Fig. 1. "Predator" with two chelipeds of *Gecarcinus quadratus* autotomized on its face. [Photo by D. Farrell]

pace and oriented their chelipeds toward the threat, closing their chelae on the bear. No amount of shaking or sharp withdrawals induced autotomy. However, when one of us tried to pull a crab out of its burrow by its cheliped, the cheliped was autotomized (*4*).

Eriphia squamata and *Xanthodius sternberghii* are both found in the intertidal zone, *E. squamata* under stones and in shallow pools and *X. sternberghii* under stones. When *E. squamata* was disturbed, 15 out of 25 crabs encountered ran for cover, holding the chelae above the carapace and displaying. The display was similar to the startle display of many insects (*1*) with the chelipeds maximally extended laterally; this display increases their apparent size and reveals the striking coloration of the inner surfaces and of the bright red fingers. When cornered and attacked, 23 crabs displayed and counterattacked by "biting." Autotomy did not occur during the attack, but four crabs autotomized when the bear was sharply withdrawn.

Xanthodius sternberghii are extremely cryptic and, when first exposed or disturbed, remain motionless with their legs curled under them (*5*). Of the 160 crabs exposed, 127 remained motionless for more than 1 minute. The crabs then slowly edged for cover or almost imperceptibly dug into the sand. Thirty-three of the crabs ran as their initial response to disturbance; one large male displayed, holding both chelipeds over the carapace as it ran for cover. It was not possible to induce counterattacks on the predator, and when *X. sternberghii* was held in the hand, 42 out of 52 crabs feigned death.

The evolution of attack autotomy may be a factor which allows the terrestrial crab to defend itself effectively while wandering far from a burrow or retreat. Mammals which may be vulnerable to attack autotomy include otters, raccoons, and opossums, all of which occur in the crabs' habitats and are known to feed on crabs (*6*). Although the encounters between the otter and *P. richmondi* show that the autotomy of the attacking weapon is a successful form of defense, defense is not the only function of the chelipeds. Selection for retaining the cheliped will be exerted wherever this organ is important for functions other than defense. In gregarious intertidal and terrestrial crabs, the chelipeds may have acquired important functions in social signaling and fighting (*7*). In addition, the diet of the crab may affect the importance of the cheliped for feeding purposes and its consequent disposability. Some crabs can learn to feed effectively by using their walking legs (*8*), and *P. richmondi* and *G. quadratus* have been observed feeding on fallen fruit which does not require the use of chelipeds.

Autotomy, in the broad sense, in other arthropods and reptiles (and the autotomy of walking legs in crustaceans) permits the escape of the prey only if the predator chances to seize an autotomizable part. Active autotomy, as we have described it in *P. richmondi* and *G. quadratus*, is a process by which the active role belongs to the potential prey and the defense does not depend on the chance orientation of the predator's grasp.

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4. To test the response of *C. crassum* to predators in the field, we glided a black hawk model over the colony and pulled the toy bear across it on a piece of string. When the model was flown over the colony at a height of 1.2 m, all the crabs in a 1.8-m path below the flight path retreated down their holes. The first crabs appeared after 1 minute at the first flight, 45 seconds after the second, and 30 seconds after the third flight. When the bear was dragged through the colony, crabs within 0.6 m went down their burrows, those between 0.6 and 0.9 m moved to the entrance, and beyond this there was no response.
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9. The attack was maintained for 30 seconds against all crabs except *E. squamata*, which was attacked for 1 minute. After 30 seconds the crabs usually became lethargic and would not respond.

