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Overshadowing not potentiation of illness-based contextual conditioning by a novel taste

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In four experiments using rat subjects, we investigated the effects of presenting a novel flavor cue at the time of pairing an environmental context with illness. In each experiment, the subjects were allowed to spend time in a distinctive cage before receiving an injection of LiCl. For some, plain water was made available on these conditioning trials; for others, a novel taste (HCl) was presented. We measured the strength of the context aversion by assessing the ability of the contextual cues to block the acquisition of an aversion to sucrose in a further phase of training. We found that initial training with HCl present made the context less effective as a blocking cue and concluded that the HCl had overshadowed learning about the context. We suggest that this blocking procedure provides a more accurate assessment of contextual aversion than does the consumption test that has more usually been used and that taste–context overshadowing may be a more robust phenomenon than has thus far been thought.

Rats that are subjected to a nausea-inducing treatment during or immediately following exposure to a novel context will develop an aversion to that context (see, e.g., P. J. Best, M. R. Best, & Henggeler, 1977; Symonds & Hall, 1997). This phenomenon has attracted attention because of the way in which the strength of the aversion can be modulated by the presence of another cue during conditioning. In particular, it has often been reported that rats allowed to consume a novel, flavored substance during their time in the context will develop a stronger context aversion than will control subjects given plain water or nothing at all (e.g., M. R. Best, Brown, & Sowell, 1984; Boakes, Westbrook, & Barnes, 1992; Mitchell & Heyes, 1996). This *potentiation* effect is not what would be expected on the basis of standard accounts of associative learning (e.g., Rescorla & Wagner, 1972), which predict that the novel flavor cue would overshadow learning about the context; it has thus become the focus of extensive theoretical debate (see, e.g., LoLordo & Droungas, 1989). We will not discuss the various theoretical proposals here, since the purpose of the work presented in this article is to attempt to show that the evidence taken to demonstrate the potentiation effect (at least, that seen in the context aversion learning paradigm) is weak and that the usual effect of adding an extra cue during conditioning is, as in other conditioning paradigms, to produce overshadowing.

Procedures for assessing the aversive properties of a context associated with toxicosis have taken four main forms: place-preference tests, tests of instrumental performance in the context, consumption tests, and tests that make use of the blocking procedure. The last of these is used in the experiments to be described later in this article; evidence from the first three procedures will be reviewed next.

In the place-preference procedure, the rat is allowed to choose, in a version of the shuttle box, between two distinctive compartments, one of which has been associated with toxicosis and one not. It is well established that the rat will tend to avoid the poison-associated compartment on such a test (e.g., Berk & Miller, 1978; P. J. Best et al., 1977), but there is little evidence to show that the presence of a novel flavor during conditioning will enhance this effect. Experiments by P. J. Best, M. R. Best, and Mickley (1973), Klein and Elder (1987), Klein, Freda, and Mikulka (1985), and Miller, McCoy, Kelly, and Bardo (1986) have all found that subjects given access to a saccharin solution during conditioning show, at most, only a marginally greater aversion than subjects given plain water.[1] Importantly, for the interpretation of these results, P. J. Best et al. (1973) also included a condition in which the rats received no access to fluid during conditioning. These animals showed the strongest place aversion of all. It appears, therefore, that allowing the animals to consume a fluid during conditioning produces not potentiation, but overshadowing, and that this is true both when the fluid is water and when it is a novel, flavored saccharin solution.

An example of the use of an instrumental test procedure is provided by an experiment by Morrison and Collyer (1974). They trained thirsty rats to leverpress for a reward of either water or a saccharin solution. An injection of lithium chloride (LiCl) was given after the training sessions. This resulted in a decline in responding on a subsequent test session that was much more substantial in the rats that had received saccharin as the reinforcer

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than in those that had received water. This result is consistent with the possibility that the decline in responding reflects the acquisition of aversive properties by the training context and that these properties are acquired more readily when a novel flavor is presented in that context. (See also Batson, Best, Phillips, Patel, & Gilleland, 1986; M. R. Best, Meachum, Davis, & Nash, 1987.) But the results of a study by Meachum (1988) raise questions about this interpretation. Meachum's (1988) experiment was similar to that conducted by Morrison and Collyer, except that it involved a within-subject comparison, the rats having been trained with two levers, one yielding saccharin, the other water. Postsession lithium (Li) injections produced a substantial decline in responding only on the lever that yielded saccharin. An aversion to the training context would be expected to affect both levers equally. Accordingly, this result is best interpreted as an instance of the effect of reinforcer devaluation on instrumental performance (see, e.g., Dickinson, 1994), with the novel saccharin being more susceptible to devaluation than the familiar water.

It may be that the procedures used in these experiments, in addition to producing reinforcer devaluation, are also capable of establishing an aversion to the context. But their results provide no evidence that such learning is potentiated by the novel flavor; indeed, there is some evidence, from experiments using the instrumental test procedure, that the presence of a novel flavor might have quite the opposite effect. Meachum (1990) trained rats to leverpress for familiar food pellets prior to a phase of Pavlovian conditioning in which exposure to the context was followed by an injection of LiCl. Some subjects were given access to a novel sucrose solution during these context conditioning sessions; control subjects experienced the context alone. A final test of instrumental performance showed that those that had been given sucrose responded much more readily than did the control subjects. Meachum (1990) concluded that the control subjects had acquired a context aversion that tended to suppress leverpressing but that the presence of sucrose during context conditioning had acted to overshadow the formation of this aversion.

The most substantial body of evidence supporting the existence of potentiation in context aversion learning comes from experiments that make use of a consumption test. It has been shown many times that rats given access to a novel flavor, such as a saccharin or a sucrose solution (as opposed to unflavored water) during context conditioning display a marked unwillingness to consume a familiar and palatable substance (usually a saline solution) when it is presented in the conditioning context (M. R. Best, Batson, & Bowman, 1990; M. R. Best, Batson, Meachum, Brown, & Ringer, 1985, Experiment 4; M. R. Best et al., 1984, Experiment 2; M. R. Best & Meachum, 1986; Boakes et al., 1992, Experiment 3; Mitchell & Heyes, 1996). Similar results have sometimes been obtained when the control subjects are given no fluid during conditioning (M. R. Best et al., 1985, Experiment 1) and when the test flavor is itself novel (Boakes et al., 1992, Experiments 1 and 2, in which a novel dilute acid solution was used). Furthermore, reduced consumption of the test fluid in experimental subjects is seen only when the test is given in the original training context, not when it is given elsewhere (M. R. Best et al., 1985, Experiment 2; Mitchell & Heyes, 1996, Experiment 3). If we can assume that an unwillingness to drink saline or acid in the test context is an index of the acquisition of aversive strength by that context, the results just described support the notion that such acquisition is potentiated by the presence of a novel flavor during conditioning.

