SIGNALED AVOIDANCE IN THE EYE WITHDRAWAL REFLEX OF THE GREEN CRAB

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Learning in a signaled avoidance procedure was studied in the eye withdrawal reflex of the green crab, *Carcinus maenas*. A puff of air to the eye, which causes eye retraction, was used as the unconditioned stimulus (US). A mild vibration on the carapace, which has no effect on untrained animals, was used as a warning (conditioned) stimulus (CS). Eye withdrawal during the CS led to the omission of the otherwise scheduled US. Acquisition was rapid, reaching about 75% avoidance after 30 trials. Extinction occurred slowly over the course of 40 CS-only trials. Yoked controls did not perform as well. The behavior of experimental animals in the avoidance procedure was found to be essentially identical to the performance of animals subjected to a classical conditioning paradigm in which CS responses had no effect on US presentation. Additional groups of animals were subjected to experiments in which (a) avoidance conditioning (60 trials) was followed by classical conditioning (40 trials) or (b) classical conditioning was followed by avoidance. The behavior of these groups was, again, essentially identical. The results suggest that there may be an underlying Pavlovian mechanism for the learned response, although the contribution of an operant process is not excluded. The results expand the range of invertebrate animals in which fundamental conditioning phenomena can be demonstrated, and may provide a neuronal model for learning in a signaled avoidance procedure.

Key words: signaled avoidance, classical conditioning, invertebrate learning, eye retraction, crustaceans, green crab

One of the current problems in the experimental analysis of behavior is the extent to which conditioning phenomena that have been demonstrated in higher animals also exist in simple invertebrate species. One reason for such interest is that, in some cases, the underlying neuronal circuitry is comparatively simple and the behavioral analysis can be extended to the cellular or even chemical level (see Carew & Sahley, 1986; Farley & Alkon, 1985 for reviews). We have shown recently that in the green crab, *Carcinus maenas,* the eye withdrawal reflex can be controlled by two simple learning procedures. The eyes of *Carcinus,* like those of other crustaceans, are at the end of stalks (more precisely, eye-cups), which can be retracted into the carapace in response to

aversive stimuli. Extension of the eye can be suppressed by an operant procedure in which each extension of the eye, following reflex withdrawal, is punished with a brief puff of air (Abramson & Feinman, 1987). The eye withdrawal response can also be brought under classical (Pavlovian) control by pairing a mild vibration to the carapace as a conditioned stimulus (CS) with a puff of air to one of the eyes as an unconditioned stimulus (US). Animals receiving repeated pairings showed an increased probability of eye retraction during CS presentations (Abramson & Feinman, 1988).

Because eye withdrawal can be brought under operant or Pavlovian control it is of interest to study experimental situations in which these two contingencies may interact. One such manipulation is the omission (signaled avoidance) experiment. The question is of interest, first, from a comparative learning perspective (Bitterman, 1975). Some animals, in some tasks, such as rats in discrete trial shuttle-box learning, show signaled avoidance that is sensitive to response–reinforcer contingencies. Others, such as teleost fish trained in analogous situations, respond as Pavlovian animals; that is,

they show no advantage in being able to control the presentation of reinforcement. With the exception of a study of crayfish in shuttle-box avoidance (Taylor, 1971), the behavior of crustaceans in avoidance situations is largely unknown. A second area in which avoidance is of interest is the field of neuronal learning models. In general, there are few neuronal models of operant conditioning, the notable exceptions being the head-waving response in *Aplysia* (Cook & Carew, 1986) and leg position in the locust (Forman & Zill, 1984; Hoyle, 1980). One of the virtues of the crab eye preparation is the accessibility of the underlying neuromuscular circuitry, and because a simple kind of operant learning has been demonstrated in this system, it is reasonable to ask if this response is sensitive to omission contingencies. It may then be possible to look for neuronal correlates of learning using operant, Pavlovian, and omission phenomena in the same response system.

