

Simultaneous Overshadowing and Potentiation of Taste and Contextual Cues by a Second Taste in Toxicosis Conditioning

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Three experiments examined the effect of sucrose consumption in a novel context on the conditioning of an aversion to that context. In Experiment 1, rats were injected with LiCl after drinking either sucrose (Group SUC-LI) or water (Group WAT-LI) in a novel context (context 2). An unpoisoned control group consumed water in context 2 and was injected with isotonic saline solution (Group WAT-SAL). On test, when presented with saline in context 2, Group WAT-LI consumed less than Group WAT-SAL, suggesting that a conditioned aversion to context 2 developed in Group WAT-LI. Group SUC-LI consumed less than Group WAT-LI, suggesting that the sucrose had potentiated a context aversion in Group SUC-LI. Experiment 2 was similar to Experiment 1, except that rats drank a novel vinegar solution in context 1 before entering context 2 for conditioning. On test, Group SUC-LI drank more vinegar in context 1, and less saline in context 2, than Group WAT-LI, suggesting that sucrose had simultaneously overshadowed vinegar and potentiated an aversion to context 2. Experiments 3a and 3b confirmed that the results of Experiment 2 were due to potentiation rather than generalization of a sucrose aversion to familiar saline. © 1996 Academic Press, Inc.

When more than one conditioned stimulus (CS) is presented prior to the onset of an unconditioned stimulus (US), one of two possible interactions may take place between the conditioned stimuli: overshadowing or potentiation. The most widely investigated of these interactions is overshadowing. In a typical overshadowing experiment two groups are compared in which either the element A (Group A) or the compound AB (Group AB) are paired with a US, and both groups are presented with A on test. As a result of this training, it is commonly observed that responding to A in Group AB is less vigorous than that in Group A, and it is this decrement resulting from the introduction of the second cue (B) which is termed overshadowing (e.g., Pavlov, 1927; Revusky, 1971).

Several accounts of overshadowing have been proposed. Rescorla and Wagner (1972) suggested that overshadowing is a form of blocking. When a compound CS (AB) is paired with a US, the more salient CS (e.g., B) quickly becomes

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associated with the US and, having high associative strength following the first training trial, blocks further learning about the less salient cue (A). The generalization decrement interpretation of overshadowing (e.g., Pearce, 1987) is that the compound cue presented during training generalizes less well to the elements that make up that compound than do the elements themselves. According to the generalization decrement hypothesis, the decrement in responding to A shown on test in Group AB compared to that of Group A is due to the fact that the test stimulus A is perceived as highly similar to the training stimulus A (high generalization), but not as similar to the training stimulus AB (low generalization).

Wagner (1981) interpreted the overshadowing phenomenon to be the result of the allocation of limited processing resources. Thus, if only one cue were presented (A), all processing resources would be free to process that stimulus. However, if a second cue were introduced during training (B), the processing resources would have to be shared between the cues present (A and B), and therefore learning about these cues would be retarded. Other interpretations of the effect have been offered, but these three are arguably the most influential at the present time.

In contrast to the overshadowing effect, the presence of one stimulus may potentiate, rather than overshadow, the other stimuli presented during conditioning (e.g., Rusiniak, Hankins, Garcia, & Brett, 1979). This potentiation effect is particularly pronounced in toxicosis conditioning. For example, when exposure to a novel context (which may be viewed as a CS) is followed by the injection of lithium chloride, the aversion developed toward that context is greater if the animal is given access to novel sucrose during context exposure (Best, Brown, & Sowell, 1984).

At least three mechanisms have been proposed to explain potentiation. First, Garcia and colleagues (e.g., Garcia, Brett, & Rusiniak, 1989) suggested that nonfood cues presented contiguously with consumption of a novel flavor are "gated" into the feeding system. It is claimed that illness is a US specific to the feeding system and that stimuli which gain access to this system (e.g., foods, and stimuli presented contiguously with foods) are able to form strong associations with illness. A second, related hypothesis is that the presentation of a novel flavor increases the amount of attention paid to contiguous stimuli and thus increases their associability (Galef & Osborne, 1978). These first two hypotheses differ in that the former postulates a domain-specific learning mechanism, while the latter attributes potentiation to the properties of a general attentional mechanism. They are, however, similar in that they both assume that processes in addition to those thought to be acting in other associative learning phenomena are responsible for potentiation.

Durlach and Rescorla (1980) have suggested that second-order conditioning is responsible for potentiation. This view suggests that cues present when the animal consumes a novel flavored food become associated with that food. The food, in turn, becomes associated with illness. When the cues present during consumption of the food are presented on test, they elicit a representation of the

flavor which, in turn, elicits a representation of illness and leads to avoidance behavior. This associative perspective allows that a flavor can overshadow contextual cues, but that the associative strength which accrues to the contextual stimuli through second-order conditioning to the flavor will outweigh the decrement resulting from overshadowing. Thus, according to this account, the mechanism responsible for potentiation is that which underlies associative learning more generally. All three hypotheses have received some empirical support (see Lolordo & Droungas, 1989, for review).