A problem for this interpretation, however, comes from the observation that, in such experiments, the potentiation effect is not reliably found when unflavored water is used in the test. In one of the earliest studies of context aversion conditioning, Taukulis and St. George (1982) found that rats given access to saline on the training trials showed *less* of an aversion when given a water consumption test than did rats given water in training, a result that they attributed to overshadowing of contextual cues by the saline. And although Westbrook, Harvey, and Swinbourne (1988, Experiment 2) were able to demonstrate a potentiation effect with a water consumption test, a subsequent set of experiments using very similar procedures failed to replicate this result and, indeed, generated the reverse, with animals given sucrose during conditioning consuming more on the test than those given water during conditioning (Boakes et al., 1992, Experiments 1 and 2). Similarly, M. R. Best et al. (1984) were unable to replicate the results of their Experiment 1, which yielded potentiation with a water consumption test, and in their Experiment 2, they found the reverse result. It seems that when the test phase of the experiment involves a water consumption test, the outcome is as likely to be overshadowing as potentiation.

On the basis of this review, we conclude, therefore, that the potentiation effect in context aversion conditioning is a somewhat elusive phenomenon. An adequate account must be able to explain why the potentiation effect should be found only when the test procedure involves a consumption test and, even then, only when the substance presented on test has a distinctive flavor. A recent unpublished study conducted in our laboratory has produced results that are relevant to this issue. We measured contextual conditioning, using a consumption test along the lines of those just described. In the initial phase of training, all the subjects received pairings of a target context with LiCl; for half of the subjects, a solution of dilute acid (HCl) was made available on these trials, and the other half received plain water. In a subsequent test phase, consumption of a novel flavor in the target context was measured. The outcome of this test was found to depend critically on the identity of the test flavor. When sucrose was the test flavor, those subjects given the acid during conditioning consumed somewhat more than those that had received plain water, a result that might be taken to imply that the presence of the acid during conditioning

acts to overshadow, rather than to potentiate, the context aversion. But the results from a test in which quinine was the target flavor make this conclusion seem insecure. In this case, the subjects in the acid group drank less than those in the water group and, thus, appear to have formed a stronger aversion to the context; that is, an apparent potentiation effect was observed.

One possible explanation for these conflicting results is that the outcome of a consumption test will depend, at least in part, on generalization to the test flavor of any aversion formed to the fluid presented at the time of the context conditioning (see Symonds & Hall, 1997; Symonds et al., 1998). In our experiment, the group given acid would be likely to form an aversion to HCl, and the group given water might form an aversion to water. Thus, the apparent overshadowing effect that emerged during testing with sucrose could be explained, if we assume that the aversion to water generalized more readily to sucrose on the test than did the aversion to HCl. This in itself would be enough to explain why the subjects in the water group drank less of the sucrose than did those in the acid group. Conversely, the potentiation effect that emerged during the test with quinine might be the product of a stronger generalized aversion from HCl to quinine than from water to quinine; this would result in less drinking of quinine by subjects in the acid group than by those in the water group. Such a pattern of generalization is quite plausible: Water and sucrose have in common the fact that they are both palatable, whereas quinine and HCl are less so.

Similar considerations can supply an explanation for the supposed potentiation effects reported in those published experiments that made use of a consumption test. Whether or not the conditioning procedures used in these experiments produce a context aversion, they are undoubtedly effective in generating an aversion to the saccharin (or the sucrose) presented during training. If this aversion generalizes to the saline solution presented on test, a low level of consumption can be expected on this ground alone. Furthermore, this interpretation supplies an explanation for the failure of these experiments to reveal a reliable potentiation effect when water is used as the test fluid. In this case, there is likely to be less generalization in experimental subjects given the novel flavor during conditioning, and, to the extent that they have formed an aversion to water during conditioning, it is the control subjects that will tend to show a suppression of consumption on test.

This account can accommodate other features of previous experiments that appear to demonstrate a potentiation effect. The fact that suppression of consumption of the test fluid occurs only when the test is given in the training context (Mitchell & Heyes, 1996) is to be expected, given that flavor aversions can show context specificity (see, e.g., Bonardi, Honey, & Hall, 1990): A generalized aversion will transfer across contexts only to the extent that the original aversion is able to do so. The context specificity of the generalized aversion can also explain the results reported by M. R. Best et al. (1985, Experiment 1), which showed that rats given saccharin during context conditioning showed a greater aversion on a water consumption test than did control subjects given no fluid in the context, but saccharin–unconditioned stimulus (US) pairings in the home cage. Generalization from saccharin to unflavored water may be slight, but it will certainly be more likely to occur in subjects for whom the relevant contextual cues that will aid in the retrieval of the original association are available. Also consistent with this account is the finding that the degree of suppression of consumption on the test is attenuated by procedures that are likely to reduce the strength of the flavor–US association formed during context conditioning. In particular, M. R. Best et al. (1985, Experiment 3) found that extinction of the saccharin aversion formed in experimental subjects during context conditioning resulted in these animals drinking the test fluid (saline) readily in the subsequent consumption test. A similar result was found in their Experiment 2, in which the experimental subjects received preexposure to saccharin in the context prior to context conditioning trials on which saccharin was available. This latent inhibition procedure would be expected to retard the development of a saccharin–US association and, thus, limit generalization to the test fluid. That M. R. Best and Meachum (1986) found little effect of giving preexposure to saccharin in the home cage follows from the fact that the latent inhibition effect shows context specificity.

Taken together, the review of the literature presented above, along with our own experimental findings, prompts the conclusion that the consumption test might be an unreliable measure of the aversive strength of a context and that the potentiation (and overshadowing) effect it reveals might be artifactual. In order to assess with confidence, therefore, the effect produced by presenting a novel flavor at the time of conditioning to environmental stimuli, a different test procedure is needed. This is the purpose of the experiments to be reported in the present study.

EXPERIMENT 1

In this experiment, we made use of the blocking procedure, previously employed by Symonds and Hall (1997) to assess the strength of a conditioned contextual aversion. In the study by Symonds and Hall, rats received injections of LiCl after spending time in a distinctive context. The strength of any aversion to the context was then assessed in a subsequent stage of training, in which the rats received a novel flavor in the home cage before being placed in the target context and receiving an injection of LiCl. It was found that the acquisition of an aversion to the flavor was blocked by this procedure, thus indicating that the subjects had formed an association between the context and the illness in the first stage of training. In that experiment, the subjects were given only unflavored water during the context conditioning trials; in the present experiment, we compared animals given this treatment with

a group for whom a flavored solution was made available during this stage.

