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Contextual Conditioning with Lithium-Induced Nausea as the US: Evidence from a Blocking Procedure

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In two experiments, rats received injections of lithium chloride (LiCl) after spending time in a distinctive context. The acquisition of a conditioned aversion to the context was assessed in a subsequent stage of training in which the rats were given sucrose in the home cage before being transferred to the context and receiving an injection of LiCl. The acquisition of an aversion to sucrose was blocked by this procedure (Experiment 1A). The blocking effect was also found (Experiment 1B) with a procedure designed to ensure full consumption of the sucrose during compound conditioning. In Experiment 2, all subjects experienced two distinctively different contexts in the first stage of training, one associated with a LiCl injection and one not. Subjects given the former during the compound conditioning stage learned less well about sucrose than did subjects given the latter. This result is interpreted as showing that the effective cues in this blocking procedure can be those that uniquely define the particular place in which the first stage of training is given.

Although rats will readily form an association between the flavor of an ingested substance and gastric malaise (such as may be induced by an injection of a toxin such as lithium chloride, LiCl), associations with other (e.g., exteroceptive) stimuli are said to form poorly, or only in special circumstances (e.g., Domjan & Wilson, 1972; Garcia & Koelling, 1966). Thus, rats given simple exposure to a novel context accompanied by a lithium injection show little sign of forming an aversion to that context (Best, Brown, & Sowell, 1984, Experiment 1). Evidence for the formation of a context aversion can be produced, however, if the subject is allowed to consume a fluid (usually one with a novel flavor) during the period of exposure to the context (e.g., Best *et al.,* 1984; Best, Batson, Meachum, Brown, & Ringer, 1985; Boakes, Westbrook, & Barnes, 1992; Westbrook, Harvey, & Swinbourne, 1988). This

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result has been taken to be an instance of potentiation, in which an event that is low in associability (at least with respect to the particular reinforcer being employed) is able to acquire strength when it is conditioned in compound with some other event that is more highly associable (see, e.g., Durlach & Rescorla, 1980; Galef & Osborne, 1978; LoLordo & Droungas, 1989, for a review of the phenomenon).

There is, however, a problem in interpreting the results from experiments of this sort as reflecting the acquisition of an aversion to contextual cues. The standard test procedure has involved a demonstration that the presence of the contextual cues is effective in suppressing drinking, the test solution being different from that presented during training. Such a result is consistent with the notion that the context itself is aversive, but it is also compatible with the possibility that the aversion formed to the fluid presented during training generalizes directly to that presented on test (see Boakes *et al.,* 1992). This is not to say that the context has acquired no properties as a result of the training procedure. Suppression of consumption of the test fluid has been demonstrated to occur only when the test is given in the pretrained context, and not when it is given elsewhere (Mitchell & Heyes, 1996). But this result does not require us to assume that the trained context has itself become aversive. It is well established that flavor aversions formed in a particular context can become context-dependent so that they will be fully expressed only in the presence of the critical contextual cues (Bonardi, Honey, & Hall, 1990; Puente, Cannon, Best, & Carrell, 1988). The context-specificity demonstrated by Mitchell and Heyes (1996) could thus have occurred because their context acted as an occasion setter that allowed the (generalized) aversion to the test fluid to show itself.

Evidently, an adequate demonstration of the acquisition of conditioned aversion to contextual cues is difficult to obtain when the test procedure involves suppression of consumption in the presence of these cues. In the experiments reported here, therefore, we made use of a less direct measure of the associative strength of the context—that provided by assessing the ability of the context to block the acquisition of an aversion to a novel flavor when this flavor and the contextual cues are conditioned as a compound. With this procedure, evidence for the existence of an aversion governed by contextual cues would be provided by a *failure* of conditioning to the novel flavor; direct generalization from the aversion formed to the fluid present during the initial phase of context conditioning could not, therefore, generate the result.

Previous work using this general paradigm has produced a variety of results, and presents some difficulties of interpretation. Rudy, Iwens, and Best (1977) gave rats initial training in which an injection of LiCl was paired with confinement in a small black box, followed by a compound trial in which confinement in the box was followed by the presentation of a saccharin solution and an injection of LiCl. When tested subsequently in a standard cage, these

animals showed only a slight aversion from saccharin, an outcome consistent with blocking of the flavor aversion by the context. A curious feature of this experiment, however, was the finding that the pretraining procedure was capable of restricting the development of the saccharin aversion even when the contextual cues were not presented on the saccharin conditioning trial. This result is puzzling and has proved difficult to replicate (Krane, 1980), but indicates that the procedure used by Rudy *et al.* (1977) did not generate blocking as it is usually understood.

