for the first condition were satisfied.

Three of the four pigeons (B-17, B-19, and B-20) preferred the free-food cup with the accompanying stimulus change in terms of percentage of entries made (Table 1). However, the percentage of time spent in each food cup and the percentage of grain consumed from each cup did not change systematically with the location of the stimulus change. The fourth pigeon (B-18) did not demonstrate a stable preference, but tended to change his preference from side to side in a cyclic pattern across several sessions. This subject was dropped from the study after reaching the 50-session maximum without satisfying the stability criteria.

The data from experiment 1 show that responding in the presence of free food is maintained by the stimulus change which accompanies response-produced food, but which, in previous studies, has never accompanied the consumption of free food. Responding not being maintained when no stimulus change occurred with the response-produced food suggests that responses which produce food have no special intrinsic appeal or motivational properties.

Experiment 2 supports the conclusion that responding in the presence of free food is maintained by the stimulus changes which accompany the arrival of response-produced food by showing that preference for a particular free-food source can be manipulated by stimulus change. Because entry was required to produce the stimulus change, entries, but not time or consumption, changed systematically with the location of the stimulus change. This further supports the contention that the stimulus change controlled the observed preferences.

Neuringer (*3*) demonstrated that stimulus change, alone, was not sufficient to explain this phenomenon. He allowed two pigeons (which had been responding in the presence of free food) to produce the stimulus change but prevented them from consuming any response-produced grain. Both ceased pecking at the disk and ate exclusively from the free-food cup. While this manipulation showed that stimulus change would not maintain response, it did so by severing the association between stimulus change and food. In the two studies presented here we investigated the role of stimulus change without terminating the relationship between stimulus change and food and showed that responding is maintained by stimulus change accompanying food. Stimulus change in this context may be a conditioned reinforcer due to its temporal pairing with food (*7*). The results are also consistent with Herrnstein and Loveland's (*8*) recent position that the presence of food in a procedure enhances the reinforcing effectiveness of stimulus change. In any case, the relationship between stimulus change and food is apparently the crucial factor in maintaining responding in the presence of free food.

Table 1. Average preference for the food cup with accompanying stimulus change for the last five sessions of each condition, left (L) and right (R).

Pigeons	Food cup	Entries (%)	Time in each cup (%)	Grain consumption (%)	Number of sessions
B-17	L	72	49	63	20
	R	60	25	29	21
B-18	L	33*	30*	27*	50*
B-19	L	61	59	39	20
	R	59	41	43	38
B-20	L	76	78	73	21
	R	56	56	46	21

* Average for sessions 46 to 50. Not stable data.

The assumption that deprivation is a necessary antecedent of performance is an essential constituent of many learning theories. This assumption may require modification in light of the present results. These results, however, offer no problem for those who define reinforcers (rewards) in terms of their effects on behavior and without reference to inferred internal states (for example, deprivation). The major finding of these experiments is that food-producing responses have no special motivational properties. The phenomenon of responding in the presence of free food, while replicable, need not be construed as an indictment of reinforcement theory. Instead, these responses, like other operant (instrumental) responses, appear to be controlled by their associated consequences.

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Long-Term Sensitization of a Defensive Withdrawal Reflex in Aplysia

Abstract. *When a weak tactile stimulus is applied to the siphon of* Aplysia californica, *the animal withdraws the siphon between the parapodia. This defensive withdrawal reflex can be facilitated (sensitized) if the animal is previously given 4 days of training, consisting of four brief noxious stimuli each day. The sensitization of this reflex can last for up to 3 weeks after training and is mediated by the abdominal ganglion which also mediates long-term habituation. This preparation may provide a system for analyzing the neural mechanism of long-term behavioral modifications of complexity which is intermediate between habituation and associative learning.*

The defensive reflex of siphon and gill withdrawal in *Aplysia californica* (*1*) has been used to study cellular mechanisms of several short-term behavioral modifications (*2, 3*). Long-term habituation of this reflex, lasting several weeks, has been described (*4*). We now report long-term sensitization of the siphon withdrawal component of this reflex.