A critical feature of this procedure is that good learning about the context–illness association is evidenced by a *failure* of conditioning to the flavor that is presented on the blocking trials. This allows the possibility of finding unambiguous evidence of potentiation: If the presence of a novel flavor during the conditioning trials potentiates learning about the context, this would be evidenced by relatively poor conditioning to the test flavor; direct generalization from the aversion formed to the potentiating flavor could not, therefore, produce such a result. By the same token, however, this experimental design would be unable to provide good evidence for an overshadowing effect, should one occur. If the presence of the flavor during context conditioning were to overshadow learning about the contextual cues, there would be an attenuation of blocking of the aversion to the test flavor presented in the subsequent blocking phase. But direct generalization between the overshadowing and test flavor could also generate such a result.

In order to avoid this problem, we modified the basic experimental design employed by Symonds and Hall (1997). The design of Experiment 1 is shown in Table 1. There were two groups of subjects. One group (Group H) received a series of conditioning trials with a target context (A) that was paired with LiCl. On these trials, the subjects received access to a novel solution of HCl. In addition, the subjects received conditioning trials with a nontarget context (B) that was also paired with LiCl. On these trials, the subjects received access to plain water. For subjects in Group W, this arrangement was reversed, so that water was presented on the conditioning trials with the target context (A), but HCl was made available on the conditioning trials with the nontarget context (B). All the subjects then received a further phase of training, in which they received conditioning to a taste–context A compound; that is, they consumed a novel sucrose solution in the home cage before being placed in context A and injected with LiCl. The subjects were then tested in their home cages for their aversion to the sucrose flavor.

With this procedure, all the subjects receive the same number of conditioning trials with both the target (A) context and the nontarget (B) context, with water, and with HCl. The groups differ only in terms of whether HCl (Group H) or water (Group W) is presented in the target context. If the presence of HCl potentiates an aversion to the context, Group H should show more blocking of an aversion to the sucrose than should Group W. But if the HCl overshadows learning about the context, Group H should show a greater aversion to the sucrose than Group W, a result that could not be explained in terms of direct generalization from the aversion formed to HCl (since Group W also receives conditioning with HCl). It may be noted that the only previous study of potentiation in context aversion conditioning that made use of the blocking procedure (M. R. Best et al., 1984, Experiment 3) gave conditioning with the potentiating flavor only to the experimental subjects and, thus, failed to control for the effects of direct generalization.

Table 1
Design: Experiments 1 and 2

Group	Context Conditioning	Compound Conditioning	Test
Group H	A(H) → Li & B(W) → Li	Suc → A → Li	Suc
Group W	A(W) → Li & B(H) → Li	Suc → A → Li	Suc

Note—A and B designate distinctive contexts, different from each other and from the home cage; Suc refers to a sucrose solution presented in the home cage; Li indicates an injection of lithium chloride; W refers to water, H to HCl.

Method

The subjects were experimentally naive male hooded (Lister) rats. There were 16 subjects in each of two replications. In the first, the subjects had a mean free-feeding weight of 256 g (range, 230–270 g); in the second replication, the mean free-feeding weight was 346 g (range, 330–360 g). They were housed in home cages made of opaque white plastic, 35 × 22 × 19 cm. These had a wire mesh roof that held food and (when available) a water bottle; a layer of wood shavings covered the floor. The home cages were housed in a large colony room that was brightly lit from 0800 to 2000 h each day.

Two sets of cages, both distinct from the home cage, served as the experimental contexts. The first set of cages was located in a separate small room dimly lit by a single 60-W red lamp and containing a speaker supplying a constant background white noise, with an intensity of 75 db close to the cages. The wall and floors of these cages were made of transparent plastic and measured 33 × 20 × 19 cm. The floor was covered with commercially obtained cat litter. Those in the second set were larger, measuring 42 × 35 × 16 cm, and were located in a colony room in a separate part of the laboratory. The floor and walls of these cages were made of translucent white plastic, and the wire mesh roof included a section through which a drinking spout could be inserted. These two sets of cages were the same as those used in the study by Symonds and Hall (1997) and are, therefore, known to be discriminably different from each other. Inverted 50-ml centrifuge tubes equipped with stainless steel ball-bearing-tipped spouts were used to present measured quantities of unflavored tap water, a solution of 0.01 M HCl or of 0.33 M sucrose. Fluid consumption was recorded, by weighing, to the nearest 0.5 ml. The US for the conditioning trials was an intraperitoneal injection of 0.15 M LiCl administered at 10 ml per kg of body weight.

The initial stages of water deprivation were carried out with subjects housed in pairs in their home cages. The standard water bottles were first removed overnight. On the following 2 days, access to water was restricted to two daily sessions of 30 min initiated at 1100 and 1700 h. The subjects were then housed individually, and this cycle was repeated. On the last day of this cycle, water intakes were measured, and the subjects were assigned to one of two equal-sized groups, Group W or Group H, matched in their levels of water consumption. The next 12 days constituted the conditioning phase. On Day 1, all the subjects were put into the target context A for 30 min at 1200 h. Half of the subjects (Group H) received access to 10 ml of a novel solution of HCl; the remainder (Group W) received 10 ml of water. They were then removed from the context and given an injection of LiCl before being returned to the home cage. All the subjects were allowed 30 min of free access to water from the standard bottles in their home cages at 1700 h. The next day (Day 2) constituted a recovery day, in which the rats remained in their home cages and received two 30-min sessions of free access to water at 1200 and 1700 h. On Day 3, the subjects were put into the nontarget context (B) for 30 min at 1200 h. Group H received access to

10 ml of water, and Group W received 10 ml of the HCl solution. Again, the rats were injected upon removal from the context before being returned to the home cage. The subjects received free access to water for 30 min at 1700 h in the home cage, followed on Day 4 by a further recovery day. This 4-day cycle was then repeated an additional two times. Whether the small or the large cages served as the A or B contexts was counterbalanced.

The next phase of training consisted of two blocking trials. On the first of these trials, all the subjects received a 10-ml presentation of sucrose for 15 min in the home cage at 1200 h. They were then transferred to the target context (A) for 30 min (no fluids being available), were removed, and were immediately injected with LiCl before being returned to the home cage. The next day was a recovery day. This 2-day cycle was then repeated. Finally, the subjects received two nonreinforced tests, in which free access to sucrose was given in the home cage for 15 min at 1200 h. In the first replication, compound conditioning was begun immediately after the final recovery session of the conditioning phase, and it was found that sucrose consumption in both groups was somewhat suppressed, even on the first trial, perhaps because the subjects had acquired a general aversion to drinking fluid at this time of day. In the second replication, a 6-day interval was interposed between the conditioning and the blocking phases, during which the subjects received access to water twice daily (at 1200 and 1700 h) in their home cages. These subjects showed a consistently higher level of sucrose consumption on the blocking and test trials. In other respects, the results generated by the two replications were equivalent, and they are pooled in the scores presented below.