The present report focuses on the possibility that overshadowing and potentiation might occur simultaneously; that is, a single cue might overshadow a second cue and, in addition, potentiate a third cue which is present during conditioning. It has already been shown that, when a novel flavor is presented in a novel context and followed by an injection of lithium chloride, not only does the novel flavor potentiate an aversion to the novel context, but the novel context also overshadows the aversion conditioned to the novel flavor (Best & Meachum, 1986). This is clearly an example of simultaneous overshadowing and potentiation. Both stimuli in this compound conditioning procedure affected the conditioning of the other, but the effect was asymmetrical; the flavor was overshadowed by the context, while the context was potentiated by the flavor. The present experiments were an attempt to demonstrate simultaneous overshadowing and potentiation by varying the nature of the target stimuli.

Although the mechanisms postulated to underly potentiation proposed by Galef and Osborne (1978) and Rusiniak *et al.* (1979) are nonassociative, they do not exclude the possibility that a single stimulus might potentiate a second stimulus and, at the same time, overshadow a third stimulus as a result of conventional associative processes. The associative explanation of potentiation proposed by Durlach and Rescorla (1980) also allows for such an effect.

Data bearing on the issue of whether overshadowing or potentiation will occur in compound conditioning with a flavor CS and toxicosis US indicate that potentiation occurs most readily when (i) the target cue presentation is contiguous with the presentation of the flavor (Westbrook & Brookes, 1988), (ii) the potentiated stimulus is of very low salience (Davis, Best, & Grover, 1988), and (iii) the duration of compound exposure during training is long (Westbrook, Homewood, Horn, & Clarke, 1983). Thus, it would seem that if the novel flavor were presented with two further stimuli, one satisfying the conditions for potentiation (contiguity with the flavor, low salience, and extended exposure) and the other optimizing the conditions for overshadowing (noncontiguous and of high salience), then both overshadowing and potentiation should occur simultaneously. The three experiments presented below sought to demonstrate such an effect.

EXPERIMENT 1

Evidence of potentiation of a context aversion by sucrose was sought using a procedure similar to that used by Boakes, Westbrook, and Barnes (1992, Ex-

periment 3). Three groups of rats were allowed to drink in a novel context and then received an injection immediately after being taken out of the context. Two of the groups were injected with lithium chloride. Of these groups, one drank sucrose in the context while the other drank tap water. The third group was given access to tap water in the context and then injected with saline solution. It was predicted that the poisoned animals would develop an aversion toward the context as measured by a reduction in consumption of familiar saline solution in the context relative to the unpoisoned controls. It was further predicted that the animals given sucrose solution in the context would show potentiation by consuming less saline on test than poisoned animals given tap water in the context during conditioning.

Method

Subjects. Twenty-four, experimentally naive, male Sprague–Dawley rats (250–350 g) were used. They were housed in groups of four in a temperature-controlled room on a 12-h light/dark cycle, lights on at 0700 h. All animals were experimentally naive and were allowed food *ad libitum* throughout the experiment. Water consumption was controlled as shown below.

Apparatus. A rack with 12 cages in a dark experimental room was used for the animals' daily access to water. The cages were similar to the home cages in all respects except that they had wire instead of sawdust floors. These cages constituted context 1. In context 1, water was made available from 500-ml water bottles with rubber stoppers and ball bearing spouts to reduced leakage. The conditioning context (context 2) consisted of operant chambers with clear plastic walls, housed in open-fronted, sound attenuating chambers. The room containing the operant chambers was brightly lit by a combination of natural and fluorescent light, and two noisy fans were placed on the floor in front of the boxes. Thirty-milliliter water bottles were used to allow access to water and sucrose solution. Each of these had a rubber stopper and a long metal spout, again with a ball bearing, which protruded through a hole in the wall of the box. Thus, context 1 was similar to the home cages in construction and had a low level of lighting and no background noise. Context 2 was brightly illuminated and noisy and was significantly different in construction from the home cages.

Procedure. On Day 1, the water bottles in the subjects' home cages were filled with 0.9% saline solution and remained in place for 72 h. On Day 4, the saline bottles were removed from the home cages. All of the animals were then allowed 15 min access to tap water each day for 7 days in context 1 (Days 5–11). The first conditioning trial occurred on Day 12. The animals were assigned to groups by equating mean group water consumption on Days 10 and 11 as closely as possible. They were placed in context 2 for 15 min and given access to 3% w/v sucrose solution (Group SUC-LI) or tap water (Groups WAT-LI and WAT-SAL). An injection (10 ml/kg ip) of 0.3 M LiCl or 0.9% saline solution was administered immediately on removal from context 2. The rats were then re-

placed in their home cages. Days 13 and 14 were recovery days when the animals were allowed 15 min access to tap water in context 1 each day. This 3-day cycle (Days 12–14) was repeated twice across the following 6 days (Days 15–17 and Days 18–20) so that there were three conditioning trials in total. Testing was carried out on Day 21, when each animal was given 15 min access to 0.9% saline solution in context 2.