We report two omission experiments in which a mild vibration to the carapace served as a warning stimulus signaling onset of an air puff. The response, retraction of the eye into the carapace, initially observed only with the US, appeared during CS presentations after several pairings. Yoked controls showed little acquisition, indicating that the withdrawal response can be conditioned in a procedure designed to show avoidance. However, comparison with several control procedures suggested that the associative mechanism responsible for such sensitivity may have a major Pavlovian component.

EXPERIMENT 1

In the first experiment we tried to determine whether the eye withdrawal response can be controlled by omission contingencies, and, if avoidance learning could be demonstrated, whether CS termination played a significant role. One group of crabs was exposed to a standard avoidance procedure: Response to the CS terminated the CS and avoided the US. For a second group, CS responses also avoided the US but did not terminate the CS. For each group, yoked controls were subjected to the same schedule of stimuli independent of their behavior.

Method

Subjects. Subjects were 32 male green crabs (*Carcinus maenas*) with an average carapace width of 47 mm. They were fed fresh squid every other day and maintained in a flow-through seawater aquarium at 20 °C.

Apparatus. A detailed description of the apparatus is provided elsewhere (Abramson & Feinman, 1987). In all experiments a crab was selected at random from the laboratory colony, wrapped in a paper towel soaked in seawater and restrained in a clamp. The CS was a 5-s pulse of low amplitude vibration (approximately 50 Hz) provided by the shaft of a 3-V DC motor that rested on the carapace 4 mm behind the eye that was to be conditioned. At the outset of training carapace vibration elicited no perceptible movement of the eye. For half the animals the right eye was trained, and for the other half the left eye. The US was a 0.5-s puff of air (0.25 psi) directed at the eye through a nozzle located 3 mm from the eye to be conditioned. The eye almost invariably returned to the extended position immediately after cessation of the stimulus; the extended position is the normal state for the eye, and the US is a very mild stimulus. A few animals, after extended training, kept the eye retracted after cessation of the stimulus. (This appeared to be a consequence of the training rather than fatigue because other experiments (Abramson & Feinman, 1987) have shown that animals receiving more than 100 noncontingent punishments continue to bring the eye back immediately.) In cases in which the eye remained retracted, tipping the animal (geotactic reflex) returned the eye to the upright state. This was done after a few seconds so that all animals received CS presentations only when the eye was up. Contingencies of reinforcement were programed automatically. Responses were recorded manually and only large movements of the eye, similar to those caused by the US, were scored. Approximately half of the measurements were blind, and the judgments of blind observers showed no disagreement with those of informed observers.

Procedure. The 32 crabs were divided into four groups of 8 animals each. Each group received 100 trials separated by an intertrial interval of mean 1-min duration presented in random intervals with a range from 0.2 s to 2 min (to prevent fortuitous temporal or unsignaled conditioning). A trial began with the onset of carapace vibration for 5 s, at the end of which a puff of air was delivered to the eye. For Group AT (avoidance with CS termination), a response of withdrawing the eye into
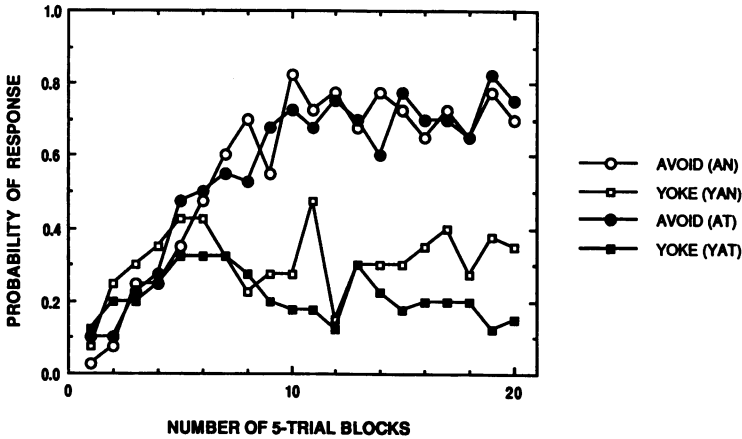
Fig. 1. Avoidance conditioning of eye withdrawal. Mean probability of response to the conditioned stimulus in successive five-trial blocks of Groups AT (avoidance with CS termination), AN (avoidance with no CS termination), YAT and YAN, yoked controls for avoidance groups.

