

Appetitive Conditioning in *Octopus cyanea*

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The performance of *Octopus cyanea* was studied in 3 appetitive conditioning situations. In Experiment 1, 2 groups were trained in a runway; a large reward produced faster acquisition when reinforcement was consistent and better subsequent performance on a partial schedule than did a small reward. In Experiment 2, activity in the vicinity of a feeder was measured, and in Experiment 3, latency and probability of response were measured in an automated version of a traditional conditioned attack situation (Boycott & Young, 1950). There was evidence of acquisition with continuous reinforcement in both experiments but in neither with partial reinforcement. All of the results can be understood in terms of growth and decline in the strength of stimulus-reinforcer associations with reinforcement and nonreinforcement.

Comparative experiments have shown similarities in the learning of honeybees and vertebrates that are surprising in view of the remoteness of the evolutionary relation and the vast differences in brain size and organization (Bitterman, 1988). Although Menzel (1983) suggested that the underlying mechanisms may be homologous "at the cellular and network levels" (p. 510), it is clear that the networks have evolved independently, and the possibility has not been ruled out that the same is true of the synaptic mechanisms. Evidence of functional convergence has been provided by the discovery in honeybees of successive negative incentive contrast (Couvillon & Bitterman, 1984), a phenomenon found in opossums (Papini, Mustaca, & Bitterman, 1988), rats (Elliott, 1928), monkeys (Tinkelpaugh, 1928), and chimpanzees (Cowles & Nissen, 1937) but not in representatives of older vertebrate lines such as goldfish (Lowes & Bitterman, 1967), toads (Schmajuk, Segura, & Ruidiaz, 1981), and painted turtles (Pert & Bitterman, 1970). For honeybees as for the mammals, the acceptability of a modest reward is reduced under conditions that in the past have yielded a preferred reward. Convergence would be suggested also by the absence in older invertebrate lines of learning phenomena, found in honeybees, that do seem to be common to vertebrates.

Not much is known about the learning of invertebrates other than honeybees. Learning has been demonstrated in a variety of invertebrates, but there has been little in the way of functional analysis (Corning, Dyal, & Willows, 1973, 1975; Sahley, 1984), in part perhaps because suitable species—available in large numbers, easily maintained, and with appropriate sensory, motor, and motivational properties—are rare. An important exception is to be found in octopuses, which do seem to meet the requirements, and which for a time at least were studied fairly intensively, mostly in rather complicated experiments on discriminative learning (see the review by Sanders, 1975). The meaning of that work is

unclear, however, because much of it was done under difficult circumstances and with training techniques that were less than ideal (Bitterman, 1975). More recently, attention has been concentrated on several other mollusks, such as *Aplysia*, *Limax*, and *Hermisenda*, selected on the ground of their suitability for neurophysiological analysis (Alkon & Farley, 1984; Carew & Sahley, 1986), but they are not very suitable for behavioral analysis, which has yet hardly begun.

In the work reported in this article, we turned again to the study of learning in octopuses, taking advantage of convenient access to a modern marine laboratory immediately adjacent to their natural habitat. Although octopuses have been maintained successfully in specially designed closed systems (e.g., Forsythe & Hanlon, 1980), the only practical way to keep large numbers of them properly is to have an open system with a constant flow of seawater through their living enclosures. It is important also that the laboratory be close to the places from which the animals are collected because of the damage that can be done by transporting them in closed containers for more than brief periods. Our purpose here simply was to examine the effects of reinforcement and nonreinforcement on the performance of one local species, *Octopus cyanea*, in several different appetitive training situations.

Experiment 1

To begin with, we used a runway like that developed by Walker, Longo, and Bitterman (1970) for *O. maya*. In work with a runway or any training situation apart from the animals' own home tanks, a nontraumatic technique of moving the animals is required, and that, too, we borrowed from the work with *O. maya*. In this first experiment we studied the performance of four groups of *O. cyanea* in a one-trial-per-day factorial experiment with two magnitudes of reinforcement and two reinforcement schedules (continuous vs. partial).

Method

Subjects. The work was done with 37 subjects, whose weights at capture ranged from 0.56 to 1.70 kg. They were collected on the

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leeward shore of Oahu, Hawaii, in the vicinity of the laboratory and quickly transferred to their individual home tanks, to which they were adapted for at least 2 weeks before training was begun. The animals took shrimp upon arrival, but strips of squid mantle like those to be used as reinforcement were taken only several days afterward. Training was not begun until pieces of squid dropped into the home tanks were taken almost immediately (in 3–5 s).