Results and Discussion

Fluid intake in context 2 on test is shown in Fig. 1. It is apparent that both poisoned groups (WAT-LI and SUC-LI) showed suppressed consumption of saline on test compared with controls (Group WAT-SAL). Moreover, Group SUC-LI drank less than Group WAT-LI. The criterion set for significance in the analyses carried out on these data, and all subsequent analyses presented here, was $p < .05$. In addition, since the group variance increased with the group means, all data presented in this paper were subject to a square-root transformation before statistical analyses were carried out. A one-way ANOVA confirmed that the groups differed in their consumption of saline on test ($F_{2,21} = 59.9$), and Newman–Keuls post hoc pairwise comparisons showed that Group WAT-SAL consumed more than Group WAT-LI and that Group WAT-LI consumed more

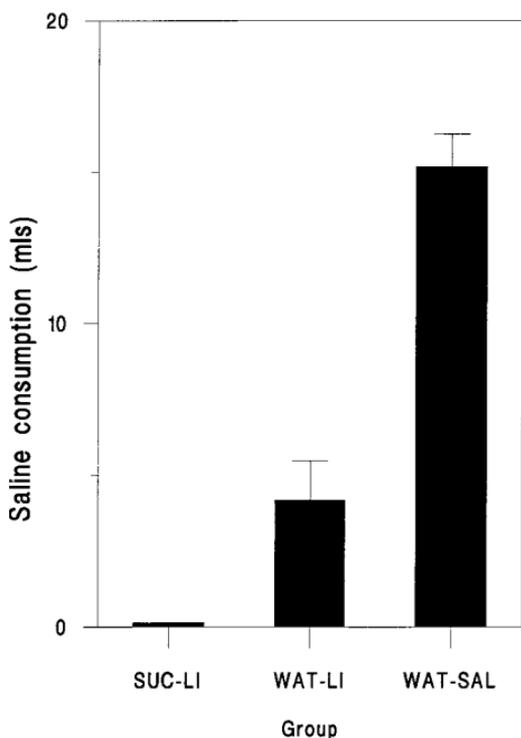


FIG. 1. Experiment 1: mean intake of saline solution in context 2 on test. Error bars indicate SEMs.

than Group SUC-LI. These results are consistent with the development of an aversion toward the context in groups WAT-LI and SUC-LI, and a stronger aversion toward the context in Group SUC-LI than in Group WAT-LI.

This experiment replicated the results of Boakes *et al.* (1992, Experiment 3) in demonstrating a stronger aversion toward a context in which a novel sucrose solution was presented than in one in which tap water was presented. The enhanced aversion was particularly pronounced since the animals in Group SUC-LI effectively failed to drink on the test trial. In addition, the pairing of this context with lithium resulted in an aversion toward the context compared to an unpoisoned control. However, this final result should be treated with caution. Group WAT-SAL were not treated with LiCl during training and thus the results may have overestimated the context aversion in Group WAT-LI; an unpaired control group in which LiCl was administered but not paired with the context would have constituted the proper control for this procedure. Nevertheless, this procedure was then used in the subsequent experiments and taken to be a valid model of the potentiation of the development of conditioned context aversions.

EXPERIMENT 2

Experiment 2 tested the prediction that when two stimuli are conditioned together and in compound with a novel flavor, the conditioning of one stimulus may increase while that of the other declines. In an attempt to obtain simultaneous overshadowing and potentiation, a third stimulus, novel vinegar solution, was chosen to be the overshadowed stimulus. One-trial overshadowing of a novel vinegar solution by a novel sucrose solution in a CTA procedure has been demonstrated (Kaye, Gambini, & Mackintosh, 1988) and there seems no reason to suppose that the use of a multitrial procedure will abolish the overshadowing effect. If the sucrose solution presented in the novel context is able to overshadow an aversion toward a previously presented vinegar solution, and at the same time, the enhancement of the aversion toward the context occurs as it did in Experiment 1, this will represent evidence that simultaneous overshadowing and potentiation can occur.

The procedure used in Experiment 2 to demonstrate simultaneous potentiation and overshadowing was similar to that of Experiment 1. On conditioning days, however, 5 min access to novel vinegar solution was given to all animals, 3 h and 15 min before exposure to context 2 and injection. It was thought that the presentation of sucrose in the context would again potentiate the aversion to the context and, in addition, reduce the magnitude of the aversion developed toward the vinegar solution. Since overshadowing is known to be a reciprocal effect (Mackintosh, 1976), it was also possible that the vinegar would overshadow the sucrose. If this were the case, the magnitude of the potentiation effect may be expected to be less than that observed in Experiment 1. However, this prediction was not tested explicitly.

Method

The design of Experiment 2 is presented in Table 1.

Subjects and apparatus. Forty-eight male, experimentally naive, Sprague-Dawley rats (250–400 g) were used. Twenty-four animals were used in each of two replications. The apparatus was as described in Experiment 1.