the carapace during CS presentations terminated the CS and led to the omission of an otherwise scheduled air puff. If no response was made, the US was presented following CS termination. Each animal in this group was yoked to an animal in the control group (YAT) in such a way that the CS duration and US omission was controlled entirely by the behavior of the master animal (in Group AT). For Group AN (avoidance with no CS termination), responses prevented onset of US, but there was no CS termination. The yoked controls (YAN) received the same pattern of stimuli as the AN group, independent of their own responses.

Results

The performance of the groups in the two avoidance procedures and the corresponding yoked controls is shown in Figure 1. The data are plotted as mean probability of response to the CS in blocks of five trials over the course of 100 training trials. The first portion of Figure 1 shows that during Trials 1 through 25 there was no difference between avoidance groups and their yoked controls; responses for all groups increased in this period. As omission training continued, the probability of making a withdrawal response during the CS increased in experimental animals but not in controls.

Figure 2A shows the total number of responses for individual animals. It is evident that the mean population behavior of the avoidance groups is a reflection of individual

performance. This is also true of the Group YAT, the yoked controls for the avoidance group with CS termination. It is significant that 3 animals in Group YAN, controls for avoidance without CS termination, showed as many responses as the experimental subjects. In one case the yoke made more responses than the corresponding master. As discussed below,
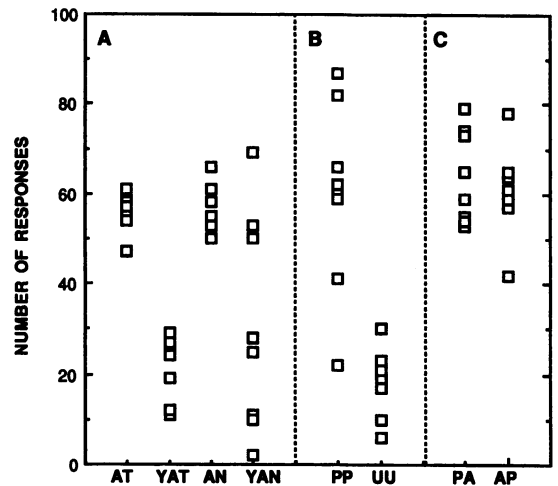

Fig. 2. Responses of individual animals in conditioning experiments. Each group contains 8 subjects; data points for some subjects overlap. (A) Total responses of animals in 100 trials of avoidance conditioning, AT, AN, YAT, YAN (see legend to Figure 1). (B) Total responses of animals in 100 trials of classical (Pavlovian) conditioning (PP and UU; see Figure 3). (C) Total responses of animals trained in avoidance and switched to classical procedure at Trial 61 (AP) and animals switched from classical to avoidance (PA) (see Figure 4).
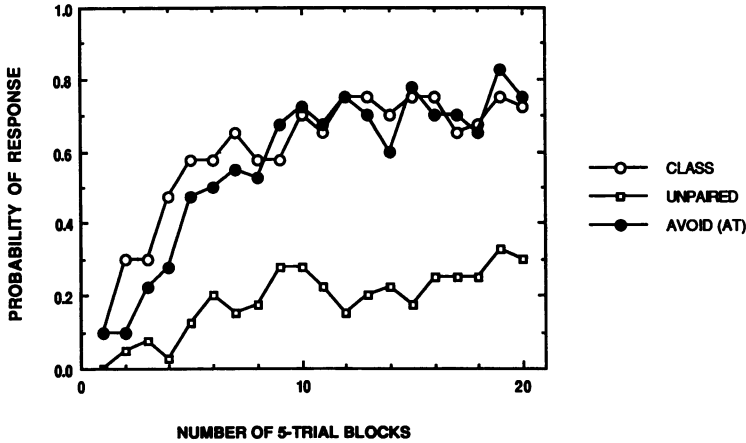
Fig. 3. Classical conditioning of eye withdrawal compared to avoidance. Mean probability of response to the conditioned stimulus in successive five-trial blocks of groups subjected to Pavlovian conditioning (PP) and training with unpaired stimuli (UU). Data of Group AT (avoidance with CS termination) from Figure 1 are shown for comparison.