Apparatus. The individual home tanks were 17.0 cm wide \times 38.0 cm long \times 34.5 cm deep (internal dimensions). The flow of seawater through each was 2–3 L/min, with a water level of 25 cm. In each tank there was a *house*—a five-sided box of clear Plexiglas—in which, because the external width of the house was only slightly less than the internal width of the home tank, the animal could be scooped up easily, whether or not it happened to be inside, for transportation to the training apparatus, and in which it could be returned to the home tank. The height of the house was 20 cm, and its depth was 16.5 cm.

The runway, constructed of resined plywood, was 1.56 m long and 34 cm high. Its internal width, which was that of the home tanks, permitted the introduction and removal of an animal in its house without significant disturbance. Seawater flowed from the goal end to the starting end at the rate of about 11 L/min, with a water level of 23 cm. As an animal was introduced into the runway, a timer was turned on. When the animal reached the goal end, its presence was detected by a column of photocells, 40 cm before the end. The clock then was stopped to provide a measure of latency, and on reinforced trials, the pieces of squid used as reinforcement were washed from a feeder down onto the body of the animal.

Procedure. The animals were assigned in quasi-random fashion to four reinforcement groups: large and continuous (LC; $n = 8$); small and continuous (SC; $n = 10$); large and partial (LP; $n = 9$); and small and partial (SP; $n = 10$). The large reinforcement was 20 pieces of squid mantle that weighed in all about 24 g, and the small was 5 pieces (about 6 g). Each piece was about 1 cm wide and 5 cm long.

Because preliminary observations showed that naive subjects of this species did not leave their houses for long periods when first introduced into the runway, the training began with an extended period of what can be thought of either as shaping or as contextual conditioning. To begin with, an animal was placed in the goal end of the runway, the feeder was operated by the experimenter, and the animal was permitted to take the food (the amount of which—25 g or 6 g—was appropriate to the animal's group membership). On subsequent days, as the animal began to leave the house before delivery of the food, the starting position was moved backward from the goal end in successive stages to a point 100 cm distant. If on any day the animal failed to approach the feeder spontaneously in 5 min, it was moved in its house to the feeder, and food was delivered. The second stage of training (with the house at the start of the runway) began after the animal had responded on 2 successive days from the terminal pretraining position of 100 cm from the feeder.

The second stage consisted of 45 daily sessions. There were 5 trials per session, with reinforcement for the continuous-reinforcement groups scheduled on each trial. Reinforcement was available to the partial-reinforcement groups on each of the first 5 training trials and for the remaining 40 trials on the following schedule: NRRNR NRRNR NRRNR RRNR NRRNR NRRNR NRRNR NRRNR (R = reinforcement and N = nonreinforcement). On reinforced trials the animals were returned to their home tanks immediately after taking all the food, which required no more than 30–40 s; on nonreinforced trials the animals were returned after 30 s in the goal region. If on any day of this training an animal failed to respond within 5 min, it was removed from the runway and returned to its home tank for a period of at least 20 min. Then it was given a second trial and, if it failed to respond, returned again to its home tank for at least 20 min. If it failed to respond on the third trial, it was moved in its house to the feeder and given whatever amount of food was

due it that day or, if no reinforcement was scheduled, simply kept in the goal area for 30 s. Differences in the amount of food received by the various groups in the runway were compensated for by postsession feeding at least 20 min after the end of each session.

Results

An effect of magnitude of reinforcement was found in the first stage of training: The animals trained with small reinforcement took about twice as long to complete training as did those trained with large reinforcement. The median number of days to criterion was 26 for small and 13 for large reinforcement (Fisher's exact $p = .0370$).

In the second stage of training, there were significant effects both of amount and schedule of reinforcement on probability of response but not on latency of response. When the animals responded, their log latencies were very much the same: The means for the four groups ranged from 1.70 to 1.94, and analysis of variance yielded neither a significant effect of magnitude of reinforcement, $F(1, 33) = 1.26$, $p = .2692$, a significant effect of schedule, $F(1, 33) < 1$, nor a significant interaction of Magnitude \times Schedule, $F(1, 33) < 1$. The animals did not, however, respond consistently, and after the first 5 days (in which reinforcement was continuous for all groups), there were more failures to respond in the partial-reinforcement groups, especially in Group SP, than in the continuous-reinforcement groups.