Procedure. On Days 1–10, all animals were treated as in Experiment 1. On the Days 11, 14, and 17 (the days before conditioning took place) all of the animals which were not due to receive the sucrose solution in context 2 during conditioning (Group WAT-LI and WAT-SAL) were given 15 min access to 3% w/v sucrose solution in context 1 in place of tap water. On each of the 3 conditioning days (Days 12, 15, and 18), each animal was given 5 min access to 3% v/v vinegar solution (distilled malt vinegar) in context 1 in the morning and then replaced in its home cage. Three hours later, they were placed in context 2 for 15 min access to 3% w/v sucrose solution (Group SUC-LI) or tap water (Groups WAT-LI and WAT-SAL). An injection (ip) of 0.3 M LiCl or 0.9% saline solution was administered immediately upon removal from context 2, and the rat was replaced in its home cage.

Two recovery days followed each of the first 2 conditioning days. On the first of these, animals were given 15 min access to tap water in context 1, while on the second day, animals received either tap water or sucrose solution in this context; animals due to receive sucrose solution during conditioning drank tap water and vice versa. Following the final conditioning day, seven 15-min exposures to context 1 were given in order to allow any aversion to context 1 to extinguish before testing for a vinegar aversion in context 1. Testing was carried out on Day 21. On this day, half the animals from each group were given 15 min access to 0.9% saline solution in context 2. The other half were given 15 min access to 3% v/v vinegar solution in context 1.

Results and Discussion

Inspection of the data for vinegar consumption (lefthand panel of Fig. 2) reveals that Group WAT-SAL drank more than Group WAT-LI. In addition, consumption of vinegar in group SUC-LI was higher than that of Group WAT-LI. A one-way ANOVA revealed a significant difference in vinegar consumption across groups ($F_{(2,21)} = 30.9$), and Tukeys post hoc comparisons indicated a

TABLE 1
The Design of Experiment 2

Group	Conditioning		Test	
	Context 1	Context 2	Context 2	Context 1
1 SUC-LI	5 min vinegar	15 min sucrose \Rightarrow LiCl	Saline	Vinegar
2 WAT-LI	5 min vinegar	15 min water \Rightarrow LiCl	Saline	Vinegar
3 WAT-SAL	5 min vinegar	15 min water \Rightarrow NaCl	Saline	Vinegar

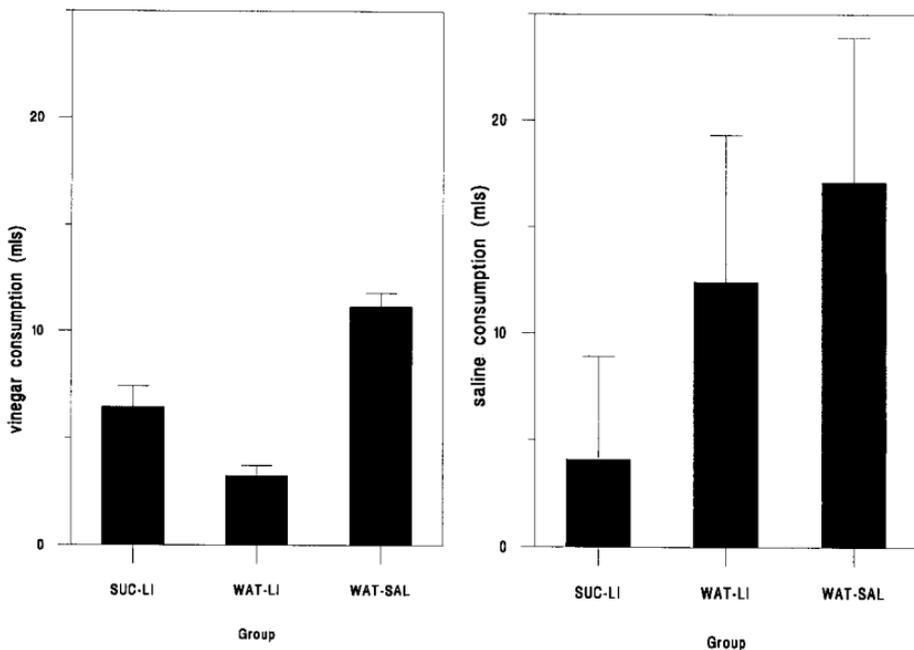


FIG. 2. Experiment 2: the lefthand panel indicates mean vinegar consumption in context 1 on test. The righthand panel indicates mean consumption of saline in context 2 on test. Error bars indicate SEMs.

difference between Groups WAT-SAL and Group WAT-LI and a difference between WAT-LI and SUC-LI. These data suggest that an aversion developed toward vinegar in Group WAT-LI due to the pairing of this flavor with lithium chloride and that the development of this aversion was attenuated due to the presence of sucrose on the conditioning trials in Group SUC-LI.