an argument can be made for a Pavlovian explanation for learning in the avoidance experiment; at least some of the yokes in group YAN may not have been able to discriminate between contingent and noncontingent stimuli.

Discussion

Results of this experiment indicate that the eye withdrawal response of the green crab can be controlled by an avoidance procedure, but that the CS termination contingency is not important for development of the conditioned response. The generally poor behavior of the yoked controls, who received the same number of stimuli and omissions but in a noncontingent fashion, suggests that the learned behavior is operant in mechanism. On the other hand, CS termination usually has an effect on operant signaled avoidance (e.g., D'Amato, Fazzaro, & Etkin, 1968), and the lack of such an effect points to the possibility of other mechanisms. To inquire into the underlying associative structure of learning in the avoidance experiment, we carried out a second series of experiments in which the avoidance learning is compared to behavior in a classical paradigm. We also studied the effect of following one of the training methods (avoidance or classical conditioning) by the other. If the observed avoidance learning in Experiment 1 is operant in mechanism, there are several predictions: (a) the operant nature of the avoidance should provide some advantage compared to animals

who are not able to control the consequences of the response (see, e.g., Kamin, 1956), (b) switching an avoidance animal to a Pavlovian situation wherein there is inevitable appearance of the US should lead to extinction of the learned response, and (c) if behavior in the two procedures is fundamentally different, then switching an animal trained in the classical procedure to avoidance should lead to weakening of the response due to partial reinforcement. We attempted to test these predictions in the second experiment.

EXPERIMENT 2

We first compared the performance of crabs in the avoidance procedure to that of crabs in classical conditioning. We then used two additional procedures in which one group of crabs received Pavlovian training prior to avoidance training and another group received avoidance training followed by Pavlovian training. Two final groups were trained in classical and avoidance procedures and then subjected to extinction trials.

Method

Subjects and apparatus. The subjects were 48 male green crabs with a mean carapace width of 4.8 cm selected and maintained as in Experiment 1. The apparatus was the same as in Experiment 1.

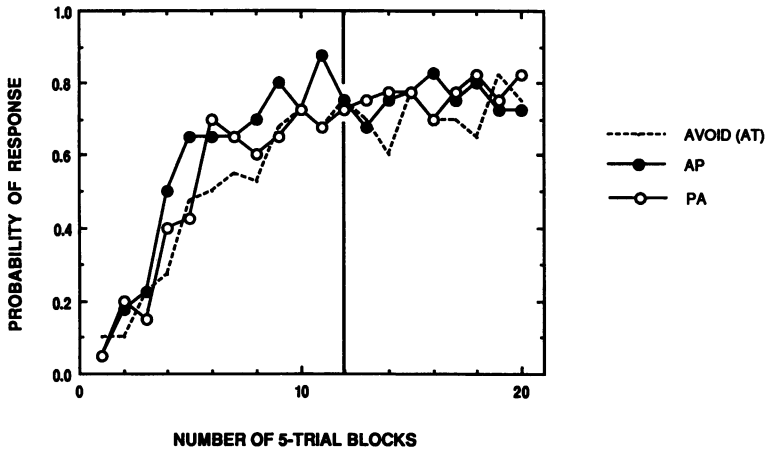*Procedure.* Handling of subjects, intertrial