In Figure 1, the performance of the four groups in the second stage is plotted in terms of the mean number of days (in blocks of 5) on which there were no failures to respond (that is, days on which the animals responded when first placed in the runway, with no reruns necessary). A Kruskal-Wallis analysis of the scores for the four groups over all 45 days in 5-day blocks shows their performance to be significantly different ($H = 11.34$, $p < .01$). Median tests showed better performance with large reinforcement only for the partial schedule: The performance of LC was not significantly different from that of SC (Fisher's exact $p = .3230$), but the performance of LP was significantly better than that of SP ($p = .0473$). Median tests also showed the octopuses' better performance on the continuous than on the partial schedule, both with large and small reinforcement: The performance of LC was significantly better than that of LP ($p = .0444$), and the performance of SC was significantly better than that of SP ($p = .0005$).

These results certainly are not typical of those to be found in the vast runway literature for rats, which prepared us neither for the greater sensitivity of the probability measure than of the latency measure nor for the marked decremental effect of intermittent nonreinforcement. Nevertheless, the octopus results are readily understandable in terms of familiar learning principles. We have only to assume: that large reinforcement produces greater associative strength than does small; that greater associative strength in Group LC as compared with Group SC is obscured by a performance ceiling; and that the decremental effect of nonreinforcement is sufficient to bring the associative strengths of Groups LP and SP below the ceiling, more so in the case of Group SP because the incremental effect of the small reinforcement is less.

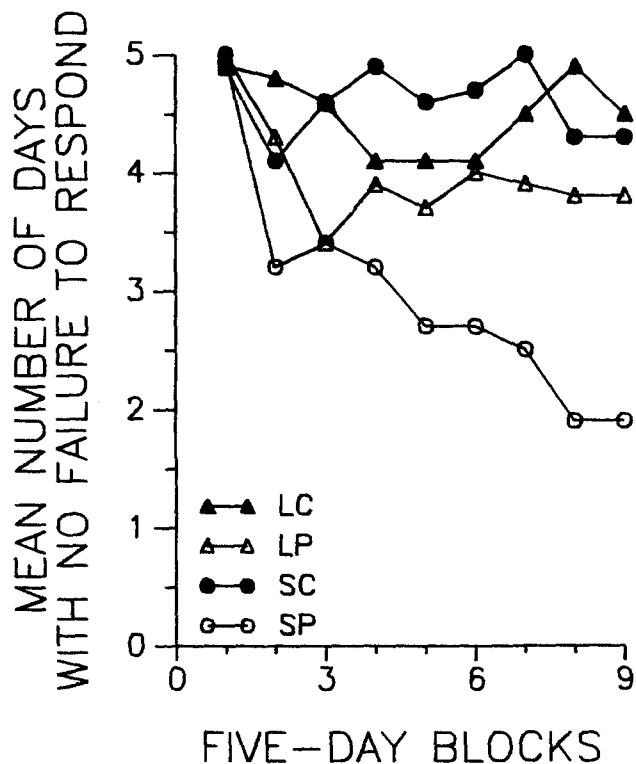


Figure 1. The performance of the four groups after consistently reinforced pretraining in Experiment 1. (LC = large, consistent reinforcement; LP = large, partial reinforcement; SC = small, consistent reinforcement; and SP = small, partial reinforcement.)

The data actually are easy to model with a linear acquisition equation (Bush & Mosteller, 1951) for computing the increase or decrease of associative strength with reinforcement or nonreinforcement and an exponential equation for computing probability of response on the basis of associative strength. Because the model is not very closely constrained by the data, several sets of parametric values may be found that provide reasonably good fits, as, for example, an incremental rate of .07 with an asymptotic associative strength of 1 for the larger reinforcement and .8 for the smaller, a decremental rate of .05, and a probability function that reaches 1 at the associative strength of .6. Data for other magnitudes of reinforcement and other reinforcement schedules would provide a stricter challenge to the model, but the runway technique proves to be so cumbersome and the measures it affords so crude—at least for this species—that the matter does not seem to be worth pursuing further.

Experiment 2

Although the runway technique is nominally instrumental, much of runway performance in general can be understood in terms of classical conditioning, and the same is true of the performance of the octopuses in Experiment 1. The extensive pretraining procedure used in that experiment certainly was purely classical at the outset. To focus on the classical process,

we now shortened the runway, eliminated the response contingency entirely, and measured anticipatory activity in the vicinity of the feeder. Continuous and partial schedules of reinforcement were compared in an equated-reinforcements design. Number of reinforcements rather than number of trials was equated in order to put the effect of intermittent nonreinforcement into clearer perspective.

Method

Subjects. The subjects were 10 octopuses, which ranged in weight from 0.50 to 1.05 kg at capture, that were collected and maintained as were those of Experiment 1. The animals were divided into two groups with different reinforcement schedules, continuous (C) and partial (P).