Better evidence for blocking by contextual cues comes from the experiments reported by Willner (1978) and Westbrook and Brookes (1988). Both demonstrated that the presence of pretrained contextual cues restricted the acquisition of an aversion to the test flavor. In both, however, it was found that rather little of the flavored solution was consumed in the presence of these cues on the conditioning trial. This in itself could be enough to explain the retarded acquisition of an aversion to the flavor (see, e.g., Bond & DiGiusto, 1975), making it unnecessary to assume that the contextual cues exerted a blocking effect. In an attempt to avoid this complication Westbrook and Brookes (1988, Experiment 2) adopted the procedure of allowing all subjects only a small, fixed amount of the target flavor on the compound conditioning trials. An alternative, used in the experiments described below, is the procedure employed by Best *et al.* (1984, Experiment 3) in which the test flavor and the pretrained context were presented serially on the compound training trial. Using this procedure, Best *et al.* (1984) were able to obtain a blocking effect in rats that consumed a normal amount of the to-be-conditioned flavor on the compound trial. Our aim in Experiment 1 was to extend and confirm the reliability of the effect demonstrated by Best *et al.* (1984). In Experiment 2 we modified this experimental design in an attempt to determine the roles played by some of the varied cues that constitute the context; in particular, we tried to demonstrate that an aversion can be controlled by those cues that define the context as being a certain place.

EXPERIMENT 1A

There were two groups of subjects. Those in the Experimental group (Group E) received a series of trials in which consumption of water in a context distinctively different from that provided by the home cage was followed immediately by an injection of LiCl. For subjects in the Control group (Group C), the injection was administered 5 h after they had been put in the context. All subjects then received serial compound conditioning trials in which they were allowed to consume a novel sucrose solution in the home cage before being placed in the target context. An injection of LiCl was administered upon removal from the context. A test trial then followed in which sucrose was presented in the home cage. If the initial context–LiCl pairings allow the context to block the acquisition of an aversion to sucrose, it can be anticipated that subjects in the Experimental group will be more willing to

consume this flavor on test than the Control subjects that had received unpaired presentations of the context and LiCl.

Method

Subjects and apparatus. The subjects were 16 male hooded (Lister) rats with a mean free-feeding body weight of 459 g (range: 375–615 g). They had previously served as subjects in an experiment using an appetitive conditioning procedure, but were naive to all aspects of the current stimuli and procedures. They were housed in home cages made of opaque white plastic, 35 × 22 × 19 cm. These had a roof of wire mesh that held food and (when available) a water bottle; a layer of wood shavings covered the floor. The home cages were kept in a large colony room that was brightly lit from 0800 to 2000 h each day.

A second set of cages located in a separate small room in the laboratory served as the experimental context. This room was dimly lit (by a single 60-W red lamp) and contained 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. The floor was covered with commercially obtained cat litter. Inverted 50-ml centrifuge tubes equipped with stainless-steel, ball-bearing-tipped spouts were used to present measured amounts of unflavored tap water, and a solution of 0.33 *M* sucrose. Fluid consumption was measured, by weighing, to the nearest 0.5 ml. The unconditioned stimulus for the conditioning trials was an intraperitoneal injection of 0.15 *M* LiCl at 10 ml/kg of body weight.

Procedure. The initial stages of water deprivation were conducted 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 1200 and 1600 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 assigned to one of two groups, Group E or Group C, matched for levels of water consumption.

The next 4 days constituted the context conditioning phase. On each of these days, all subjects were placed in the experimental context at 1200 h where they received access to 10 ml of water for 30 min. Subjects in Group E were then removed and immediately given an injection of LiCl. Subjects in Group C were returned to their standard home cages and 5 h later, at 1700 h, they were given an injection of LiCl. All subjects were given an opportunity to drink water in the standard bottles for 30 min at 1800 h.