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Reinforcement of Competing Behavior during Extinction

Abstract. *Conditioned behavior declines in frequency when reinforcement is discontinued. In two experiments this extinction process was facilitated when competing behavior was reinforced as the original response was extinguished. When reinforcement for competing behavior was withdrawn, however, rats resumed their original behavior and there were no overall savings in total responses to extinction.*

There are many ways to suppress behavior including physical restraint, satiation, punishment, and extinction. Restraint physically prevents the organism from engaging in the old behavior; satiation involves a procedure such as previous feeding and implies that the deprivation motivating the old behavior has been relieved; punishment involves the delivery of aversive stimuli following the old behavior; and extinction consists of the withdrawal of the former consequences (reinforcers) of the old behavior. Except for physical restraint, which hardly needs any refined analysis, each of these procedures has been studied extensively (*1*). A less frequently explored method for suppressing behavior involves reinforcing behavior incompatible with the old response (*2*). Terms such as competing behavior, reciprocal inhibition, interference, counterconditioning, and antagonistic responses refer to the same issue: How can performance of one behavior prevent the performance of another behavior?

Unfortunately, competing responses

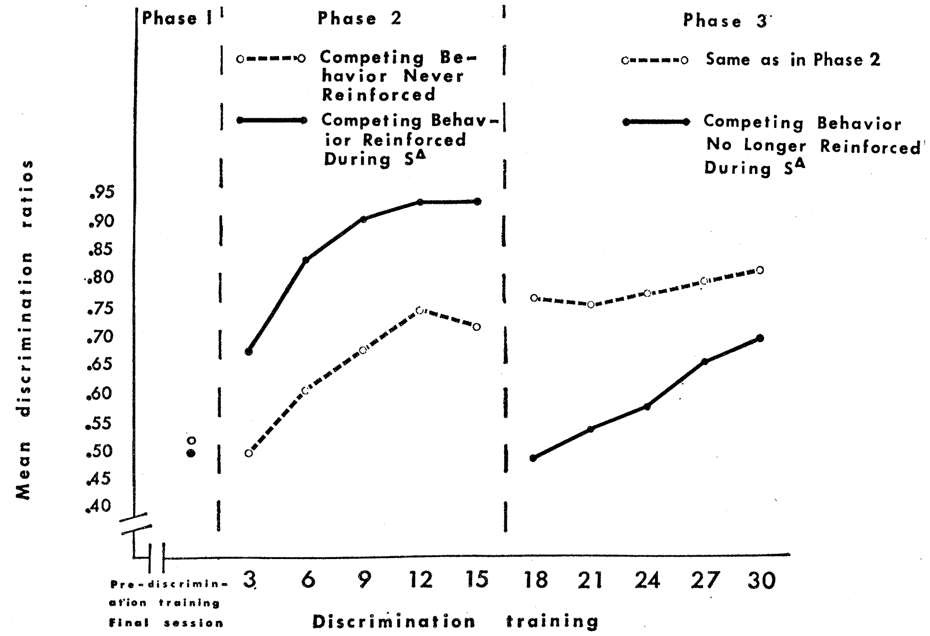

Fig. 1. Discrimination learning as a function of (i) reinforcement of competing behavior during S^Δ and (ii) subsequent withdrawal of this reinforcement. The ratios were computed according to the formula $S^D/(S^D + S^\Delta)$ and plotted in blocks of three sessions.

have too often been inferred rather than measured and manipulated directly. For example, they have been used as handy ghosts in theoretical explanations of the suppressive effects of punishment (*3*), extinction (*4*), and systematic desensitization (*5*). An experimental analysis, instead of a theoretical or a correlational analysis, is necessary to determine if and how reinforcement of competing behaviors contributes to the suppressive effects produced by other procedures such as punishment and extinction.

A good start has been made in the case of punishment. A series of studies involving different species and different aversive stimuli has shown that punishment can be made more effective if an alternative behavior to the one being punished is available and is reinforced (*6*). A similar extensive analysis, however, has yet to be made in the case of extinction. We have asked two questions about the possible facilitating effects of competing behavior during extinction: (i) When reinforcement is withdrawn for one response (extinction procedure), is this response reduced in frequency more rapidly and more permanently if an alternative (competing) behavior is reinforced simultaneously? The results from two control groups without punishment in the Boe (*7*) experiment suggest that an affirmative answer to this question can be expected. (ii) What happens to the extinguished response when reinforcement for competing behavior is stopped?