The results for saline consumption in context 2 on the test day are presented in the righthand panel of Fig. 2. These data were first tested for an effect of replication and treatment. Although the effect of replication was significant ($F_{(1,17)} = 3.2$), as was the effect of treatment ($F_{(2,17)} = 11.8$), there was no replication by treatment interaction ($F_{(2,17)} = 1.6$). Therefore, since the effect of replication was not different across groups, the data from the two replications were pooled. Consumption of saline appears to have been suppressed in both poisoned groups (Groups WAT-LI and SUC-LI) compared to the unpoisoned controls (Group WAT-SAL). However, suppression was greatest in Group SUC-LI. It would seem then, that the pattern of data from this experiment with regard to saline consumption in context 2 is similar to that shown in Experiment 1; poisoned groups showed a suppression of consumption in context 2 which was the strongest in Group SUC-LI. A one-way ANOVA was carried out on the square-root-transformed data which indicated a reliable variation between the three groups ($F_{2,21} = 8.7$). Newman-Keuls post hoc comparisons showed that there was a difference between Group SUC-LI and Group WAT-SAL, and also

a difference between Group SUC-LI and Group WAT-LI. No other effects were reliable.

In combination, the results of the vinegar and saline tests suggest that a novel sucrose solution can simultaneously potentiate and overshadow other stimuli which are present on conditioning trials and that the effect is dependent on the nature of those stimuli; contiguous contextual cues were potentiated, while a noncontiguous flavor cue (vinegar solution) was overshadowed. Poisoned animals given vinegar and sucrose solution on the conditioning days showed a greater tendency to drink vinegar when it was offered than those given vinegar and water, thus demonstrating overshadowing. In contrast, animals treated in an identical manner showed a greater aversion to the context in which the sucrose was presented as measured by their reluctance to drink familiar saline in context 2, thus demonstrating potentiation.

EXPERIMENTS 3a AND 3b

The results of Experiment 2 have been interpreted as showing that a novel sucrose solution may simultaneously give rise to overshadowing and potentiation. However, if an aversion to novel sucrose solution generalizes to familiar saline solution, then it is possible that the difference between Groups SUC-LI and WAT-LI in Experiment 2 is due, not to potentiation of a context aversion by sucrose, but to a simple sucrose aversion. Although the saline solution used here was familiar and the sucrose novel, it is still possible that sucrose–lithium pairings in group SUC-LI led to a greater saline aversion than did the water–lithium pairings in group WAT-LI. Experiment 3 examined this possibility, using essentially the same procedure as that of Experiment 1, but controlling for the occurrence of sucrose–lithium pairings.

Two experiments were carried out in order to test whether the potentiation effect apparently found in Experiment 2 could, in fact, be the result of the generalization of a sucrose aversion to the saline solution used on test. Experiment 3a was an attempt to show that sucrose–lithium pairings in one context would not lead to suppression of consumption of a familiar saline solution presented in another context. Two groups of animals were used. In one group, sucrose presentation was followed by LiCl on three occasions in context 1 and, in the second group, three water–lithium pairings were given in context 1. The rats received the same amount of context 2 exposure as did the animals in Experiments 1 and 2 (15 min, three times) before being tested for saline consumption in this context. If an aversion to novel sucrose generalizes to familiar saline solution, a suppression in consumption of saline would be expected to be demonstrated in the animals which received sucrose–lithium pairings in training.

Experiment 3b sought to confirm that potentiation of context 2 by sucrose would occur when the control and experimental groups received an equivalent number of sucrose–lithium pairings. Both groups received three sucrose–LiCl pairings and a further three water–LiCl pairings. The difference between the two

groups was that group POT (the group expected to show potentiation of an aversion toward context 2) was given sucrose in context 2 before an injection of lithium, while group CONT (the control group) received water in context 2 before lithium injection. Both groups were injected with lithium a further three times after exposure to context 1 in which they received either water (group POT) or sucrose (group CONT) before injection. Context 2 aversions in both experiments were measured by the level of consumption of familiar saline solution in that context. A summary of the design is presented in Table 2.

Method

Subjects and apparatus. Thirty-two experimentally naive male, Sprague-Dawley rats (400–600 g) were used. They were housed in groups of three in a temperature-controlled room on a 12-h light/dark cycle, lights on at 0700 h. All animals were allowed food *ad libitum* throughout the experiment. Water consumption was controlled as shown below. The apparatus was that described in Experiment 1.

Procedure. The procedure for Days 1 to 11 in Experiments 3a and 3b was the same as that used in Experiment 1, and assignment to groups was on the same basis. Thus, all animals were familiarized with 0.9% saline solution and given 7 days drinking experience in context 1. Experiments 3a and 3b differed in the procedure applied from Day 12 onward.