On the next day (Day 5) the subjects received the first blocking trial. On this trial, all subjects were given free access to the novel sucrose solution in the home cage for 15 min starting at 1200 h. The bottles were then removed and the subjects were transferred to the experimental context where they received 10 ml of water for 30 min. Removal from the context was immedi-

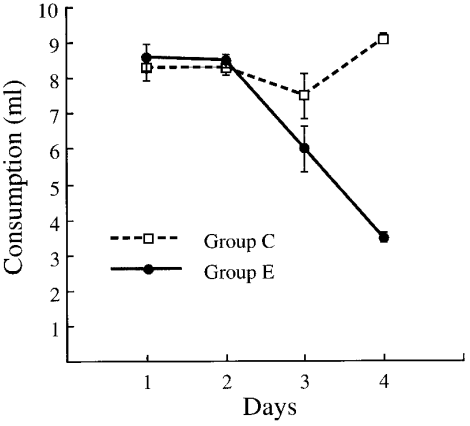

FIG. 1. Experiment 1A: Group mean (±SE) quantities of water consumed during context conditioning. For Group E, drinking water in the context was followed, on removal from the context, by an injection of LiCl; for Group C the injection was given 5 h later.

ately followed by an injection of LiCl for all animals. After a recovery day (Day 6) on which the subjects received two 30-min sessions of free access to water in the home cage (at 1200 and 1700 h), a further compound conditioning trial was given. A further recovery day was followed by a single test trial (Day 9) in which subjects were given a 15-min presentation of sucrose in the home cage at 1200 h.

Results and Discussion

When first put in the training context, animals in both groups drank almost all the 10 ml of water provided. This level of consumption was maintained in Group C, but, as Fig. 1 shows, declined dramatically in Group E. An analysis of variance (ANOVA) conducted on the data summarized in Fig. 1 showed there to be a significant difference between the groups, $F(1,14) = 9.16$, a significant effect of trial, $F(3,42) = 16.5$, and a significant interaction between these factors, $F(3,42) = 24.59$. (In this and all subsequent analyses a significance level of $p < .05$ was employed.) An analysis of simple main effects showed that the groups differed on the third trial, $F(1,36) = 4.28$, and on the final trial of this phase, $F(1,36) = 58.79$. These results are consistent with the possibility that the contextual cues were acquiring aversive properties for Group E, but, as has already been noted, other explanations are possible, such as the acquisition of a context-specific water aversion by this group.

Consumption of the sucrose solution on the two blocking trials and on the test trial is shown in Fig. 2. It is clear that on the first trial, subjects in Group C consumed substantially more of the sucrose solution than those in Group E. But on the second trial, which presumably reflects the conditioning that

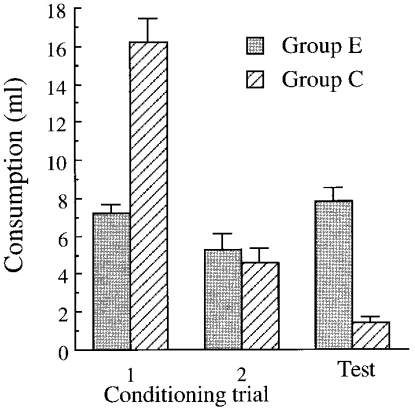

FIG. 2. Experiment 1A: Group mean (+SE) quantities of a sucrose solution consumed on each of two conditioning trials, and on a nonreinforced test trial. On each conditioning trial, the serial flavor-context compound was followed by an injection of LiCl; on the test trial, only sucrose was presented. For subjects in Group E, the context had previously been paired with illness; subjects in Group C had received noncontingent presentations of the context and LiCl.

occurred as a consequence of the first, this pattern was reversed, with Group E consuming slightly more than Group C. On the test trial (i.e., after two reinforced trials), the aversion was clearly stronger in Group C than in Group E. An ANOVA conducted on these data with Group and Trial as the factors revealed no significant effect of group ($F < 1.5$), but a significant effect of trial $F(2,28) = 54.09$, and a significant interaction between these two factors, $F(2,28) = 50.88$. The interaction was explored using an analysis of simple effects. This showed that the groups differed on the first blocking trial, $F(2,28) = 68.46$, and on the test trial, $F(2,28) = 33.90$.

It is not clear why the groups differed in the amount of sucrose solution they consumed on the first conditioning trial. Such a difference has been found in previous studies that have made use of this general experimental design; but in these the test solution was presented in the pretrained context itself on the conditioning trial. It was in the hope of ensuring that the two groups would consume the same amount of the to-be-conditioned flavor that we followed Best *et al.* (1984) and gave the animals access to the flavor before putting them in the target context. We can only speculate why the group difference should still appear in these circumstances. One possibility is that time of day at which the compound conditioning trials were given might have acquired conditioned properties in those subjects (Group E) that received effective context–illness pairings at this time in the first stage of training. (For subjects in Group C this time cue would not develop conditioned properties, as their LiCl injections were administered 5 h after experience of the target context). A conditioned response to this temporal cue might have

augmented the subjects' normal neophobic response to the novel sucrose (see also Boakes *et al.*, 1992). Alternatively, subjects in group E might have developed an aversion to fluid, or to the drinking spout used to present it, that was dependent on temporal cues. This too could result in a reduction in the amount consumed on the blocking trials.