Sensitization is an elementary form of learning in which reward or punishment facilitates an animal's preexisting response to another stimulus (*5*). While

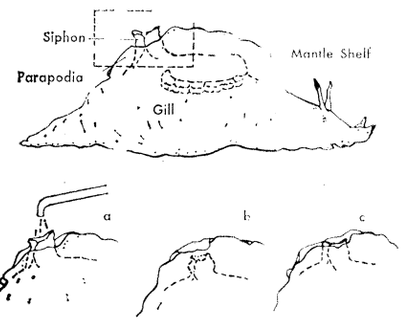

Fig. 1 (top). Side view of an unrestrained *Aplysia*. The siphon normally protrudes between the parapodia, whereas the gill (dashed lines) is normally hidden underneath the mantle shelf between the parapodia. Fig. 2 (bottom). Method of tactile stimulation and operational definition of siphon withdrawal reflex. (a) The tip of the Water Pik is aimed, from a fixed distance, down the lumen of the siphon and an 800-msec jet of seawater is delivered. Timing of the response is begun at the offset of the stimulus. (b) In response to the tactile stimulus, the siphon withdraws between the parapodia, out of view of the observer. Often, siphon withdrawal is also accompanied by closure of the parapodia. (c) Timing is terminated as soon as the observer can unambiguously identify the siphon when it becomes visible again between the parapodia.

Table 1. Median duration of siphon withdrawal, sum of trials one to ten. The values in parentheses are the first and third quartiles. The surgery itself produced no significant change in sham-operated scores.

	Median duration of siphon withdrawal (seconds)					
	a. Not sensitized			b. Sensitized		
	N	Pre-operative	Post-operative	*N*	Pre-operative	Post-operative
Sham-operated	13	78 (40–118)	98 (45–151)	11	61 (42–116)	268 (124–429)
Deganglionated	14	83 (53–141)	0 (0–4)	6	54 (24–103)	0 (0–0)

habituation involves a decrease in reflex responsiveness to repeated presentation of the same stimulus, sensitization involves an increase in reflex responsiveness due to the presentation of a second stimulus, usually to a different site. Sensitization resembles classical conditioning in that activity in one pathway enhances activity in another, but it differs from classical conditioning in that the reflex enhancement does not require the temporal association of the two stimuli. Because of its similarity to classical conditioning some workers (*6*) suggest that sensitization is the basic adaptive mechanism from which associative learning evolved. An understanding of the neural mechanisms of sensitization might, therefore, be a useful step in understanding neural mechanisms of associative learning.

A tactile stimulus applied to the siphon produces concomitant contraction of both gill and siphon. The gill withdrawal component of this reflex can be monitored only in restrained animals and is, therefore, difficult to study in long-term experiments. However, the siphon can be seen in unrestrained animals (Fig. 1), and, therefore, the siphon withdrawal component of the reflex can be used for investigating the long-term effects of chronic stimulation.

To examine whether the siphon withdrawal reflex could undergo long-term sensitization we matched 38 animals by weight (100 to 360 g) and by initial responsiveness to siphon stimulation, and assigned them to experimental and control groups. To determine their baseline responsiveness we gave both groups a habituation training session which consisted of ten consecutive tactile stimuli to the siphon (*4*). The strength of each reflex response was measured by the time that the siphon remained withdrawn between the parapodia (Fig. 2).

A 0-second response on a given trial indicated that the siphon never disappeared from view, although it may have moved when stimulated. In all animals, the series of ten stimuli produced a progressive decrement in reflex responsiveness characteristic of short-term habituation (Fig. 3a). After recovery from the habituation session prior to training, experimental animals received sensitization training, consisting of four brief noxious electrical shocks applied to the anterior mantle region on four consecutive days (*7*). Control animals received no sensitization training. Retention of sensitization was measured 1 day, 1 week, and 3 weeks after training by comparison of siphon withdrawal time of experimental and control animals using a blind procedure (*8*).

In the 1-day and 1-week retention tests (Fig. 3, b and c), the experimental animals showed significantly longer siphon withdrawal times as compared to the controls ($P < .01$). Also, in both retention tests the responses of the experimental animals were significantly longer as compared to their responses in the preshock session [1 day, $P < .005$; 1 week, $P < .025$ and $P < .005$ (Fig. 3, b and c)], whereas the control group was unchanged. In the 3-week retention test, although there was no longer a significant difference between the groups, an intragroup comparison revealed that the responses of the experimental animals were still significantly longer than those in the pretraining session ($P < .005$), whereas the control animals were still unchanged.