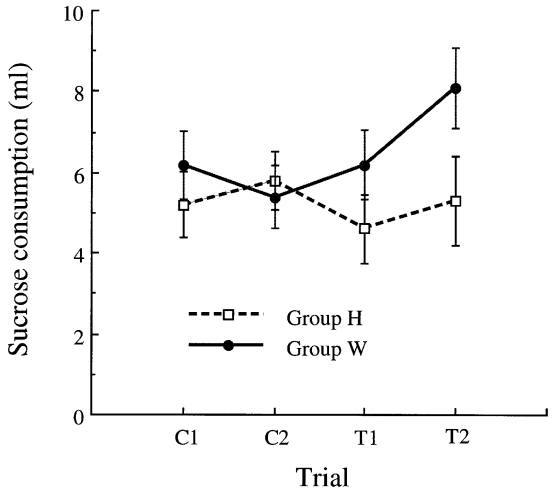

Figure 1. Group mean scores for sucrose consumption in the home cage in Experiment 1. On the conditioning trials (C1 and C2), consumption of sucrose was followed by exposure to a distinctive context and an injection of LiCl. T1 and T2 were nonreinforced test trials. All the subjects had previously received training in which exposure to the context was followed by an injection of LiCl. For Group W, water was presented on these context conditioning trials; for Group H, an HCl solution was presented.

Results and Discussion

At the start of context conditioning, the subjects drank most of the fluid offered, although consumption of HCl was consistently somewhat less than consumption of water. The mean for all the subjects was 8.8 ml on the first session with water and 7.1 ml on the first session with HCl. Consumption declined over the course of conditioning, and the corresponding means for the final sessions were 1.9 ml for water and 0.6 ml for HCl. An analysis of variance (ANOVA) conducted on these data, with trial (first or last) and fluid (water or HCl) as the variables, revealed significant effects of flavor [$F(1,30) = 32.40$] and of trial [$F(1,30) = 713.72$], but no interaction between these variables ($F < 1$).

Group mean scores for sucrose consumption in the home cage on the two compound conditioning trials and on the test trials are shown in Figure 1. Neither group drank the full amount offered on the conditioning trials, but there was no difference between the groups at this stage. On the free-access test trials, however, consumption in Group H remained suppressed, whereas that in Group W began to increase. An ANOVA conducted on these data, with group and trial as the variables, revealed there to be a significant effect of trial [$F(1,30) = 14.13$] and a significant effect of group [$F(1,30) = 4.37$]. The interaction between these two variables was not significant [$F(1,30) = 2.56$]. The greater aversion shown by Group H indicates that blocking of the acquisition of an aversion to sucrose was more profound in Group W than in Group H and suggests that the context aversion was less well formed in the latter group.

The results of this experiment are clear-cut. At least with the particular contexts and stimuli that we have chosen, the subjects given the opportunity to consume a novel flavored solution (in this case, a sour taste) during pairings between a context and LiCl showed less evidence of an aversion to the context than did those that received only plain water on the conditioning trials. The presence of the novel flavor appears to overshadow, rather than potentiate, the acquisition of aversive properties by the context.

These results contrast with those of a previous study of potentiation that made use of the blocking procedure. In an experiment of similar design to ours, M. R. Best et al. (1984, Experiment 3) found that blocking of the acquisition of an aversion to a new flavor (coffee, in this case) was greater in rats allowed to consume a saccharin solution in the reinforced context than in control subjects for whom only water was available during context conditioning. We are unable to account for this discrepancy. A curious feature of the Best et al. (1984) study, however, is that the rats in this control condition showed no learning about the context at all (as compared with control subjects given experience of the US outside the context). In previous work (see Symonds & Hall, 1997), we have used a procedure broadly similar to that of Best et al. (1984), in which the experimental animals received access to only plain water during the conditioning phase, and in this case, a perfectly robust contextual conditioning effect was revealed by a subsequent blocking test.

Given this discrepancy and the fact that the outcome of the present experiment contradicts the conclusion that has usually been drawn on the basis of experiments using the consumption test procedure (although, as we have already argued, there is reason to doubt the reliability of

this procedure as an assay of contextual conditioning), we thought it worthwhile to conduct a further experiment, to demonstrate the reliability of our results and to extend their generality.

EXPERIMENT 2

In Experiment 2, we wanted to confirm the reliability of the overshadowing effect that we have just described, using a slightly modified experimental procedure. In particular, there is reason to suppose that the procedure used in Experiment 1 might have underestimated the size of the overshadowing effect. For the subjects in Group H, the amount of HCl drunk in the context declined over the course of the four conditioning trials (and was almost zero by the final trial). As a consequence, the extent to which these subjects were exposed to the putative overshadowing stimulus was dramatically reduced over the course of context conditioning, and on the final trial, they received a context–US pairing in the absence of any experience of HCl—a circumstance that may have been less than optimal for generating an overshadowing effect.

Previous work (admittedly, with a different training preparation) has shown that it is possible to obtain an overshadowing effect when subjects receive only a single conditioning trial with a compound stimulus (e.g., James & Wagner, 1980). In Experiment 2, therefore, we repeated the procedure employed in Experiment 1, except that the subjects were given only one conditioning trial with the target context. For half of the subjects, HCl (Group H) was available on this trial, and for the other half (Group W), water was presented. In addition, the subjects also received a conditioning trial with the nontarget context, in which, as in Experiment 1, they were allowed to consume the fluid that had not been presented in the target context. The advantage of this one-trial procedure is that, for subjects in Group H, there would be no opportunity for their consumption of the overshadowing flavor to decline across subsequent trials, and this might allow the overshadowing effect to emerge more readily than in Experiment 1.

Method

The subjects were 16 experimentally naive male hooded (Lister) rats with a mean free-feeding weight of 383 g (range, 345–430 g). They were maintained in the same way as the subjects of the previous experiment. After a schedule of water deprivation had been established, they were assigned to one of two groups, Group H or Group W. All the subjects received a single conditioning trial, in which placement into the target context (A) was followed by an injection of LiCl. For the subjects in Group H, HCl was made available on this trial, and for the subjects in Group W, only plain water was made available. This was followed by a recovery day, on which the subjects were allowed two 30-min sessions of free access to water in the home cage. All the subjects then received a single conditioning trial, in which experience of the other context (B) was followed by an injection of LiCl. For the subjects in Group H, water was made available on this trial, and for the subjects in Group W, HCl was presented in this context. After a recovery day, the subjects then remained in the home cage for a 6-day period, during which they received access to water in the centrifuge tubes for 30 min at 1200 h and a 30-min presentation of water at 1700 h in the standard bottles.