Whatever the source of the difference on the first blocking trial, the results of central interest are those from the final test trial on which subjects in Group E consumed substantially more sucrose than those in Group C. This suggests that contextual conditioning had indeed occurred in Group E and that the context–illness pairings given to these subjects were able to block the subsequent acquisition of an aversion to sucrose. This interpretation should, however, be treated with caution. As we have already acknowledged, the amount of fluid consumed on a conditioning trial may in itself be important in determining the size of the subsequent aversion. In the next experiment we modified our training procedure in an attempt to eliminate this problem.

EXPERIMENT 1B

The aim of this experiment was to replicate the blocking effect of Experiment 1A, but using a modified experimental procedure that would eliminate the group differences in sucrose consumption that were observed on the first blocking trial. In order to achieve this, a 6-day interval was interposed between the context conditioning and the blocking phases of the experiment. During this time, the rats remained in the home cage where they were allowed to consume water from the same drinking bottles as those used during the context conditioning sessions, and at the same time of day as the conditioning sessions had been given. We hoped that this procedure would allow extinction of any conditioned properties that these features might have acquired and that could have been responsible for the initial group differences in sucrose consumption seen in Experiment 1A.

Method

The subjects were 16 male hooded (Lister) rats with a mean free-feeding weight of 395 g (range: 355–440 g). They had a similar experimental history and were maintained in the same way as the subjects in Experiment 1A; they were naive to the current stimuli and procedures. The subjects were water deprived, divided into equal-sized E and C Groups, and then given the context conditioning treatment just as in Experiment 1A. This was followed by an interval of 6 days spent in the home cage during which the subjects received, in the centrifuge tubes, access to water for 30 min at 1200 h. The amount consumed was recorded. As usual, all subjects received supplementary water in the standard bottles for 30 min at 1700 h daily.

On each of the subsequent blocking trials, the subjects received a fixed 10 ml of sucrose, followed by a context–LiCl pairing; the procedure was the same as that used in the previous experiment except that in this experiment

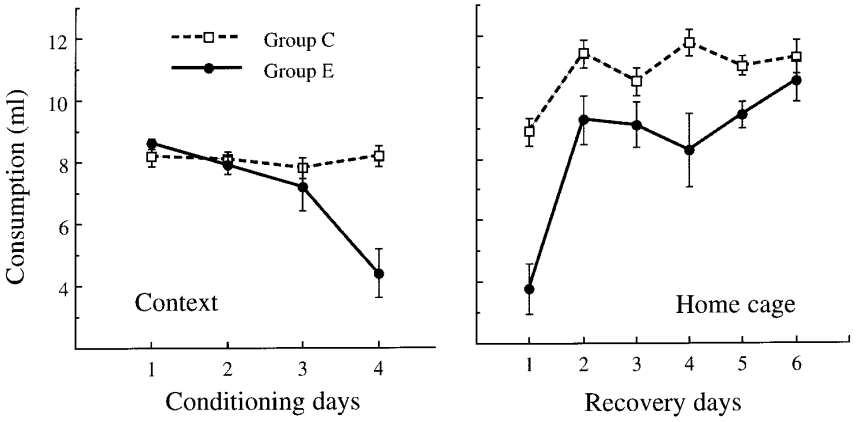

FIG. 3. Experiment 1B: left panel shows group mean (±SE) quantities of water consumed during context conditioning. For Group E, drinking water in the context was followed, on removal from the context, by an injection of LiCl; for Group C the injection was given 5 h later. The right panel shows the amount of water consumed in the home cage during the recovery phase that followed context conditioning.

we followed the procedure used by Best *et al.* (1984) and did not make water available in the experimental context during this stage. The two blocking trials were again followed by a nonreinforced test in which the subjects received free access to sucrose for 15 min in the home cage. Any procedural details not specified here are identical to those described for Experiment 1A.