Fig. 4. Effect of switching conditioning procedures on eye withdrawal. Mean probability of response to the conditioned stimulus in successive five-trial blocks for animals trained in avoidance and switched to a classical paradigm at Trial 61 (AP) and animals switched from classical to avoidance at Trial 61 (PA). Data of Group AT (avoidance with CS termination) from Figure 1 are shown for comparison.

interval, and CS and US parameters were the same as in Experiment 1. The 48 crabs were divided into six groups of 8 subjects each. Subjects in Group PP received Pavlovian training for 100 trials as described previously (Abramson & Feinman, 1988). The intertrial interval was as described for Experiment 1. Those in a specifically unpaired control Group UU received unpaired presentations of vibration and air puff for 100 trials. The stimuli were presented in a pseudorandom sequence so that no more than two consecutive stimuli were of the same type. The intertrial interval was random as described above with a mean duration of 1 min. Animals in Group AP received 60 avoidance trials followed by 40 Pavlovian trials, whereas those in Group PA received 60 Pavlovian trials followed by 40 avoidance trials. The effect of CS-alone extinction trials on avoidance training was assessed by giving animals in Group AE 60 avoidance trials followed by 40 vibration-alone trials. Extinction of Pavlovian responses was assessed by giving subjects in Group PE 60 Pavlovian trials followed by 40 CS-alone trials.

Results

Figure 3 compares the performance of crabs in classical conditioning with the data for avoidance (with CS termination) from Figure 1. It is evident that there is no additional gain derived from the avoidance contingency compared to the classical procedure; the two ex-

perimental groups had the same rate of acquisition and reached the same final level of performance. Thus, contrary to the prediction of an operant mechanism, animals in avoidance do not appear to benefit from being able to control the US. Unpaired controls (Figure 3) also show that, as previously demonstrated (Abramson & Feinman, 1988), learning in the classical procedure is pairing-specific. The similarity of the two curves for experimental subjects in Figure 3 suggests that operant avoidance and classical conditioning share some common step or that the mechanism of the observed avoidance is at least partly Pavlovian in nature. Individual subject data in Figure 2A and 2B emphasize the similarities of the behavior of the avoidance and classical groups. It is possible that the two procedures are governed by different mechanisms but fortuitously have the same rate of acquisition. Figures 4 and 2C show data for groups switched from Pavlovian to avoidance and avoidance to Pavlovian training. The figures show that the performance of animals switched between the two contingencies is not disrupted and is not significantly different from the avoidance experiment that is shown for comparison.

The rationale of the experiments in which avoidance conditioning is switched to the classical procedure is that if reinforcement occurs because it leads to the omission of an otherwise expected US, then switching to a condition in which it has no control should lead to extinc-

tion. The fact that no such decrement in performance was found (Figure 5) means that one must also show as a control that the responses are capable of extinction in this time period. Figure 5 shows that, in fact, a decrease in responses in both avoidance and classical paradigms can be affected by CS-only presentation.

Discussion

The results of Experiment 2 do not fulfill the predictions of an operant mechanism that were suggested by the efficacy of the yoked control procedure in the first experiment. Although not in direct contradiction to an operant interpretation, the results seem to show that carapace vibration comes to elicit eye withdrawal whether or not the response prevents presentation of the air puff. This is seen from simple comparisons of Pavlovian and avoidance performance both in acquisition and extinction, the inability of CS termination to have any beneficial effect on performance and the lack of disruption in performance in crabs switched from avoidance to Pavlovian contingencies. It should be emphasized that, traditionally, reinstating unavoidable US is much more effective in causing rapid extinction than a CS-alone procedure (Bolles, Moot, & Grossen, 1971; Davenport & Olson, 1968).