These results indicate that in *Aplysia* repeated exposure to brief noxious stimuli for 4 days produces long-term sensitization of defensive siphon withdrawal which persists for at least a week and is not fully recovered after 3 weeks. To examine whether the amplitude and persistence of the sensitization could be further enhanced, we increased the number of noxious stimuli and spaced the training sessions, delivering two stimuli a day for 10 days. Animals so trained (Fig. 4) showed more dramatic sensitization 1 day after training than animals that received only 4 days of sensitization training (Fig. 3), and the difference between sensitized and control animals persisted for at least 3 weeks. There was also a suggestion that the kinetics of habituation changed since they showed buildup across some trials rather than the typical accelerating decrement (compare Figs. 3b and 4a).

The possibility existed that the sensitized behavior was primarily closure of the parapodia over the siphon rather than siphon withdrawal (Fig. 2b). To rule out this possibility we surgically removed the parapodia from 19 animals and used the procedure of experiment 1 (Fig. 3). Siphon withdrawal was measured as the length of time following the tactile stimulus that the siphon remained contracted; when the siphon reversed direction (that is, began to relax) the response was scored as terminated. Using this score, we found that 24 hours after sensitization training the experimental animals ($N = 9$)

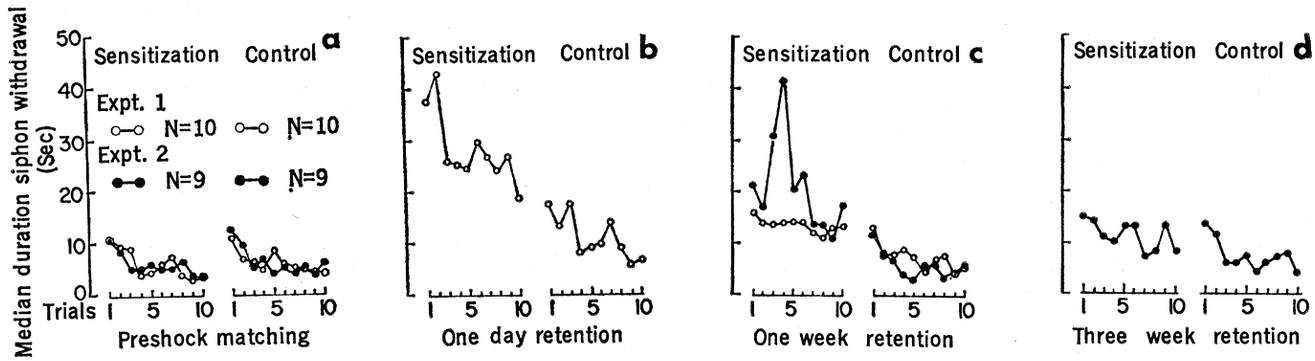

Fig. 3. The median duration of siphon withdrawal is shown for each trial of a ten-trial block. A minimum intertrial interval of 30 seconds was used. The results of two independent experiments are shown, but they are pooled for discussion in the text (a). Animals were matched on the basis of the initial duration of siphon withdrawal during a pretraining habituation session of ten trials. Thirteen days after matching, the experimental animals were given four shocks per day for 4 days, whereas the controls received no shocks. In experiment 1, retention of sensitization was tested 1 day (b) and 1 week (c) after the last shock. In experiment 2, retention was tested 1 week (c) and 3 weeks (d) after the last shock.

showed significantly longer siphon withdrawal times than controls ($N = 10$) ($P < .025$) and than before sensitization ($P < .025$). These findings demonstrate that siphon withdrawal is sensitized, although they do not eliminate the possibility that closure of the parapodia might also be sensitized.