Results and Discussion

The left panel of Fig. 3 shows the group mean amounts of water consumed over the 4 days of the context conditioning phase. As in Experiment 1A, consumption in Group E declined, but remained constant in Group C. An ANOVA revealed significant effects of group, $F(1,14) = 7.19$, trial, $F(3.42) = 9.44$, and a significant interaction between these factors, $F(3,42) = 9.89$. This difference between the groups was not confined to the pretrained context. As the right panel of Fig. 3 shows, Group E drank less than Group C when water was presented at 1200 h in the home cage on the day following the last context conditioning session. But with repeated home cage presentations at this time, the difference between the groups disappeared, with Group C coming to consume as much as Group E by the final day of this stage. An ANOVA conducted on the data for the recovery sessions showed there to be significant effects of group, $F(1,14) = 19.43$, of trial, $F(5,70) = 17.06$, and a significant interaction between these factors, $F(5,70) = 4.04$. Analysis of simple main effects confirmed that the groups differed on the first trial of this phase, $F(1,66) = 31.39$, but not on the last ($F < 1$).

The group mean amounts of sucrose consumed on each of the two com-

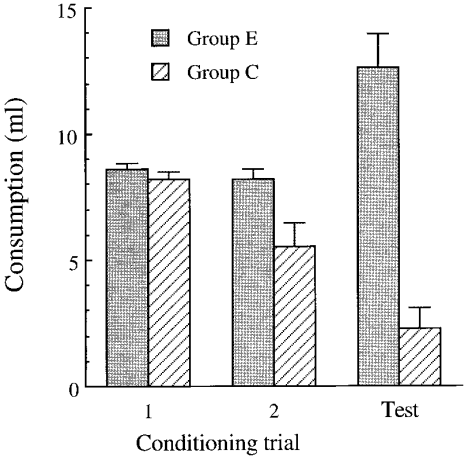

FIG. 4. Experiment 1B: Group mean (+SE) quantities of sucrose consumed on each of the two compound conditioning trials, and on the test trial. On each conditioning trial, the serial flavor-context compound was followed by an injection of LiCl; on the test trial, only sucrose was presented. For subjects in Group E, the context had previously been paired with illness; subjects in Group C had received noncontingent presentations of the context and LiCl.

pound conditioning trials and on the nonreinforced test trial are shown in Fig. 4. There was no difference between the groups on the first blocking trial, but on the second blocking trial, and on the nonreinforced test trial, Group E consumed more than did Group C. This interpretation was confirmed by statistical analysis. An ANOVA conducted on the data with Group and Trial as the factors revealed there to be a significant effect of group, $F(1,14) = 32.98$, no effect of trial ($F < 3$), and a significant interaction between these two factors, $F(2,28) = 27.75$. An analysis of simple main effects showed that the groups differed on both the second blocking trial, $F(2,28) = 5.77$, and on the test trial, $F(2,28) = 84.93$.

The results of this experiment confirm those of Experiment 1A (and of Best *et al.*, 1984) in showing that the context–illness pairings will block the acquisition of an aversion to sucrose when the sucrose and the context cues are subsequently trained as a (serial) compound. They thus support the conclusion that the pairing of contextual cues with an interoceptive US (illness) will allow those cues to acquire conditioned aversive properties.

A new finding to emerge from our experiments concerns the group differences in consumption of sucrose (Experiment 1A) and water (Experiment 1B) that were observed on the day that followed the context conditioning phase of the experiment. In both cases, Group E showed a suppressed level of fluid intake, relative to Group C, in a test given outside the pretrained context. This difference implies that the conditioning regime given to Group E must have allowed the acquisition of associative strength (or of occasion-

setting properties) by cues other than those that constitute the physical properties of the experimental context. It was suggested, for instance, that the drinking spout, or a specific time cue may have acquired conditioned properties for subjects in Group E. That the blocking effect can survive a procedure (repeated presentation of the drinking bottles at the critical time) that appears to be effective in producing extinction of these cues suggests that other features of the context must be acquiring strength during the initial conditioning phase. Experiment 2 attempted to specify more precisely what these features might be.