Apparatus. The training enclosure, 18.0 cm wide × 75.0 cm long × 33.5 cm deep, was made entirely of black Plexiglas except for the wall at one end of the enclosure where food was delivered by an automatic feeder. That wall was made of translucent Plexiglas and was diffusely illuminated (11.8 ftl [40.4 cd/m²] at 30 cm) throughout each experimental session. At the feeding end, too, there were three vertical columns of photocells, 9, 17, and 25 cm from the illuminated wall, the function of which was to monitor general activity in the region; each column contained three photocells, 4.5, 8.0, and 11.5 cm above the floor, respectively. The level of the water, which flowed from side to side through the enclosure at the rate of about 8 L/min, was 24 cm.

Procedure. Each daily session was 18 min long. The first 3 min of each session always were unreinforced, and thereafter, in reinforced sessions, single, 1.2-g strips of squid were delivered on a variable-time 45-s schedule; in nonreinforced sessions the animals were kept in the situation for the same period of time. The training began with 5 nonreinforced (habituation) sessions followed by 3 reinforced sessions for all animals. Then there were 17 sessions for the 5 animals in Group P, 9 reinforced and 8 nonreinforced in the sequence NRRNR RNNRN RRNNR NR. The 5 animals of Group C had reinforced sessions on reinforcement days for Group P and remained in their home tanks on nonreinforcement days (an equated-reinforcement design), with differences in amount of food provided in the experimental situation compensated for in the postsession feeding. In the procedure of this experiment, unlike that of the previous one, the interval between reinforced sessions was the same for both groups, which ruled out the possibility that poorer performance with partial reinforcement might be due in part to retention decrement.

Results

Our primary interest in this experiment was in *anticipatory activity*, which was measured as the total number of photo-beam interruptions in the first 3 min of each session (before the initial introduction of food in reinforced sessions). That activity was highly variable to begin with, but the animals seemed to settle down by the end of the habituation period. Activity increased again after 2 reinforced sessions and continued to increase in the animals of Group C as training continued but did not do so in the animals of Group P. Figure 2 shows the mean anticipatory activity scores of the two groups at the end of the habituation phase (activity in the last habituation session and the first conditioning session combined), after the two initial reinforcements (activity in the second and third conditioning sessions combined), and in the subsequent 9 sessions in which both groups were reinforced.

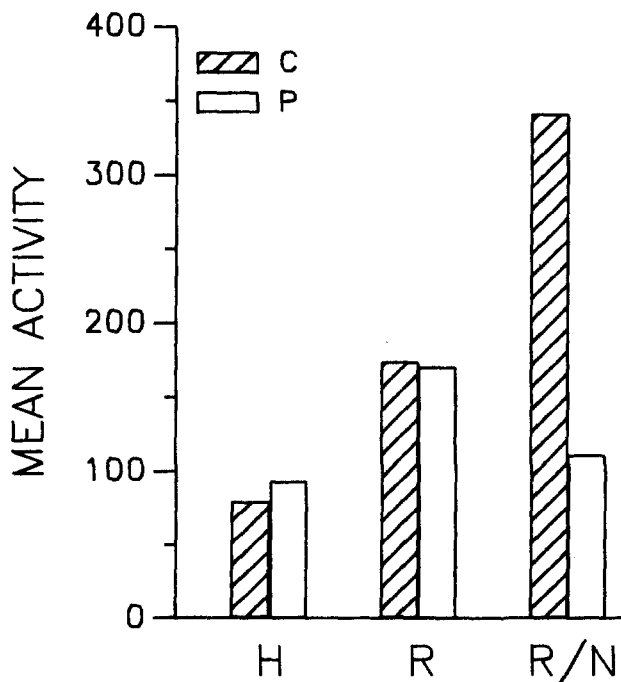


Figure 2. The activity of the two groups (C [continuous reinforcement] and P [partial reinforcement]), as measured in terms of the number of photobeam interruptions, in three stages of Experiment 2. (H = end of habituation period; R = after two reinforced sessions; R/N = in reinforced sessions after partial reinforcement began for Group P.)

The scores for the two groups were very much the same until differential treatment began, when anticipatory activity was significantly greater in Group C than in Group P, $F(1, 8) = 6.09$, $p = .0388$. Mean activity (photobeam interruptions) during the 15-min periods in which food was delivered tended to be higher in Group C ($M = 1,611$) than in Group P ($M = 1,336$) but not significantly so, $F(1, 8) < 1$.

These results complement those of Experiment 1, in which the performance established by extensive continuous reinforcement declined with the shift to equated-trials partial reinforcement. Here, after little continuous reinforcement, the effect of intermittent nonreinforcement was to impair acquisition, even though the number of and distribution of reinforcements was the same. The extent of the impairment was unexpected, but in retrospect it may not be surprising that the effects of unreinforced 18-min exposures to the training situation in this one-trial-per-day experiment were so strong. In the following experiment, partial and continuous reinforcement were studied in relatively massed trials.