The blocking phase then followed, in which all the subjects received two compound conditioning trials, on each of which consumption of sucrose in the home cage preceded placement in the target context (A), followed by an injection of LiCl. This was followed by three nonreinforced test trials, in which the subjects received free access to sucrose in the home cage. All other details of the stimuli, apparatus, and procedure were identical to those of Experiment 1, unless otherwise specified.

Results and Discussion

On the context conditioning trial in which the subjects were placed in the target context (A), Group H consumed a mean of 9.1 ml of the HCl solution, and Group W consumed a mean of 9.1 ml of water. On the conditioning trial with the nontarget context (B), Group H consumed 8.3 ml of water, and Group W consumed 7.8 ml of HCl.

The data of central interest are those from the two compound conditioning trials and the three nonreinforced test trials in which the sucrose solution was presented. These data are displayed in Figure 2. They show that both groups drank the sucrose readily on the first trial but that consumption quickly became suppressed, so that by Trial 3 (after two reinforced trials), little was consumed by either group. This rapid acquisition (compare Experiment 1) presumably reflects the fact that, after just one context conditioning trial, the context was not fully effective in blocking acquisition to sucrose. Nonetheless, a slight difference between the groups appeared on Trials 2 and 3, and this became more substan-

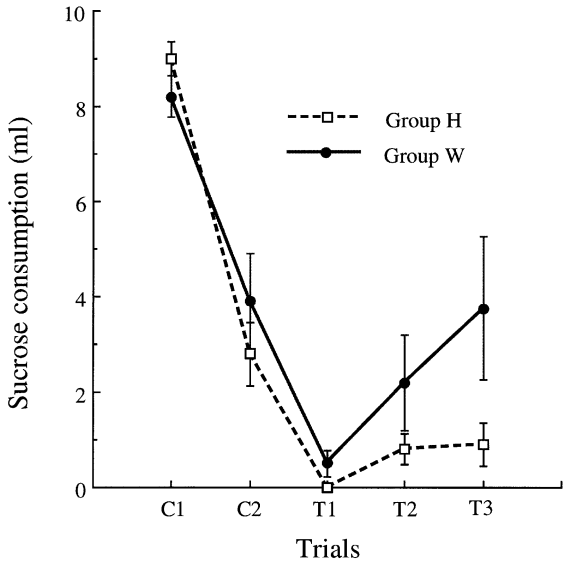

Figure 2. Group mean scores for sucrose consumption in the home cage in Experiment 2. On the conditioning trials (C1 and C2), consumption of sucrose was followed by exposure to a distinctive context and an injection of LiCl. Trials T1–T3 were nonreinforced test trials. All the subjects had previously received training in which exposure to the context was followed by an injection of LiCl. For Group W, water was presented on this context conditioning trial; for Group H, an HCl solution was presented.

tial as consumption began to recover to some extent over the test trials. As in Experiment 1, Group H showed evidence of more profound aversion to sucrose than did Group W (i.e., blocking by the context was less effective in Group H). An ANOVA conducted on the data summarized in Figure 2, with group and trial as the variables, served to confirm this impression. This analysis showed there to be no significant main effect of group ($F < 1.5$), but a significant effect of trial [$F(4,56) = 85.08$] and a significant interaction between these two variables [$F(4,56) = 3.60$]. This interaction was explored, using an analysis of simple main effects, which revealed that the groups differed significantly on the third test trial [$F(1,30) = 6.99$].

The overshadowing effect obtained in this experiment was not notably more substantial than that observed in Experiment 1, despite our argument suggesting that the use of a one-trial context conditioning regime might enhance the magnitude of the effect. Perhaps, with just one trial of conditioning, the associative strength acquired by the context is sufficiently small that the scope for overshadowing is restricted. More important, however, is the fact that, despite the procedural changes introduced here, the basic finding of the previous experiment was replicated. Thus, this result confirms the conclusion that, when the strength of the context aversion is assessed by means of a blocking test, the effect of presenting a novel flavor during context conditioning is to overshadow, rather than to potentiate, learning about the context.

EXPERIMENT 3

The training procedure used in Experiments 1 and 2 was based on that used by Symonds and Hall (1997) in their demonstration of blocking by contextual cues. These experiments differ from the earlier study, however, in that certain control conditions included by Symonds and Hall were omitted here. As a consequence, it is possible to argue that the effects obtained in Experiments 1 and 2 might be a consequence of second-order conditioning, rather than of blocking. In these experiments, the target flavor, sucrose, was followed on the compound conditioning trials by a poison-associated context. We have assumed that contextual cues served to block association between the sucrose and the Li injection that then followed and did so more successfully in Group W than in Group H. But an alternative interpretation is that any aversion acquired to the sucrose was a consequence of the formation of an association between that flavor and the context that followed it (i.e., of second-order conditioning). If so, the greater aversion to sucrose shown by Group H would indicate that, for this group, the context was a more effective conditioned reinforcer—that the presence of HCl in the first stage of training had potentiated learning about the context.

We are inclined to reject this alternative explanation for two reasons. First, we have conducted a set of unpublished studies in this laboratory specifically designed to demonstrate second-order flavor aversion conditioning, with a context as the second-order reinforcer, and have been quite unsuccessful in obtaining such an effect. Second, the experiments reported by Symonds and Hall (1997) included control conditions that allowed the conclusion that the compound conditioning procedure used in their experiments (and reproduced here) is effective in producing blocking. Nonetheless, since the central point of the experiments reported here is to establish that the presence of HCl during initial training results in overshadowing, rather than in potentiation, it seemed important to conduct a further study to demonstrate an overshadowing effect that would not be open to an alternative interpretation in terms of second-order conditioning.

This experiment was essentially identical to Experiment 2, with one major exception. As in the previous experiment, two groups received context conditioning with HCl present in one context and not in the other. They then received compound conditioning involving the HCl-associated context for Group H and the other context for Group W. In contrast to the procedure adopted in Experiment 2, however, the order of presentation of the stimuli was reversed in this phase—that is, the animals experienced the context first, followed by sucrose presented in the home cage, prior to the lithium injection. To the extent that backward pairings are ineffective in generating excitatory associations, this procedure is unlikely to generate an excitatory sucrose–context association, and thus, no difference between the groups can be expected on these grounds. Blocking, however, should still be possible, and if HCl overshadows the acquisition of context aversion, the aversion established to sucrose should again be less substantial in Group W than in Group H.