To analyze the neural mechanisms underlying long-term sensitization of the siphon withdrawal reflex, it is necessary to relate these behavioral changes to activity changes in identified neural circuits that mediate siphon withdrawal (*9*). The understanding of the neuronal circuits within the abdominal ganglion that mediate the central components of gill and siphon withdrawal (*10*) makes this possible. Gill withdrawal can be elicited by siphon stimulation without recruiting the peripheral nerve net of the gill (*11*). However, siphon withdrawal, elicited by direct stimulation of the siphon, invariably involves some activation of the peripheral nerve net of the siphon (*12*). In order to evaluate the relative contribution of peripheral and central components to the siphon withdrawal reflex, we first examined the effect on this reflex of removing the abdominal ganglion. Twenty-seven animals were matched on the basis of a ten-trial siphon habituation session and assigned to a deganglionated or sham-operated group. Eight days after the initial session, the deganglionated group had the abdominal ganglion removed (*13*) and the sham-operated group underwent similar surgery except for the actual removal of the ganglion. On the day after surgery, siphon withdrawal was measured using a blind procedure (Table 1a). The deganglionated animals showed significantly less siphon with-

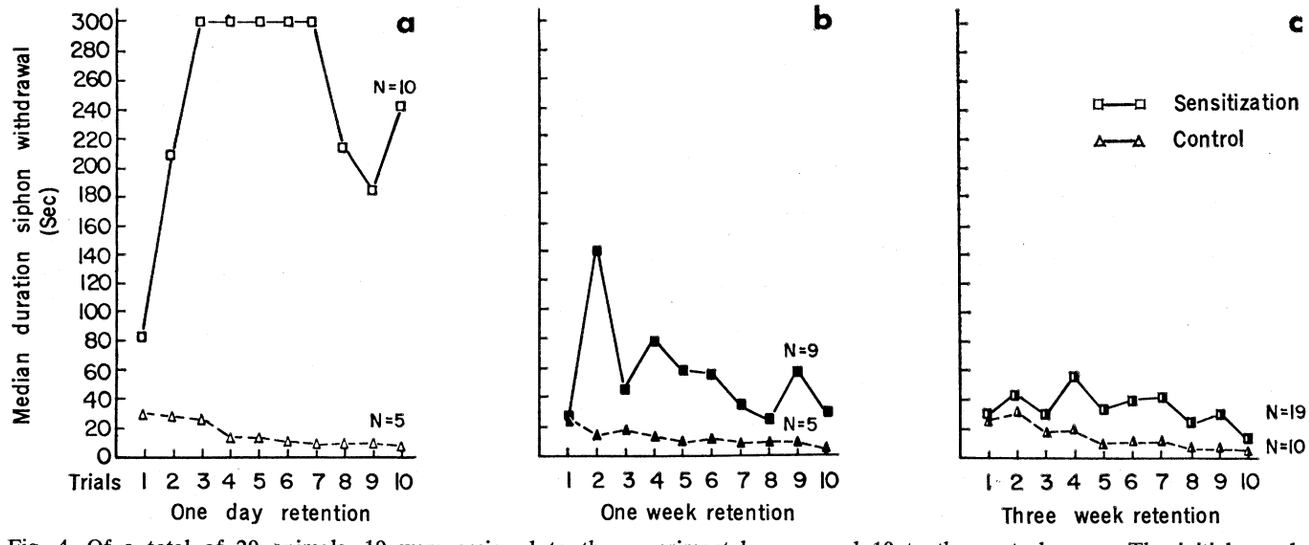

Fig. 4. Of a total of 29 animals, 19 were assigned to the experimental group and 10 to the control group. The initial matching prior to shock (not shown) was based on only two trials separated by about 1 hour. Beginning 5 days after matching, the experimental group was given two shocks a day for 10 days. During training, all animals were given a single siphon test stimulus each day and, on the basis of this information, subjects in each group were assigned at the end of the 10 days to either the 1-day retention or the 1-week retention group. Half of the animals in each group were tested for retention of sensitization 1 day after the last shock (a), whereas the other half were tested at 1 week (b). Three weeks after the last shock, all animals were tested for retention (c). In all comparisons, the sensitized animals showed significantly greater siphon withdrawal than controls. There is also a difference in the duration of siphon withdrawal in these animals compared to those illustrated in Fig. 3. The flat peak of the sensitization group on the 1-day retention test results from more than half of the animals exceeding a limit of 300 seconds on those trials.

drawal after surgery ($P = .025$), while the responses of the sham-operated were not significantly changed. After the operation the scores of the deganglionated group were significantly lower than the scores of the sham-operated group ($P = .013$). These results suggest that the siphon withdrawal component of the defensive reflex is mediated primarily by the central nervous system. This does not mean that all siphon withdrawal is centrally mediated. In the absence of the abdominal ganglion, the peripheral plexus is still able to move the siphon when it is directly stimulated. However, deganglionated animals are unable to perform an integrated withdrawal reflex that removes the siphon from view.