Experiment 3

Most frequently used in work on visual discrimination in octopuses (Sanders, 1975) are variations of a technique developed by Boycott and Young (1950), in which attack on one object is rewarded with food and attack on a different object is punished with shock. The procedure is nominally instrumental, and there is in fact some initial tendency on the

part of the animals to attack moving objects that can be thought of as strengthened by reward, but a common shaping procedure has been simply to pair an object with a crab, and the possibility of a thoroughgoing Pavlovian interpretation of the change in behavior has by no means been ruled out. In Experiment 3, we used an automated version of the technique to study the conditioning and extinction of the attack response to a single stimulus. Continuous and partial reinforcement were compared, again in what was nominally at least an equated-reinforcements design (the same number of scheduled reinforcements for both groups).

Method

Subjects. The subjects were 14 octopuses, ranging in weight from 0.35 to 1.60 kg at capture, that were collected and maintained as were those of our previous experiments. The animals were divided into two groups with different reinforcement schedules, continuous (C) and partial (P).

Apparatus. The training situation used in Experiment 2 was modified in one respect: The clear Plexiglas panel at the feeder end was no longer diffusely illuminated throughout but set before a monitor screen on which moving stimuli could be presented under the control of a computer in an adjacent room.

Procedure. In the pretraining, with the monitor screen diffusely illuminated (11.75 ftl [40.26 cd/m²] at 30 cm), the animals learned to take food. There were 5 unsignaled reinforcements (4 strips of squid that weighed in all about 5 g) in each session at intervals of at least 100 s but frequently longer, because no scheduled reinforcement was delivered until the animal had been away from the feeding area (i.e., had activated none of the photocells) for 20 s. The number of pretraining sessions required before food was taken almost immediately ranged from 4 to 9 for the different animals.

In 12 acquisition sessions the animals of Group C ($n = 7$) had 5 continuously reinforced conditioning trials at an intertrial interval (ITI) of at least 100 s, although the interval could be longer because each scheduled trial was delayed as in the pretraining until the animal had been away from the feeding area for 20 s. The brightness of the monitor screen was 1.57 ftl (5.38 cd/m²) during the ITI. At the beginning of each trial, the screen brightness changed to 11.75 ftl (40.26 cd/m²), and on that background, 5 circles were presented in positions that varied randomly from trial to trial. Each circle grew from a point to a diameter of 6.2 cm in 9.6 s, collapsed to a point, grew again, and so forth, until the animal responded by activating any photocell in the column closest to (9 cm from) the screen. (The behavior of the animals was not observed during the experiment, but pilot work showed responses ranged from gradual approach to full-blown attack.) Activation of a photocell triggered the feeder, which washed the pieces of squid down onto the body of the animal and then restored the ITI screen brightness. The animals of Group P ($n = 7$) had 10 trials of which only 5 were reinforced (an equated-reinforcements design) in Gellermann orders that varied from session to session. The nonreinforced trials were exactly like the reinforced trials except that the feeder was not activated by response. The measure of performance was latency of response. If on any trial an animal failed to respond in 60 s, the trial was terminated, and any scheduled food that was not delivered was compensated for in the postsession feeding.

For the animals of Group C, there were 3 more training sessions with continuous reinforcement followed by 12 extinction sessions. In each extinction session there were 5 nonreinforced trials exactly like those previously given the animals of Group P.

In the final phase of the experiment, 6 animals of Group C and 3 of Group P were trained in 12–15 sessions of continuous reinforce-

ment under the same conditions as had previously been used for Group C. Then, when performance had stabilized, there was an unreinforced test session, 3 more days of continuous reinforcement, and a second unreinforced test session. In each test session, there were 16 trials, four of each of the following types in balanced orders: (a) blank trials, in which there was no change in stimulation; (b) trials like the training trials, in which the circles were presented against a background of increased brightness; (c) trials with the circles but no increase in background brightness; and (d) trials with increased background brightness but no circles. Each trial terminated with a response or after 60 s if there was no response.