Method

The subjects were 16 naive male hooded (Lister) rats with a mean free-feeding weight of 430 g (range, 400–470 g) at the start of the experiment. All the subjects received a conditioning trial, in which the target context (A) was followed by an injection of LiCl, and after a recovery day, a trial in which experience of the other context (B) was followed by an injection. For the 8 subjects in Group H, HCl was available in Context A, and water in Context B; for the remaining subjects (Group W), this arrangement was reversed. After a further recovery day, all the subjects received a compound conditioning trial organized as follows. At 1200 h, the subjects were transferred to Context A, where they remained for 30 min; they were then returned to their home cages, where they received access to the sucrose solution for 15 min; this was followed by an injection of LiCl. With this procedure, a single reinforced trial was sufficient to establish a sizeable aversion to the sucrose (two compound conditioning trials were given in Experiment 2). After 2 additional recovery days, all the subjects received a series of daily, nonreinforced test trials consisting of free access to sucrose presented in the home cage. Suppression of the consumption of sucrose was initially quite profound, making it necessary to give four such trials (rather than the three given in Experiment 2). Details of the procedure not specified here were identical to those described for Experiments 1 and 2.

Results and Discussion

On the context conditioning trial in which the subjects were placed in the target context (A), Group H consumed

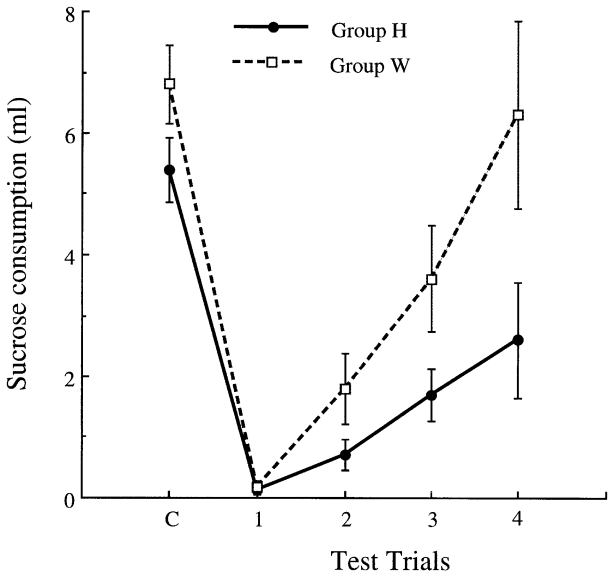

Figure 3. Group mean scores for sucrose consumption in the home cage in Experiment 3. On the conditioning (C) trial, the sucrose was followed by an injection of LiCl and preceded by exposure to a distinctive context. The remaining trials were nonreinforced test trials. Prior to this, all the subjects had received training in which exposure to the context was followed by an injection of LiCl. For Group W, water was presented on this context conditioning trial; for Group H, an HCl solution was presented.

a mean of 6.3 ml of the HCl solution, and Group W a mean of 8.6 ml of water. On the conditioning trial with the nontarget context (B), Group H consumed 7.3 ml of water, and Group W consumed 5.5 ml of HCl.

Group means for sucrose consumption on the compound conditioning trial and the test trials are shown in Figure 3. It is apparent that both groups acquired a substantial aversion to sucrose as a result of the compound conditioning trial, that consumption recovered over the course of testing, and that the recovery was slower in Group H than in Group W. An ANOVA conducted on the data summarized in the figure showed there to be a significant main effect of trial [$F(4,56) = 35.68$] and of group [$F(1,14) = 4.91$] and a significant interaction between these variables [$F(4,56) = 2.75$]. Analysis of simple main effects showed that the groups differed reliably on Test Trial 4 [$F(1,43) = 12.72$]. For Trial 3, $F(1,43) = 3.51$; for all others, Fs < 2.

As in Experiments 1 and 2, the aversion to sucrose was greater in Group H than in Group W. We interpreted the result of the earlier experiments as indicating that the context was less effective as a blocking stimulus for Group H than for Group W and thus concluded that the presence of HCl during the first phase of context conditioning was able to overshadow the acquisition of associative strength by the context. We acknowledged, however, that the aversion shown to sucrose could, in principle, derive from an association formed between context and sucrose during the compound conditioning phase. If so, the greater aversion shown by Group H might be taken to suggest that, for them, the context was actually more aversive than it was for Group H. The results of the present experiment disconfirm this alternative account by showing that the effect can still be found when the training procedure used in the compound conditioning phase is one that is unlikely to generate a sucrose–context association.

EXPERIMENT 4

Experiment 3 was designed to evaluate the possibility that the aversion to sucrose seen in the test phase of these experiments might be a consequence, at least in part, of the formation of a sucrose–context association. The procedure used in that experiment, of presenting the context prior to the sucrose in the compound conditioning phase, adequately addresses this matter, but it raises a further issue. We have argued that the first phase of conditioning gives the context aversive properties (e.g., makes the context capable of evoking a state of nausea). If we further assume that the nausea induced by exposure to a conditioned context can persist for some time after the animal has been removed from the context, the procedure used in Experiment 3 is one that will result in the animal's consuming sucrose while in a nauseous state. This experience could contribute to the rejection of sucrose seen in the test. Thus, the enhanced aversion shown on the test by Group H would again indicate that the presence of HCl in the initial phase of training has actually enhanced the aversiveness of the context—the reverse of the conclusion drawn on the basis of the assumption that blocking is occurring in the compound conditioning phase of these experiments.

The present experiment was designed to assess this interpretation. Two groups of rats received training identical to that given to the subjects in Experiment 3, except that no Li injection was given on the compound conditioning trials. If the aversion to sucrose depends on the formation of a sucrose–Li association (that may be blocked to greater or lesser extent by the contextual cues that are also presented), it was predicted that the groups would not differ on test, neither group showing an aversion. But if test performance is critically determined by an association between sucrose and context-elicited nausea, an aversion might still be evident, particularly in Group H. Since one possible, theoretically important outcome of this experiment is a null result, we thought it worthwhile to include two further groups that would be given just the same treatment as that given Groups H and W in Experiment 3, in order to confirm that the effect seen in that experiment when the Li injection was included during compound conditioning could be replicated in this experiment.