GENERAL DISCUSSION

The results presented here demonstrate clearly that the green crab is capable of learning in a discrete-trial signaled avoidance procedure. The underlying mechanism of this learning, however, is difficult to characterize. This is a general problem due, in part, to the fact that performance in avoidance is affected by species and task, and has given rise to several theories to explain learning in avoidance procedures. These may be roughly divided into three classes: (a) operant mechanisms in which learning is attributed to the response–reinforcer contingencies of the procedure, (b) Pavlovian mechanisms in which the animals learn by virtue of the stimulus–stimulus associations and do not benefit from the omission, and (c) mechanisms, such as two-factor theory, that have both operant and Pavlovian components. Several criteria have evolved for testing whether a particular animal or response system follows one or another of these mechanisms. These

include the use of yoked controls, comparison of avoidance with classical procedures, and the effect of switching classical and avoidance paradigms. Although none of these criteria are unambiguous, we will discuss the behavior of the eye withdrawal reflex in terms of the tests for mechanism.

Yoked Controls

It is generally considered that the best procedure for demonstrating an operant mechanism is the use of yoked controls. On this basis, the generally poorer behavior of yoked animals (Figure 1) argues for an operant basis for learning in the crab. On the other hand, there is no general agreement that a yoked control is sufficient, by itself, for demonstrating operant behavior. For example, Woodard and Bitterman (1973) studied shuttle-box learning in the goldfish and found that experimental subjects performed better than yoked controls in avoiding shock. They nonetheless argued for a Pavlovian explanation for the observed learning on the basis of comparison with classical procedures (see below). They showed that a Pavlovian interpretation can still be consistent with poor performance of yoked animals. In their analysis, one assumes differential conditioning where S+ is the CS alone (vibration in our case). S− is a compound stimulus composed of CS (vibration) plus feedback from the conditioned response (the retracted state). For experimental subjects, S+ reliably signals the US and S− is reliably followed by an omission. For yokes, these relationships do not hold. The eye withdrawal response is known to proceed without proprioceptive feedback (Burrows & Horridge, 1968) but because the eye can see when retracted the retracted state might correspond to the change in visual field. For experimental animals, then, vibration plus the retracted state is never paired with air puff (omission), whereas vibration without a withdrawal response (during the CS) is always followed by air puff. For yoked crabs, vibration alone is sometimes followed by the US and, at other times, not. In this regard it should be noted in Figure 1 that yoked animals do show some acquisition, and, as shown in Figure 2, one yoked animal actually performed better than its corresponding master. Experimental–yoke differences also appear in an avoidance procedure using the nictitating membrane response of the rabbit in which these differences
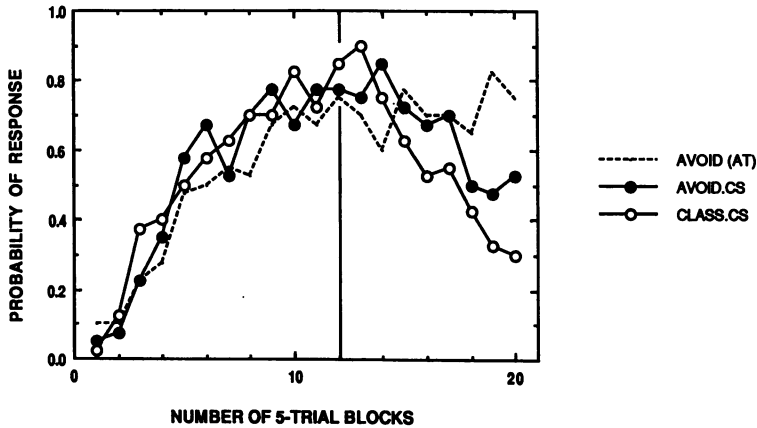
Fig. 5. Extinction of avoidance and classical conditioning. Mean probability of response to the conditioned stimulus in successive five-trial blocks of Groups AE and PE. Animals in Group AE were trained in avoidance procedure (with CS termination) and exposed to CS-only trials at Trial 61. Animals in PE were trained in classical conditioning procedure; CS-only presentations were instituted at Trial 61. Data of Group AT (avoidance with CS termination) from Figure 1 are shown for comparison.

are rationalized with an overall classical interpretation (Gormezano, 1965).