EXPERIMENT 2

For subjects in the E groups of the previous experiments the LiCl-induced illness was preceded by a range of cues any or all of which could, in principle, have acquired associative strength. Some of these cues (e.g., the handling involved in the injection procedure) would also be present for Group C and thus could not be responsible for the difference between the groups observed on the blocking test. Of those that are unique to Group E some can be extinguished without eliminating the blocking effect (as we have just noted). What remains is the set of cues associated with the training context for Group E. This will include not only the visual, olfactory, and tactile properties of the room and cage used in the training phase but also the cues that arise when animals are removed from their home cages and transferred to the experimental context in another part of the laboratory. For subjects in Group E, these handling cues are a reliable predictor of the US, whereas the handling cues that predict reinforcement for Group C are quite different (subjects in this group were removed from the home cage immediately prior to the injection).

The aim of this experiment was to determine if the blocking effect could still be observed when any contribution from associative strength acquired by handling/transportation cues is eliminated. A positive result would allow the conclusion that rats are able to associate at least some of the features that define a particular place with illness.

This experiment employed a discrimination procedure during the pretraining phase. (Westbrook & Brookes, 1988, Experiment 3, used a similar design, but their experiment failed to control for group differences in consumption of the flavor during the blocking phase). Specifically, all subjects received a series of trials in which the experience of a distinctive environmental context was paired with an injection of LiCl. In addition, all received a no-injection day on which they were allowed to consume water in a second context (also distinctively different from the home cage) before being returned to the standard housing racks. For half of the subjects (Group E), the extent to which the illness-paired context could block the acquisition of an aversion to sucrose was measured. For the remaining subjects (Group C), the no-injection context was presented after the target flavor on the compound condi-

tioning trials. It was anticipated that Group E would acquire a weaker aversion to the sucrose than Group C, since only an illness-paired context should be able to block conditioning to sucrose. The critical feature of this design is that the associative strength acquired by time cues, the drinking spouts, and handling/transportation cues is equated in the two groups. Any differences observed should then be a consequence of the ability of distinctive contextual cues to serve as predictors of illness.

Method

The subjects were 16 male hooded (Lister) rats with a mean free-feeding weight of 457 g (range: 400–500 g). They had previously served as subjects in a study in which an appetitive conditioning regime had been used, but were naive to the current stimuli and procedures.

Two sets of cages, both distinct from the home cage, served as the experimental contexts. One set was identical to that used in the previous experiment. Those in the second set were larger, measuring 42 × 35 × 16 cm, and were located in a colony room situated in a separate part of the laboratory. The walls and floor of the cage 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 are known to be discriminably different from each other, as they have been used in previous studies that have successfully demonstrated a role for contextual factors in flavor aversion conditioning (e.g., Bonardi *et al.*, 1990).

A schedule of water deprivation was established as in the previous experiment. Subjects were assigned to two equal-sized groups (E and C), matched for baseline levels of fluid consumption. The next 8 days constituted the conditioning phase. On Day 1, all subjects were put into the conditioning context for 30 min at 1200 h and given access to 10 ml of water. They were then removed from the context and immediately given an injection of LiCl before being returned to the standard housing racks. As in the previous experiment, the subjects were allowed, in the home cage, 30 min of free access to water in the standard bottles at 1700 h. On Day 2, the subjects were placed in the no-injection context at 1200 h, given 10 ml of water for 30 min, and then returned to the standard home cages, no injection having been given. Again, the subjects were given free access to water in the home cage at 1700 h. This 2-day cycle was then repeated a further three times. For half the subjects in each group the large cages served as the conditioning context and the smaller cages as the no-injection context; for the remainder this arrangement was reversed.

As in Experiment 1, there was a 6-day interval between context training and the compound conditioning phase during which the rats were given access to water, twice daily, in their home cages. On the first compound conditioning trial, subjects received a 10-ml presentation of sucrose for 15 min in the home cage. They were then transferred to one of the experimental contexts for 30

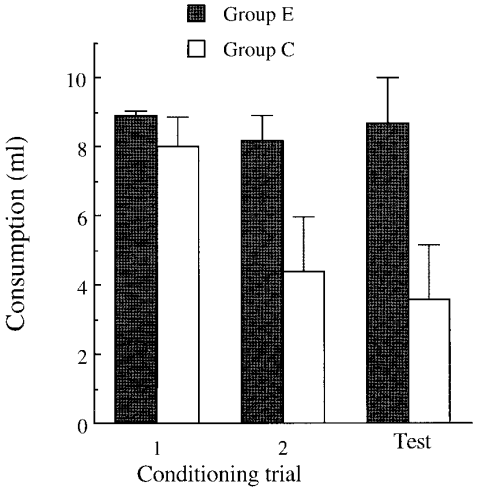

FIG. 5. Experiment 2: Group mean (+SE) quantities of sucrose consumed on each of two conditioning trials, and on the test trial. On each conditioning trial, the serial flavor-context compound was followed by an injection of LiCl; on the test trial only sucrose was presented. For subjects in Group E, the context was that which had previously been paired with illness, for subjects in Group C, this was the no-injection context.