Results

There was in both groups an initial tendency to respond—with a probability of about .4—that was strengthened by consistent but not by partial reinforcement. Plotted in Figure 3 are the mean log latencies of response for the two groups in each of the 12 acquisition sessions. The curves show a decline in the consistent group but not in the partial group. Analysis of variance yields a significant group effect, $F(1, 12) = 15.85$, $p = .0018$, a significant session effect, $F(11, 132) = 2.02$, $p = .0311$, and a significant interaction, $F(11, 32) = 2.85$, $p = .0022$. The two groups differed also in probability of response, which became greater in Group C than in Group P, $F(1, 12) = 14.39$, $p = .0026$ —with overall values of about .8 versus .4. Given that a latency score of 60 s was assigned for each failure to respond, one may suspect that the difference in probability of response accounts entirely for the difference in latency, but

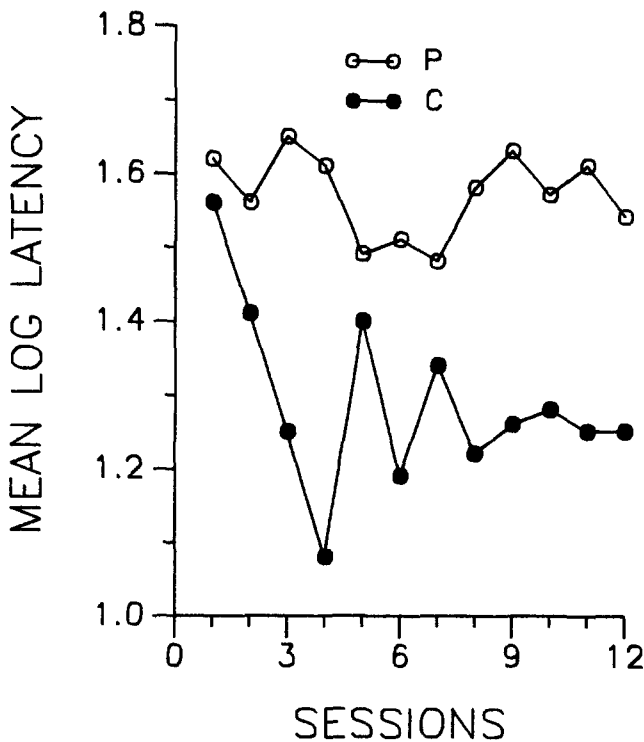


Figure 3. The performance of the two groups (C [continuous reinforcement] and P [partial reinforcement]) during acquisition in Experiment 3.

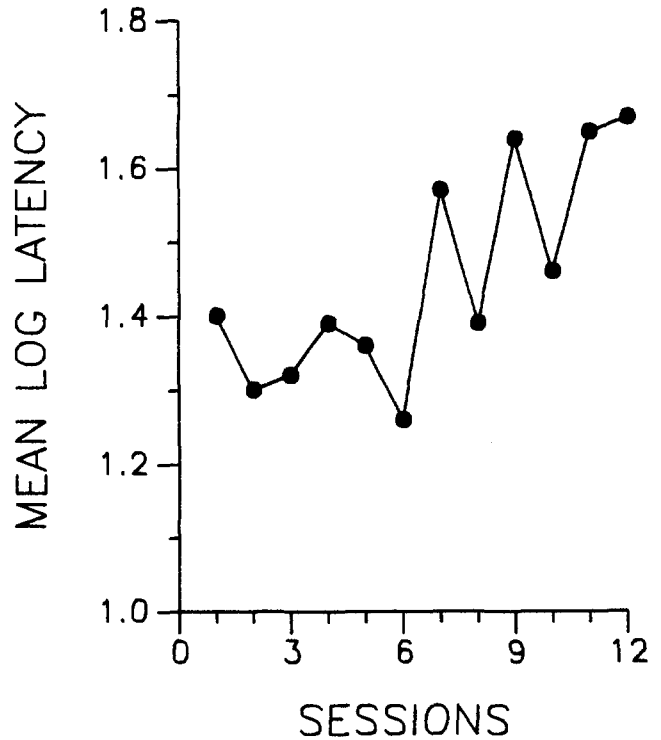


Figure 4. The performance of Group C (continuous reinforcement) during extinction in Experiment 3.

it does not. Even with failures excluded, Group P responded more slowly than did group C, $F(1, 12) = 10.73$, $p = .0066$. Neither is the difference in the performance of the groups due simply to the greater number of trials given the animals of Group P. Although the mean log latency for Group P was somewhat less in Trials 1-5 than in Trials 6-10, $F(1, 6) = 13.71$, $p = .0101$, it was greater than that for Group C even in Trials 1-5, $F(1, 12) = 11.59$, $p = .0052$.