EXPERIMENT 3a. On Day 12, half of the animals from each group were placed in context 2 and received 15 min access to tap water before they were replaced in their home cages. The other half were placed in context 1 for 15 min access to 3% w/v sucrose solution (Group SUC) or tap water (Group WAT) and then injected with 0.3 M lithium chloride (10 ml/kg) and replaced in the home cage. A second conditioning trial followed on Day 13. On this day, the animals which had been given context 2 exposure on Day 12 were placed in context 1 and presented with 3% w/v sucrose solution (Group SUC) or tap water (Group WAT) and then injected (0.3 M LiCl, 10 ml/kg). Those animals that were conditioned in context 1 were placed in context 2 for 15 min access to tap water before being replaced in the home cage. Following the second conditioning day, there were 2

TABLE 2
The Designs of Experiments 3a and 3b

Group	Conditioning		Test
	Context 1	Context 2	Context 2
Experiment 3a			
1 SUC	Sucrose \Rightarrow LiCl	Water	Saline
2 WAT	Water \Rightarrow LiCl	Water	Saline
Experiment 3b			
1 POT	Water \Rightarrow LiCl	Sucrose \Rightarrow LiCl	Saline
2 CONT	Sucrose \Rightarrow LiCl	Water \Rightarrow LiCl	Saline

recovery days (Days 14 and 15) in which 15 min access to tap water was given in context 1. This 4-day cycle (2 conditioning days and 2 recovery days) was repeated twice more across Days 16 to 23. Thus, all animals received three exposures to context 2 and three injections of lithium chloride following either sucrose consumption (Group SUC) or tap water (Group WAT) in context 1. Testing was carried out in context 2. All animals were given familiar isotonic saline solution to drink for 15 min.

EXPERIMENT 3b. On Day 12, half of the animals in each group were placed in context 2 for 15 min access to 3% w/v sucrose solution (Group POT) or tap water (Group CONT). An injection of 0.3 M LiCl (10 ml/kg, ip) was administered immediately upon removal from context 2, and the rats were replaced in their home cages. The other half of the animals from each group was given 15 min access to water (Group POT) or sucrose solution (Group CONT) in context 1 followed by an injection of 0.3 M LiCl (10 ml/kg, ip). Days 13 and 14 were recovery days on each of which the animals were allowed 15 min access to tap water in context 1. On Day 15, the procedure for Day 12 was repeated. However, the animals that had been exposed to context 1 on Day 1 were exposed to context 2 on Day 15 and vice versa. Again, animals in group POT received sucrose if they were in context 2 and water if they were in context 1, and animals in group CONT received the opposite treatment. Another 2 days recovery followed this conditioning day.

Thus, in Experiment 3b, both groups received one sucrose–LiCl pairing and one water–LiCl pairing, and both were given one context 1–LiCl pairing and one context 2–LiCl pairing. This 6-day cycle (2 conditioning days and 4 rest days) was repeated three times giving the animals a total of 6 conditioning days. It was necessary to give supplementary water in the home cage on the recovery days during the final cycle in order to keep the animals above 95% of their free feeding weight. Thus, each animal was allowed 1 h access to tap water in the home cage on each of these 4 days in addition to the 15 min access they received in context 1. On completion of the final 6-day cycle, all animals were tested for their aversion to context 2 in terms of their willingness to drink familiar saline in that context.

Results and Discussion

The test data from Experiment 3a are presented in the lefthand panel of Fig. 3. Both Group SUC and Group WAT readily consumed saline solution in context 2. A one-way ANOVA was carried out on the square-root-transformed data. While Group SUC appears to have consumed less than Group WAT, the difference was not reliable ($F_{(1,14)} = 2.6$). Thus, it would appear that sucrose–lithium pairings do not lead to an aversion to familiar saline, and therefore the effect on saline consumption observed in Experiment 2 is unlikely to have been due to generalization from sucrose to saline rather than potentiation of a context aversion by sucrose.

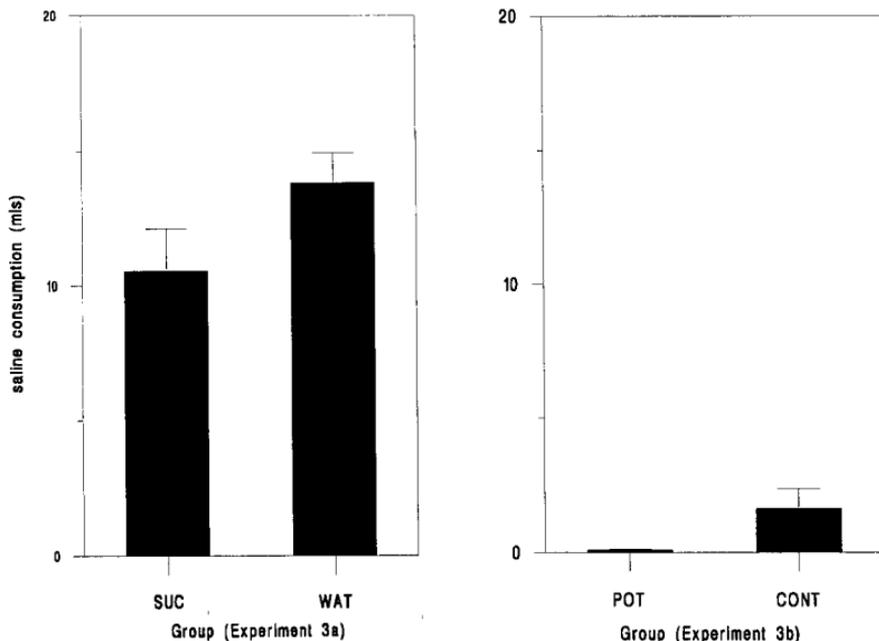


Fig. 3. Experiment 3: the lefthand panel shows consumption of saline in context 2 on test for Experiment 3a. The righthand panel shows consumption of saline in context 2 on test for Experiment 3b. Error bars indicate SEMs.