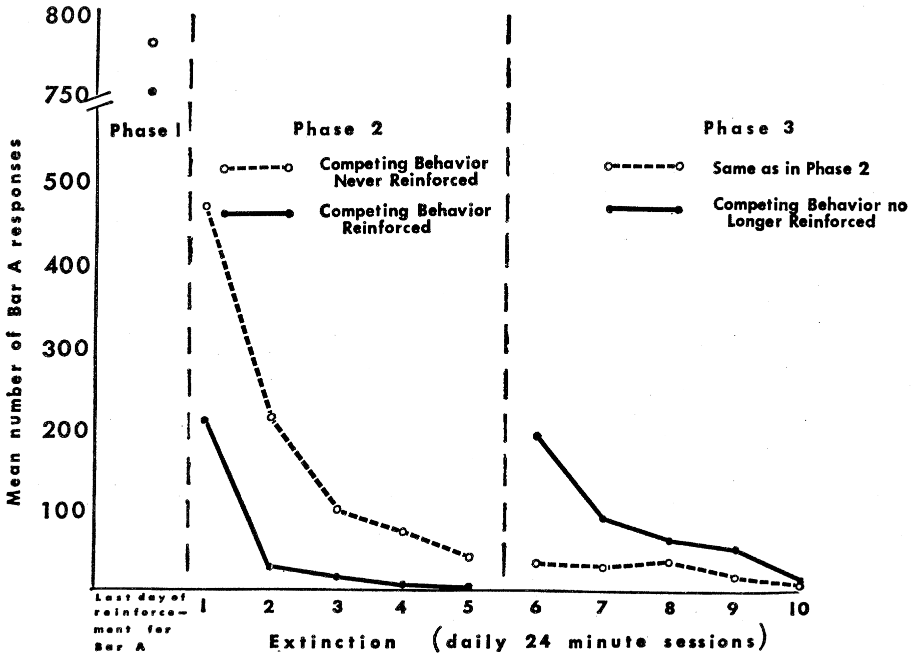

Fig. 2. Extinction as a function of (i) reinforcement of competing behavior and (ii) subsequent withdrawal of this reinforcement.

These questions were first studied in the context of a typical discrimination training procedure. Twenty-four male hooded rats kept at 80 percent of their weight when given unlimited access to food were initially trained (using food reinforcement) to press a single lever during alternating periods of light on and light off. After 5 days the animals were pressing the lever (lever A) equally often in the presence of each stimulus and phase 2 was begun. An alternative lever (lever B) was added to the box, and reinforcement was no longer provided for the original response (pressing lever A) when the light was off (S^Δ). When the light was on (S^D)the original response continued to be reinforced on a 30-second schedule of variable intervals. This conventional discrimination training procedure usually causes the animals to gradually stop pressing the lever during S^Δ (nonreinforced periods) and to continue pressing during S^D (reinforced periods). We determined whether the original response was inhibited more quickly during S^Δ if an alternative response was rewarded during this time. Accordingly, lever B responses during S^Δ were reinforced on a fixed-ratio schedule for one-half the subjects. (We started out by rewarding every lever B response, then every third response, every fifth response, and eventually every tenth response. This was done for experimental subjects only and then only during S^Δ periods when pressing lever A went unreinforced.) Lever B responses were recorded for control subjects, but these responses were not reinforced in either S^Δ or S^D. In the final phase of the experiment reinforcement for lever B responses was withdrawn for all subjects. Experimental and control groups were now treated the same: Lever A responses were reinforced when the light was on, and not reinforced when the light was off. Lever B responses in both groups were not reinforced in either stimulus condition.

High discrimination ratios in Fig. 1 mean that the animal seldom presses lever A during S^{Δ} (when the light is off and lever A responses are not reinforced). The experimental subjects that were reinforced for pressing lever B during S^{Δ} made fewer lever A responses during this period than did the control subjects (Fig. 1). The experimental group was up to a ratio of .65 within the first 3 days, whereas the control group was still around .50. At the end of this phase the experimental subjects had stabilized at about .90, whereas the control group had stabilized at about .70. These differences were statistically significant ($t = 7.67$, $P < .01$).