Since the siphon can move in the deganglionated animal, we sought to determine whether the sensitization of the reflex might be due to the facilitation of the relatively small peripherally mediated siphon movements. Twenty-four animals were matched as in previous experiments and all animals were given sensitization training (four shocks per day for 4 days) beginning 6 days after the habituation session. On the day after the last shock, half of the animals were deganglionated and the other half were sham-operated. All animals were given a 1-day postoperative retention test using a blind procedure (Table 1b). The deganglionated animals failed to show any effect of the previous sensitization training. In fact, these animals showed significantly less siphon withdrawal than they did previously ($P = .025$) (Table 1b). By contrast, the sham-operated animals showed significant sensitization ($P = .005$) despite the intervening anesthetic and surgical procedure. Two days after the last shock, the median value of the sham-operated group was about 440 percent of the presensitization value. These results suggest that long-term sensitization of siphon withdrawal is centrally mediated.

The demonstration of long-term sensitization of defensive siphon withdrawal in *Aplysia* is a further extension of the short- and long-term forms of behavioral modifications that this simple reflex can undergo. Whereas habituation is perhaps the most elementary behavioral modification, sensitization is more complex because it involves changes in one reflex pathway as a result of activity in another one. As Groves and Thompson (*14*) have pointed out, sensitization represents an aspect of arousal, or a "state variable," characteristic of vertebrates. By developing a simple system for the analysis of sensitization, it may become possible to gain some understanding of the cellular mechanisms of arousal and elementary forms of learning.

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7. Each shock (6 ma a-c between bipolar electrodes in seawater) lasted about 1 second and successive shocks within a day were separated by a minimum of 2 hours. The anterior mantle region is innervated by the branchial nerve, whereas the siphon region is innervated by the siphon nerve. It has been shown that reflex habituation produced by repetitive tactile stimulation of the siphon does not generalize to the anterior mantle region (*3*). This suggests that the electrical shock reached the central nervous system via a different pathway than the tactile stimulus.
8. Each animal contributed a single score, the sum of the duration of siphon withdrawal for all ten trials. Nonparametric statistics were used to compare scores either within a group (Wilcoxon matched-pairs signed-ranks test), or between groups (Mann-Whitney U test).
9. Using a restrained preparation, we attempted to relate sensitization of siphon withdrawal to sensitization of gill withdrawal (*4*). We found no significant difference in gill withdrawal between experimental and control animals. It may be that restraining the animals caused sufficient sensitization to obscure group differences.
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Heritability of IQ by Social Class: Evidence Inconclusive

In her provocative article on race and intelligence (*1*), Scarr-Salapatek may give the mistaken impression that "two major, competing hypotheses," or some combination of them, are the only plausible explanations of the relation among social class, race, and IQ (intelligence quotient). Either (i) racial differences in intelligence result from environmental disadvantage that simultaneously retards mental development and prevents full expression of genetic differences or (ii) racial differences reflect genetic differences that contribute a similar proportion of variance in all social classes. Scarr-Salapatek attempts to exclude the second hypothesis and thereby, perhaps, to strengthen the environmental explanation of race differences.

It is sometimes supposed that an optimum environment will result in maximum expression of genetic factors, but the fallacy of this view becomes apparent when one asks, "Optimum for what?" or "Expression of which genetic factors?" Different environments elicit the expression of different sets of genes. Scarr-Salapatek's restriction of explanations to two models tends, albeit unintentionally, to affirm the above fallacious view and to perpetuate the widespread idea that genetic factors set limits on an individual's potential, while the environment determines how closely he will approach these limits. Neither heredity nor environment sets absolute limits on quantitative traits.

If we discard simplistic formulations, many more than two models have to be considered in any attempt to understand racial and class differences in intelligence. A complete and testable model should predict at least three things: the effect of socioeconomic environment on intelligence test scores,