This experiment also allows us to address a further issue. Although it may not be likely, it is, in principle, possible that the effects obtained in the preceding experiments do not depend on the formation of context–illness associations at all. Assume that phase-one training for Group H establishes associations only between the context and HCl and between HCl and illness. In the com-

pound conditioning phase, the presence of the context would then activate the HCl representation at a time when the animal is consuming sucrose. The formation of an association between sucrose and this representation (or with the US representation that it evokes, or both) would supply a reason for rejection of sucrose on the test. The enhanced aversion shown by Group H would then be interpreted as indicating simply that the relevant phase-one associations are better formed when HCl is used than when unflavored water is presented. It may be noted that this interpretation predicts that it should be possible to observe a difference between the groups in their test performance even when no Li injection is given during compound conditioning.

Method

The subjects were 32 male hooded Lister rats with a mean free-feeding weight of 455 g (range, 400-500 g). They had previously served in a study using the conditioned suppression procedure with a footshock US, but were naive to all aspects of the stimuli and procedures used in this experiment.

The subjects were introduced to a regime of water deprivation, in which they received, over a period of 3 days, free access to water for two 30-min periods a day at 1000 and 1600 h. Presentations of fluids continued to be given at these times throughout the remainder of the experiment. The animals were then assigned at random to one of four equal-sized groups. Two of these groups, Groups W and H, received training similar to that described for the equivalent groups in Experiment 3. Thus, they received context conditioning with Contexts A and B, HCl being presented in Context A for Group H and in Context B for Group W. Compound conditioning consisted of exposure to Context A followed by a single reinforced trial with sucrose presented in the home cage. There were six daily test trials, on each of which sucrose was presented in the home cage for 15 min. The other groups (Groups H− and W−) received an identical training regime, except for the fact that no Li injection was given on the compound conditioning trial. They then received three test trials with sucrose presented in the home cage. The last of these was followed by an injection of LiCl. After a recovery day, they received a series of six nonreinforced test trials with sucrose presented in the home cage.

Training, compound conditioning, and test trials were initiated at 1600 h, and on each day of the experiment, water was made available in the home cage for 30 min at 1100 h. Any procedural details not specified here were the same as those described for Experiment 3.

Results and Discussion

All the subjects readily drank the fluid presented during the context conditioning phase, although, as in previous experiments, the amount consumed on HCl trials was slightly less than that consumed on trials when water was available. The groups did not differ in the amount of sucrose they consumed when it was presented following exposure to Context A in the second phase of training. The group means were 6.5 ml for Group H and 7.8 ml for Group W; 7.0 ml for Group H− and 7.1 ml for Group W−. An ANOVA, with training condition (H or W) and presence or absence of reinforcement following on this trial as the variables, revealed no significant effects (all Fs < 1).

Figure 4 shows the mean amounts of sucrose consumed by Groups H and W over the six nonreinforced test trials. The results match exactly those reported for the equiva-

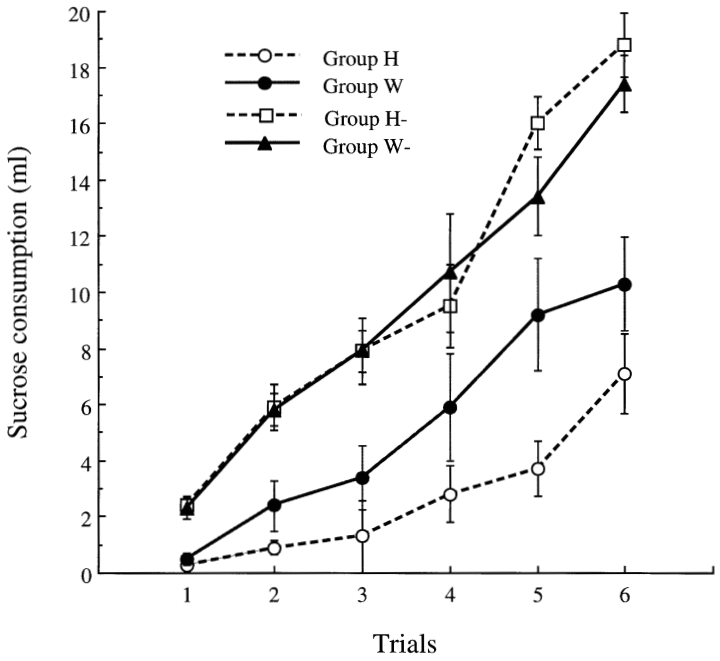

Figure 4. Group mean scores for sucrose consumption in the final test phase of Experiment 4. Groups H and W had received a single trial, on which consumption of sucrose had been followed by an injection of LiCl and preceded by exposure to a pretrained context. Groups H− and W− received similar treatment, except that no injection was given on this trial.

lent groups in Experiment 3. Both groups showed a strong aversion initially, but a difference emerged over the course of the test, with Group H showing evidence of having a stronger aversion. Groups H− and W−, on the other hand, differed not at all on the test. Group mean scores for sucrose consumption over the three test trials given prior to the Li injection were 14.3, 17.3, and 17.0 ml for Group H− and 14.6, 17.6, and 17.8 ml for Group W−. (The relatively low level consumption shown by both groups on Trial 1 of this test presumably reflects a neophobic reaction that has habituated by Trial 2.) An ANOVA, with group and trial as the variables, revealed only a significant effect of trial [$F(2,28) = 12.23$]; neither the effect of group nor the interaction of group with trial was reliable (Fs < 1). The injection given after the last of these trials produced a strong aversion that extinguished over the subsequent six nonreinforced test trials. The result for these trials are also shown in Figure 4. It is evident that Groups H− and W− did not differ on this test, and this was true over the range of consumption levels that revealed a difference between Groups H and W. An ANOVA was conducted on the data summarized in Figure 4, the variables being trial, training condition (H or W), and presence or absence of reinforcement in the compound training phase. The critical outcome of this analysis was a significant interaction among all three variables [$F(4,140) = 2.95$]. In order to evaluate this interaction, separate analyses were conducted on pairs of groups, which for Groups H− and W−, showed a significant effect only of trial [$F(5,70) = 93.39$]. For the interaction of group and trial, $F(5,70) = 1.23$, and for the main effect of group, $F < 1$. For Groups H and W, the analysis produced a significant effect of trial [$F(5,70) = 29.99$], a near significant effect of group [$F(1,14) = 3.74$, $p < .1$], and a significant group × trial interaction [$F(5,70) = 2.47$]. An analysis of simple main effects showed that the groups differed reliably on Trial 5 [$F(1,34) = 10.46$]. For Trial 4, $F = 3.38$; for Trial 6, $F = 3.65$; for others, Fs < 2.