The most dramatic results, however, took place in the third phase of the experiment. When reinforcement for the competing behavior was withdrawn, the experimental subjects resumed pressing lever A when the light was off, even though such behavior was still not being reinforced in the presence of this stimulus. The discrimination ratios deteriorated drastically for the experimental subjects and there was only a gradual recovery over the next 15 days. In other words, lever A responses for experimental subjects had not been extinguished during S^{Δ} conditions in the previous phase; they had been temporarily supplanted by lever B responses. When this competing behavior was no longer reinforced the experimental animals still had to learn what the control animals had already learned. No savings in total number of errors (lever A responses during nonreinforced periods) was indicated. In fact, the trend was in the opposite direction; the mean number of errors made by the experimental subjects in phases 2 and 3 combined was greater than that made by the control subjects (978 compared to 682). This difference, however, was not statistically significant ($t = 1.40$, $P > .05$).

An almost identical finding was obtained in a second experiment where, instead of studying the same phenomenon within the context of discrimination training, we used a simple extinction procedure. Twenty-four male hooded rats maintained at 80 percent of their weight when given free access to food served as subjects. In phase 1 only lever A was available and all subjects were reinforced for pressing this lever on a variable-interval, 30-second food schedule. In phase 2, lever A responses were no longer reinforced and lever B was available. During this phase the experimental subjects ($n = 12$) were reinforced after every tenth lever B response, whereas the control subjects ($n = 12$) underwent the typical extinction procedure, that is, neither lever A nor lever B was reinforced. In phase 3 experimental subjects were no longer reinforced for lever B responses. They were now in the same situation as the control subjects; neither response was reinforced (Fig. 2).

In phase 2 when the extinction procedure for experimental subjects was supplemented by reinforcement of competing behavior, lever A responses declined more rapidly and more substantially than was the case for the control subjects undergoing a conventional extinction procedure ($t = 8.12$, $P < .01$) (Fig. 2). When reinforcement of competing behavior was discontinued in phase 3, however, the experimental subjects resumed pressing lever A and exhibited an extinction curve similar to that of the control subjects in the preceding phase. Again, there was very little overall savings from the previous reinforcement of competing behavior. Although the experimental group responded on lever A less often than the control group in phase 2, they responded significantly more often in phase 3 ($t = 2.97$, $P < .01$). When the two extinction phases are combined, there is no significant difference in the number of lever A responses made by the two groups ($t = 1.42$, $P > .05$).

These findings correspond to the reports of Skinner (*8*) and Estes (*9*). They found that mild punishment did not hasten the course of extinction; likewise our results indicate that extinction may not be hastened by the reinforcement of competing behavior. In fact both punishment and reinforcement of competing behavior suppress the behavior to be extinguished and thus may prevent extinction from taking place. When punishment is stopped or reinforcement of competing behavior is stopped, the extinction procedure still needs to be carried out. This is not true, however, in the case of more intense punishment (*10*) and it may not be true if competing behavior is reinforced for a longer period before being terminated, or if a different schedule of reinforcement for the competing behavior is used, or if reinforcement for competing behavior is discontinued more gradually, or if the competing response has a topology different from the response being extinguished.

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Means and Variances of Average-Response Wave Forms

John *et al.* (*1*) reported that, during generalized responding, the stimulus for such generalization releases a neural process representing the previous experience of the animal—that is, the engram associated with the original conditioning. I am not questioning this conclusion—in fact it would appear to be a likely hypothesis. However, I do question certain aspects of the methodology employed in reaching the conclusion.

My first point concerns the comparison of average evoked responses to the generalization stimulus; evoked responses to generalization stimuli eliciting the instrumental response for food were compared to evoked responses to generalization stimuli eliciting avoidance. A number of *t*-tests (the number was not specified) were used to compare amplitudes at similar latency points of individual average-response wave forms. The variance estimates for these *t*-tests