The explanation of Woodard and Bitterman (1973) actually consitutes a criticism of the yoked control in that it points out that it is not simply the contingencies that are changed, but rather that experimentals and yokes are exposed to different stimuli (retracted and extended states). We have made a similar criticism of the yoked procedure in punishment (Abramson & Feinman, 1987). It is interesting that, in that case, we were able to use a delay procedure to show that a Pavlovian mechanism was excluded. This indicates that the eye withdrawal reflex is capable of at least one type of operant learning.

Comparison with Classical Conditioning

Although it is not a necessary requirement of operant avoidance, it is to be expected that animals will benefit from being able to control the omission of aversive stimuli when compared to animals subjected to unavoidable stimuli in classical conditioning. Numerous examples in the literature support this prediction. Rats (Bolles, Stokes, & Younger, 1966; Kamin, 1956), dogs (Wahlsten & Cole, 1972), and guinea pigs (Brogden, Lipman, & Culler, 1938) show markedly better performance in avoidance procedures than in classical conditioning. Other systems, such as the goldfish work cited above (Woodard & Bitterman, 1973), do not show differences in behavior in

the two experiments, and this is usually taken as evidence that the response has Pavlovian origins. The absence of such differences in the eye withdrawal in the crab does not preclude an operant mechanism, however. Plausible explanations consistent with operant avoidance mechanism are that the two processes may show the same acquisition curve fortuitously, or more likely, that they share a common rate-determining step, presumably at the level of the common motor output. In other words, the (presynaptic) circuitry for operant and classical procedures may be different, but the level and rate of change in the probability of movement of the eye–cup per se may be fixed by motor neurons or muscles regardless of the training procedure.

In trying to rationalize the results in experiments with yoked controls and those comparing classical conditioning, one might argue that the classical training actually has an underlying operant mechanism because the eye withdrawal response attenuates the US. This is unlikely to be a major component of the mechanism because we have shown that the restrained eye can be conditioned (Abramson & Feinman, 1988; Feinman, Abramson, & Forman, 1987), indicating that attenuation of the stimulus is not required.

Switching Procedures

In addition to yoked controls and simple comparison with classical procedures, a useful

test of mechanism of learning avoidance is to measure the effect of switching the two procedures. In Experiment 2, when a classical procedure was followed by avoidance, or avoidance by classical, crabs showed no change in the probability of responding when the procedures were switched. These results argue for a similar mechanism in the behavior in the two procedures, and is different than the behavior of rats in a shuttle-box or in a lever-press situation. In that case, when signaled avoidance training was followed by a classical procedure (unavoidable US) responses extinguished much more rapidly than when the US was omitted entirely (Bolles et al., 1971; Davenport & Olson, 1968). Such a weakening in the response is expected if the mechanism is operant. Likewise, the introduction of an omission has been found to reduce the probability of response in classically conditioned rats pressing a lever (Locurto, Terrace, & Gibbon, 1976) or salivation in dogs (Herendeen & Shapiro, 1975; see also Mackintosh, 1974, pp. 113, 302). Although the absence of changes in behavior in Experiment 2 suggests that the behavior of crabs in the two procedures is due to the same underlying mechanism, one might argue, as above, that there are two different processes controlled by a common step. According to such an analysis, in the switch from classical to avoidance or avoidance to classical, the expected change in performance is not revealed because the process of extinction may be slow, or because extinction and the effect of new training produce a net change of zero.

CS Termination

Traditional theories of avoidance (e.g., two-factor theory) suggest that reinforcement is provided by CS termination. This predicts that a procedure in which responses terminate the CS will lead to improved performance compared to one in which responses simply prevent the onset of the US. This phenomenon is frequently observed (D'Amato et al., 1968; Kamin, 1956), and its absence in the eye withdrawal of the crab is not supportive of this mechanism although it does not exclude it.