That the difference in the performance of the two groups was not a nonassociative effect of the difference in density of reinforcement is shown by the extinction results for Group C, which continued for several sessions to respond rapidly in the absence of any food whatsoever. (The animals of Group P were not extinguished because their performance did not improve during acquisition.) The results for Group C are plotted in Figure 4 in terms of mean log latency of response over the 12 extinction sessions. Performance in the absence of all reinforcement remained quite good for several sessions before gradually deteriorating to the pretraining level, $F(11, 44) = 2.44$, $p = .0180$. The probability of responding also declined significantly to the pretraining level, $F(11, 44) = 3.06$, $p = .0040$. There is, then, abundant evidence of conditioned facilitation of the attack response in Group C, and none at all in Group P.

In Figure 5, performance in the unreinforced test sessions given after retraining with consistent reinforcement is shown in terms of mean log latencies of response on trials of the four types for the 2 test days combined. Analysis of variance yields a significant effect of trial type, $F(3, 24) = 18.16$, $p < .0001$.

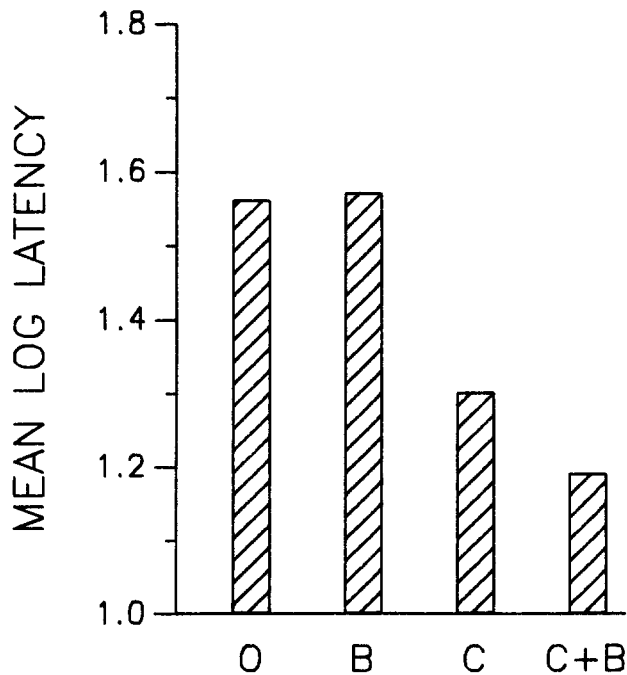


Figure 5. Analysis of response to separate components of the conditioned stimulus in Experiment 3. (O = blank trials; B = change in background; C = presentation of circles; and C+B = presentation of circles plus change in background.)

Clearly, the circles were the most effective feature of the conditioned stimulus. Response to the circles alone was significantly more rapid than to the change in background brightness alone, $F(1, 8) = 27.02, p = .0008$, which was not in itself effective as compared with response on blank trials, $F(1, 8) < 1$. The change in background did, however, seem to potentiate response to the circles; although the difference in mean log latency of response is not significant by analysis of variance, $F(1, 8) = 2.90, p = .1270$, 8 of the 9 subjects responded more rapidly to the compound than to the circles alone, a frequency significantly greater than would be expected by chance ($p = .040$, two-tailed).

Discussion

In these experiments, appetitive conditioning in *O. cyanea* was studied in three different situations, two of which were nominally instrumental: Reinforcement was contingent on approach to a feeding area in Experiment 1 and on approach to a moving stimulus in the feeding area (a response with a substantially higher initial probability of occurrence) in Experiment 3. Nevertheless, stimulus-reinforcer rather than response-reinforcer contiguity may have been largely responsible for the behavioral changes observed in both of them. In Experiment 2, the procedure was nominally classical, but the possibility cannot be discounted that adventitious response-reinforcer contiguity played an important role. The problems are familiar to students of vertebrate learning, of course, as

are the somewhat complicated techniques for dealing with them that were not incorporated in these exploratory experiments. For the moment, we can say no more than that the results thus far obtained in all three situations are at least capable of being understood entirely in Pavlovian terms, that is, in terms of association between the feeding area and food in Experiments 1 and 2 and between the moving stimulus and food in Experiment 3.

The one feature of the results that may be surprising to students of classical conditioning is the absence in Experiments 2 and 3 of any sign of acquisition with 50% partial reinforcement. In vertebrates, performance in acquisition usually is impaired to some extent when trials are equated, but when reinforcements are equated (as in Experiments 2 and 3) there is considerably less impairment and often none at all (reviewed in Gibbon, Farrell, Locurto, Duncan, & Terrace, 1980; see also Papini & Overmier, 1985). As for other invertebrates, little information is available. With reinforcements equated, modest impairment has been found in honeybees (Ammon, Abramson, & Bitterman, 1986), and in earthworms no impairment even with trials equated (Wyers, Peeke, & Herz, 1964). There is, however, some equated-reinforcements work by Farley (1987) in which *Hermisenda*, another mollusk, showed acquisition when reinforced consistently but not on a 33% schedule.