The results for Groups H and W confirm those reported for our previous experiments. Reinforcing the context–sucrose serial compound generates an aversion to sucrose, the size of which depends on the conditions under which context conditioning was given in an earlier stage of training. Specifically, making a novel flavor available during this first phase of context conditioning results in the development of a stronger aversion to the sucrose. No such effect is seen when no reinforcement follows exposure to the serial compound. Groups H− and W− showed almost identical levels of consumption on all the test trials. It may be possible to argue that no effect was seen on the first three of these trials, since a difference between the groups that is based on mediated conditioning effects will show itself only against the background of a directly conditioned aversion; but the final series of test trials (Figure 4), given after an injection of LiCl had been introduced, similarly revealed no sign of a difference. We conclude, therefore, that the aversion observed on test in Groups H and W depends on the formation of an association between the sucrose and the effects of the Li injection that directly followed it. The difference between these groups reflects the extent to which the context, experienced before the conditioning trial with sucrose, is able to block the formation of the sucrose–Li association. A greater aversion in Group H indicates that the context was a less effective blocking stimulus for this group and, thus, confirms the conclusion, derived from our previous experiments, that the presence of HCl in the first phase of context conditioning was able to overshadow the acquisition of associative strength by the context.

GENERAL DISCUSSION

The aim of the experiments reported in this paper was to investigate the consequences for context aversion learning of allowing rats to consume a novel flavor in a context that is paired with illness. Our starting point was the commonly reported finding that this treatment will potentiate learning about the context. The potentiation effect has been accorded some importance because it has been taken to imply that learning about the relationship between exteroceptive cues and illness might involve mechanisms and principles different from those engaged by other forms of conditioning (e.g., Garcia, Brett, & Rusiniak, 1989). We have, however, identified some problems with the basic experimental procedure that has been used to generate the potentiation effect.

In brief, potentiation has been found only in experiments that assess contextual conditioning by means of a consumption test. Although it is quite reasonable to suppose that a context aversion might cause animals to suppress their drinking in that context, we have argued (see, also, Symonds & Hall, 1997) that simple generalization could equally be responsible for the result. The aversion that will be formed to a novel flavor presented in the conditioning phase can be expected to generalize, to some degree, to the flavored substance presented on test. This in itself would mean that test consumption would be less in subjects given the novel flavor than in control subjects that experienced only unflavored water during conditioning. Both pilot work and published data from our laboratory have given us grounds to believe that this can indeed be a major problem for the interpretation of the outcome of a consumption test procedure.

Accordingly, in the experiments in the present study, we assessed the strength of the contextual aversion by means of a blocking test, a procedure that, we have argued, avoids the problems that are inherent in the consumption test. We found, in all these experiments, that the presence of a novel flavor during context conditioning overshadowed learning about the context; that is, subjects given the opportunity to consume HCl in the target context showed less evidence of a context aversion than did those given plain water. This outcome is consistent with the results produced by previous experiments that have used test procedures other than the consumption test (i.e., place-preference tests and tests of instrumental performance).

We conclude, therefore, that there is no good evidence to support the view that the context–illness associations are potentiated by the presentation of a novel flavor in the context and that the usual effect of this procedure is to produce overshadowing.

This conclusion does not compel us to assert that potentiation can never occur. Although the effect is by no means always found (see, e.g., Bouton & Whiting, 1982; Mikulka, Pitts, & Philput, 1982), there is good evidence that, in some circumstances, the presence of a salient flavor cue can enhance the formation of an association between a less salient cue (such as an odor) and illness (e.g., Rusiniak, Hankins, Garcia, & Brett, 1979). The results that lead to this conclusion are not susceptible to alternative explanations of the sort offered above for the apparent potentiation of context conditioning. One possible explanation for such results (see, e.g., Durlach & Rescorla, 1980) invokes the notion of second-order conditioning, suggesting that a potentiated odor is able to elicit a conditioned response because it is able to contact a representation of the US via its association with the (highly salient) flavor. This account requires there to be strong associations both between the target cue and the flavor and between the flavor and the US. The absence of potentiation in our experiments presumably indicates that one or the other of these associations is formed only poorly with our (standard) context conditioning procedures. It remains possible, therefore, that some change in the context conditioning parameters might be found that would increase the strength of the relevant association and thus produce potentiation. At this stage, however, our conclusion remains that there is no convincing evidence that the presence of a novel flavor potentiates context–illness learning and that there is, thus, no reason to accord contextual cues any special status with regard to learning about internal events, such as gastric malaise.

Finally, it may be worth mentioning the possible clinical applicability of our findings. In particular, it has been shown that patients receiving a regime of chemotherapy can develop a range of what have been referred to as psychological side effects. They may develop aversions to foods consumed prior to the therapy session, and the cues of the clinic itself can sometimes come to elicit anticipatory nausea and vomiting (ANV). It is suggested that these effects are a consequence of Pavlovian conditioning in which the nausea produced by the chemotherapy serves as the US (e.g., Hall, 1997; Morrow, Lindke, & Black, 1991; Stockhorst, Klosterhalfen, & Steingrüber, 1998). The parallel with phenomena observed in the animal conditioning laboratory suggests possible ways in which these unfortunate side effects might be eliminated or ameliorated. Thus, for example, Bernstein (e.g., Broberg & Bernstein, 1987) has investigated the possibility that persuading patients to ingest a novel food prior to a therapy session might overshadow the formation of aversions to foodstuffs in the normal diet. It has also been suggested that a similar overshadowing intervention might be helpful in alleviating ANV (Stockhorst, Wiener, et al., 1998). But here a problem seems to arise. The obvious candidate for an animal model of ANV is contextual conditioning of the sort studied in the present experiments, and as we have noted, the existing literature on this form of learning has been taken to suggest that the ingestion of a novel substance is as likely to potentiate as to overshadow context conditioning; if so, the intervention might make ANV worse rather than better. Our new data give grounds for hope on this matter. Our demonstration that the effect of a novel flavor is, in fact, to produce overshadowing, rather than potentiation, should give encouragement to those who want to develop procedures of the sort introduced by Stockhorst, Wiener, et al. as a clinical procedure for the amelioration of ANV. To this extent, analysis of the processes underlying taste–context overshadowing (and potentiation) could be of use in devising an effective management program for the psychological side effects of nausea-inducing agents in the clinical population.

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NOTE

1. Martin and Ellinwood (1974) found a clear spatial aversion only in rats given saccharin during conditioning. In their test procedure, however, they made saccharin available in both compartments of the shuttle box. Thus, the place preference observed could be a by-product of the rat's aversion to saccharin's being more marked in the compartment in which it was paired with illness. (It is known that flavor aversions show context dependence; Bonardi, Honey, & Hall, 1990.)

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