The test day data from Experiment 3b are presented in the righthand panel of Fig. 3. It is clear that all animals were reluctant to drink saline in context 2 but that animals in Group POT were less willing to drink than those in Group CONT (mean consumption in group POT = 0.1 ml, mean consumption in group CONT = 1.6 ml). A one-way ANOVA on the square-root-transformed data showed a difference in saline consumption between the groups ($F_{(1,14)} = 6.81$), and this difference is consistent with a potentiated context aversion.

The results of Experiments 3a and 3b indicate that the difference between Groups SUC-LI and WAT-LI in Experiment 2 is unlikely to have been due to generalization rather than potentiation. Experiment 3a provided no evidence that sucrose-LiCl pairings lead to an aversion toward familiar saline solution presented in context 2, and, consistent with this result, even when they have had equal numbers of sucrose-lithium pairings, rats which have drunk sucrose in a context before poisoning subsequently consume less saline in that context than rats that drank water in that context before poisoning.

GENERAL DISCUSSION

The data presented here provide evidence that the same flavor cue presented in a novel context before poisoning can both enhance an aversion toward that context and, at the same time, reduce an aversion toward a previously presented flavor cue. From Experiment 1, there was some suggestion that an aversion can

be conditioned toward a novel context through the administration of lithium chloride, and potentiation of a context aversion was shown as a result of the presentation of a novel sucrose solution in that context before injection. Simultaneous potentiation and overshadowing was demonstrated in Experiment 2; the novel sucrose solution both overshadowed a novel vinegar solution and potentiated an aversion toward a novel context. Finally, the potentiated context aversion was shown not to be the result of generalization between the aversive sucrose solution and saline, the flavor used to test the magnitude of the aversion toward the context.

In one respect, the results of Experiment 2 do not seem to be consistent with those of Experiment 1. In Experiment 1, not only was a potentiated aversion toward the context demonstrated in Group SUC-LI, but an aversion was also demonstrated toward context 2 in group WAT-LI. However, in Experiment 2, the difference in saline consumption in context 2 between groups WAT-LI and WAT-SAL was not found to be significant. Procedurally, the major difference between Experiments 1 and 2 was the presentation of vinegar solution before exposure to context 2 in Experiment 2. It is possible that the vinegar overshadowed context 2 in Group WAT-LI. Since the novel vinegar flavor was not presented contiguously with context 2, it would not be expected to potentiate an aversion to this context (Westbrook *et al.*, 1983) and therefore may overshadow this aversion.

Alternatively, context 1 may have overshadowed the aversion toward context 2 in this group. Although all animals received 7 days preexposure to context 1 in Experiment 2, and context 1 would not therefore be expected to condition well due to latent inhibition (Lubow, 1973), it is possible that the presentation of vinegar solution in this context on the conditioning days represented a context change. Thus, novel vinegar became the context for the conditioning of context 1. Since latent inhibition is known to decline with transfer across contexts, this would allow context 1 to become associated with toxicosis and therefore overshadow context 2. In addition, conditioning of context 1 might be further enhanced through potentiation as a result of the presence of the novel vinegar solution during conditioning.

It was pointed out in the introduction to Experiment 2 that the presentation of vinegar solution prior to the sucrose-context 2 compound during training may have overshadowed an aversion to the sucrose solution. There was no control in Experiment 2 for the effect of the presentation of vinegar solution of the aversion which developed toward context 2. Were the presentation of vinegar to have overshadowed an aversion to the sucrose solution then a concomitant reduction in the aversion demonstrated toward context 2 would have been consistent with a within compound analysis of potentiation. According to Durlach and Rescorla (1980), the strength of the aversion toward the context is dependent on the strength of the aversion toward the flavor presented within that context.

In contrast, the hypothesis presented by Garcia and his colleagues suggests that the potentiation of a nonfood cue by the presence of a food cue is independent

of the associative strength of the food cue (Palmerino, Rusiniak, & Garcia, 1980). Thus, altering the degree to which the food cue is associated with illness through overshadowing should leave the aversion toward the context intact. The evidence presented here is not conclusive in this respect; the presentation of a vinegar solution prior to the sucrose–context compound did not abolish the potentiation effect. However, the presence of the vinegar solution may have reduced the magnitude of the potentiation effect but the relevant control group (in which a sucrose–context compound was presented in the absence of the vinegar solution) was not included in Experiment 2.

Overall, it has proven possible to demonstrate simultaneous overshadowing of a flavor cue, and potentiation of contextual cues by the same flavor cue. This is consistent with the theories of overshadowing and potentiation presented above. The principles of overshadowing have recently been applied in the alleviation of CTA in humans, induced by emetic cancer chemotherapy. Broberg and Bernstein (1987) gave cancer patients a novel flavor prior to infusion of the toxic drugs in order to overshadow an aversion to a previously eaten meal. They found that target food items eaten before drug infusion were less likely to be rejected on test if a novel flavor had been consumed by the patient after consumption of the target and before receiving treatment. This would imply that the novel flavor presented before treatment overshadowed an aversion toward the previously consumed food.