Farley's (1987) results are interesting because they indicate that our results for *O. cyanea* are not unique, but neither set of results in fact presents any great explanatory difficulty. Training with one or several nonreinforced trials for each reinforced trial may produce no change in behavior because the associative strength that is generated does not exceed the performance threshold—in our third experiment, for example, the associative strength required to potentiate the preexisting tendency to attack the conditioned stimulus. Given the instrumental contingency in Experiment 3 (which meant that the moving stimulus was paired with food only when the animal responded to it) and the greater probability of response in the consistent-reinforcement group, reinforcements actually were not equated; the consistently reinforced animals had (on average) about 4 times as many reinforced trials as the partially reinforced animals and only about $\frac{1}{8}$ the number of nonreinforced trials.

Assume, for example, that associative strength grows with reinforcement (to an asymptote of 1) at the rate of .02 and declines (to zero) with nonreinforcement at the same rate. The associative strength for the partial group does not exceed .185; the associative strength of the consistent group at the beginning of extinction is .625 and declines gradually to .185 over 30 nonreinforced trials. If the associative strength required to produce a measurable increment in the basal level of performance were, say, .2, the observed pattern of results would follow nicely. It must be emphasized that these calculations are given only to illustrate the proposed explanation. We do suppose, however, that it is feasible with equations relating associative strength to latency and probability of response to estimate the parameters in a specially designed set of experiments and then to make detailed predictions of performance in further experiments, both classical and instrumental.

The first two of the three training techniques used in these experiments did not yield very satisfactory data. The run-way—chosen on basis of experience with *O. maya* (Walker et al., 1970)—seems inappropriate for our species because of the long period of pretraining required and because of the all-or-none nature of the response (probability rather than latency being the effective measure). It may be well to note that *O. cyanea* has failed also to perform as anticipated in a potentially fruitful consummatory situation developed by Henderson, Woodard, and Bitterman (1975) for *O. ornatus*, another local species (which, unfortunately, is not found in any numbers near our present laboratory). The technique used in Experiment 2 yielded measurements more variable than we should have liked, but it may be useful with certain modifications. It may be better, for example, to have a smaller enclosure, with activity measured over all of it. In subsequent experiments, it seems feasible to program multiple trials per session, in which the delivery of food is signaled with the onset of light or other stimuli. A valuable piece of information provided by Experiment 2 is that the animals show sustained interest in single small strips of squid, which they capture easily and ingest immediately. The small live crabs traditionally used, which are more difficult to obtain and to feed automatically, proved to be unnecessary.

The technique of Experiment 3 yielded the most satisfactory data, although there is a good deal of room for improvement. For one thing, the unconditioned probability of response to the stimulus used is too high; other stimuli to which untrained animals are much less likely to respond but which are nevertheless clearly discriminable from each other must be sought (cf. Messenger & Sanders, 1972). In the study of perceptual learning in octopuses, computer-generated stimuli represent a substantial improvement over the traditional plastic cutouts inserted into the tank at the ends of rods when there was no simple way to bring the animal to the training apparatus instead of bringing the apparatus to the animal (Walker et al., 1970). Another problem encountered in Experiment 3—and in the traditional experiments as well—was that there was a strong tendency to remain in the feeding area; because a trial did not begin until the animal had moved back from the feeding area, intertrial intervals were often rather long. A rather questionable solution to the problem in the traditional experiments, as Bitterman (1975) reported, was simply to drive the animal back by beating on the tank with some heavy object. A solution that we are considering is to have a monitor screen and feeder at each end of the enclosure, with stimuli presented at the end further from where the animal happens to be when a trial is scheduled. It probably will be wise in further work on conditioned attack to begin with purely Pavlovian contingencies.

In general, we continue to believe that octopuses are promising animals for the comparative analysis of invertebrate learning, although the particular species available to us here in any substantial quantity seems somewhat less tractable than other species that have been studied in the past. There are, of course, many technical problems still to be solved before we can hope to begin a rigorous, systematic study of learning on octopuses, and even when the problems are solved the work can be expected to proceed only very slowly. For a

variety of reasons related to the nature of the animals, it will be impossible, given the same limited resources, to accomplish in work with octopuses even a substantial fraction of what has been accomplished in the work with honeybees during the past dozen years or so (Bitterman, 1988). Nevertheless, the need for a detailed picture of learning in another, markedly divergent, invertebrate species justifies continuation of the work with octopuses. At the same time, it may be best to continue also to explore the possibilities of other species that, like honeybees, are more widely available.

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