General Considerations and Summary

The eye withdrawal response of the green crab is a classic example of a defensive reflex. In the literature of avoidance, it is frequently held that learning in an avoidance procedure will have a classical basis when the required response is part of the unconditioned defensive behavior of the animal rather than more arbitrary movements such as lever press (Bolles, 1970). Of course, both operant and classical mechanisms may contribute to the learned response; it should be pointed out that for a behavior that has an initially low probability, as is the case here, the first conditioned response always arises from a Pavlovian association.

In summary, then, a simple invertebrate animal can be conditioned in an avoidance procedure. As in many avoidance experiments, the underlying mechanism is difficult to establish. In comparison with other systems, the results more closely resemble the behavior of goldfish in a shuttle-box or the nictitating membrane response of the rabbit, rather than the behavior of rats in several avoidance situations. We have summarized the pros and cons of attributing the learning to operant, Pavlovian, or a combination of mechanisms: The yoked control experiments suggest the involvement of an operant mechanism but some of the predictions of operant mechanisms are not realized. Although the arguments above do not permit an unambiguous conclusion, we are inclined to believe that the conditioning of the eye withdrawal reflex is predominantly Pavlovian, although some component of the learning may be operant in nature.

Invertebrate Learning

With the exception of a study of shuttle-box behavior in the crayfish (Taylor, 1971), the present work is the first study of the ability of crustaceans to learn in a signaled avoidance situation. Although, in our view, Taylor's study lacked adequate controls for sensitization, he was able to demonstrate an increased probability of shuttling. It is interesting that one behavior associated with the conditioned response to light was eye retraction.

In other invertebrates, there is an insufficient number of well-controlled experiments to say much about the generality of the process responsible for avoidance. Learning in a signaled avoidance procedure has been demonstrated in ants (Abramson, unpublished data) and honeybees (Abramson, 1986). It has been less convincingly demonstrated—because of lack of control procedures—in roaches (Chen, Aranda, & Luco, 1970), earthworms (Ray,

1968), and planarians (Ragland & Ragland, 1965). Negative results have been obtained with house flies (Leeming, 1985) and roaches (Pritchatt, 1970).

With regard to the possible origins of invertebrate learning in avoidance, there is some suggestive support for the notion of a Pavlovian mechanism. In an experiment designed to vary the CS termination and US avoidance contingencies, carpenter ants were trained in a shuttle box with vibration as the CS and peppermint odor as the US. Animals learned to shuttle whether or not the response avoids odor (Abramson, unpublished data). In another study, honeybees were trained to fly back and forth between the hive and the sill of an open laboratory window to take sucrose solution from a target. The target was constructed so that shock could be delivered while the proboscis was in contact with the solution, and subjects learned to fly off the target when stimuli signaling shock were presented (Abramson, 1986). Although it is not possible to control for the response–shock contingency in free-flying honeybees, the results from an unpaired control group and a differential conditioning group suggest that the honeybee avoidance results can be interpreted in Pavlovian terms.

The major significance of this work is that an animal with a simple nervous system can be studied in the context of conditioning procedures used with higher animals. The simplicity and accessibility of the neuronal circuitry of the eye withdrawal system in the crab may, in fact, permit further investigation of the relative contribution of operant and Pavlovian mechanisms to avoidance learning. The retraction of the eye per see is under the control of only two motor neurons, one of which has been studied by both extracellular and intracellular recording (e.g., Fraser, 1974; Sandeman, 1969). The major muscle involved in the retraction is innervated by the larger neuron and is not involved in any of the complex movements of the eye (e.g., the optokinetic response; Burrows & Horridge, 1968). Preliminary studies show that electromyograms can be recorded during classical conditioning, and because of the absence of proprioceptive feedback, conditioning can be demonstrated even if the eye is not moving (Feinman et al., 1987). This feature may be very useful in the present case. As noted above, it has been suggested that the feedback from the retracted state may be

used to rationalize the behavior of yoked controls in a Pavlovian interpretation. It may thus be possible to study behavior in the avoidance procedure under conditions in which there is no feedback. Experiments of this type are currently under way in this laboratory.

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