The results of the present experiment raise the probability that, as well as overshadowing the aversion to the previously eaten food, the presentation of a novel flavor before treatment also potentiated an aversion to the context in which the drug was given, the chemotherapy clinic. As well as conditioned taste aversions, cancer patients receiving emetic chemotherapy treatment have also been shown to develop aversions toward the clinic in which the treatment is given (Redd, Burish, & Andrykowski, 1985). The aversiveness of the context was not tested in the experiment carried out by Broberg and Bernstein; thus, further work would be necessary to establish that simultaneous overshadowing and potentiation may, in fact, occur in this human population.

REFERENCES

- Best, M. R., Brown, E. R., & Sowell, M. K. (1984). Taste-mediated potentiation of noningestive stimuli in rats. *Learning and Motivation*, **15**, 244–258.
- Best, M. R., & Meachum, C. L. (1986). The effects of stimulus preexposure on taste-mediated environmental conditioning: Potentiation and overshadowing. *Animal Learning and Behaviour*, **14**, 1–5.
- Boakes, R. A., Westbrook, R. F., & Barnes, B. W. (1992). Potentiation by a taste of toxicosis-based context conditioning: Effects of varying the test fluid. *Quarterly Journal of Experimental Psychology*, **45B**, 303–325.
- Broberg, D. J., & Bernstein, I. L. (1987). Candy as a scapegoat in the prevention of food aversions in children receiving chemotherapy. *Cancer*, **60**, 2344–2347.
- Davis, S. F., Best, M. R., & Grover, C. A. (1988). Toxicosis-mediated potentiation in a taste/taste compound: Evidence for within-compound associations. *Learning and Motivation*, **19**, 183–205.
- Durlach, P. J., & Rescorla, R. A., (1980). Potentiation rather than overshadowing in flavour aversion

- learning: An analysis in terms of within-compound associations. *Journal of Experimental Psychology: Animal Behavior Processes*, **6**, 175–187.
- Galef, B. G., & Osborne, B. (1978). Novel taste facilitation of the association of visual cues with toxicosis in rats. *Journal of Comparative and Physiological Psychology*, **92**, 907–916.
- Garcia, J., Brett, L. P., & Rusiniak, K. W. (1989). Limits of Darwinian conditioning. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 181–203). Hillsdale, NJ: Erlbaum.
- Kaye, H., Gambini, B., & Mackintosh, N. J. (1988). A dissociation between one-trial overshadowing and the effect of a distracter on habituation. *Quarterly Journal of Experimental Psychology*, **40B**, 31–47.
- Lolordo, V. M., & Droungas, A. (1989). Selective associations and adaptive specializations: Taste aversions and phobias. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 145–179). Hillsdale, NJ: Erlbaum.
- Lubow, R. E. (1973). Latent inhibition. *Psychological Bulletin*, **79**, 398–407.
- Mackintosh, N. J. (1976). Overshadowing and stimulus intensity. *Animal Learning and Behavior*, **4**, 186–192.
- Palmerino, C. C., Rusiniak, K. W., & Garcia, J. (1980). Flavor-illness aversions: The peculiar roles of odor and taste in memory for poison. *Science*, **208**, 753–755.
- Pavlov, I. P. (1927). *Conditioned reflexes*. Oxford: Oxford Univ. Press.
- Pearce, J. M. (1987). A model for stimulus generalization in Pavlovian conditioning. *Psychological Review*, **94**, 61–73.
- Redd, W. H., Burish, T. G., & Andrykowski, M. A. (1985). Aversive conditioning in cancer chemotherapy. In T. G. Burish, S. M. Levy, & B. E. Meyerowitz (Eds.), *Nutrition, taste aversion, and cancer: A biobehavioral perspective* (pp. 117–132). Hillsdale, NJ: Erlbaum.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current theory and research* (pp. 64–99). New York: Appleton-Century-Crofts.
- Revusky, S. (1971). The role of interference in association over a delay. In W. K. Honig & P. H. R. James (Eds.), *Animal memory*. New York: Academic Press.
- Rusiniak, K. W., Hankins, W. G., Garcia, J., & Brett, L. P. (1979). Flavor-illness aversions: Potentiation of odor by taste in rats. *Behavioral and Neural Biology*, **25**, 1–17.
- Wagner, A. R. (1981). SOP: A model of automatic memory processing in animal behavior. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 5–48). Hillsdale, NJ: Erlbaum.
- Westbrook, R. F., & Brookes, N. (1988). Potentiation and blocking of conditioned flavour and context aversions. *Quarterly Journal of Experimental Psychology*, **40B**, 3–30.
- Westbrook, R. F., Homewood, J., Horn, K., & Clarke, J. C. (1983). Flavour-odour compound conditioning: Odour-potentiation and flavour attenuation. *Quarterly Journal of Experimental Psychology*, **35**, 13–33.

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