min, removed, and immediately injected with LiCl before being returned to the standard housing racks. For subjects in Group E, the context employed on the blocking trial was the context that had been previously paired with illness. For subjects in Group C, this context was the no-injection context. On the next day, subjects were given a recovery day on which they received two 30-min sessions of free access to water in the home cage, at 1200 and 1700 h. This 2-day cycle was then repeated. Finally there was a non-reinforced test in which free access to sucrose was given in the home cage for 15 min at 1200 h. Any other procedural details are identical to those described for Experiment 1.

Results and Discussion

Water consumption during the context-conditioning phase provided little evidence of the development of an aversion. For the first 3 days in each context, the animals consumed almost all the water offered. Some indication of an aversion became evident on the final session, but the aversion was only marginally greater in the conditioned context (group mean consumption being 7.3 ml) than in the no-injection context (7.8 ml). This difference was not statistically reliable ($F < 1$).

Figure 5 shows the group mean quantities of sucrose consumed on each of the two blocking trials, and on the test trial. The amount consumed by the two groups was similar on the first trial, but on the second blocking trial and

the non-reinforced test trial, Group E consumed more of the sucrose solution than did Group C. An ANOVA conducted on these data with Group, Cage type (small or large), and Trial as the factors confirmed the reliability of these effects. There was a significant effect of group, $F(1,12) = 5.47$, and trial, $F(2,24) = 5.86$, and a significant interaction between these two factors, $F(2,24) = 3.87$. The factor Cage type had no effect ($F < 1$), and there were no other significant interactions. The Group $\times$ Trial interaction was explored further with an analysis of simple effects. This revealed that sucrose consumption differed between the two groups on both the second blocking trial, $F(1,22) = 5.34$, and on the test trial, $F(1,22) = 9.41$.

These results confirm the central finding of Experiment 1 that context–LiCl pairings can be effective in blocking the subsequent development of an aversion to a flavored solution (sucrose) that is conditioned in compound with the target context. They extend the previous finding by showing that a context given exactly the same pretraining, but with the LiCl injection omitted, will not be effective in producing blocking. Our within-subject training procedure, in which all subjects experienced both the reinforced and the nonreinforced contexts, means that the correlation with illness of cues not specific to a given place (e.g., time of day, transportation cues, features of the drinking spouts) was the same for all subjects. The difference in sucrose conditioning between groups E and C must thus be a consequence of the associative strength acquired by other cues such as those that defined the particular place in which the injection was given.

It should be acknowledged that what we have called nonspecific cues could have played a role in the blocking effects demonstrated in Experiment 1. Indeed the dramatic suppression of water consumption that developed in the reinforced context in that experiment (no such effect was seen in Experiment 2) could well reflect the acquisition of an aversion to such cues. What Experiment 2 shows is that context aversions can form to the cues that remain when the contribution from these other cues is ruled out; also that an effective aversion can exist (as shown by the blocking test) even when a direct measure (water consumed in the context during the conditioning phase) fails to reveal it.

GENERAL DISCUSSION

The experiments reported in this paper were intended to establish a training procedure that could supply unambiguous evidence that LiCl-induced illness associated with a particular place can lead to the development of an aversion to that place. Our starting point was the possibility that a more sensitive (and potentially less artifactual) measure of such contextual conditioning may be indexed by the extent to which the illness-paired cues could block the subsequent development of an aversion to a novel flavor (see also Best *et al.*, 1984).

In Experiment 1 we established that context–illness pairings will allow

the target context to block the acquisition of conditioning to a novel flavor that is presented in compound with the context. We were able to show (Experiment 1B) that this result is not to be explained in terms of group differences in consumption of the sucrose flavor on the first blocking trial; also that the blocking effect persists after the extinction of certain cues (those that characterize the drinking bottles; those associated with the time of day at which injections were given). Experiment 2 was conducted in order to establish more precisely what the critical cues might be. In this experiment it was demonstrated that cues that defined the particular place associated with the injection were effective in producing blocking.

Our demonstration of context conditioning in this flavor aversion procedure has implications for several other, related, phenomena. For example, preexposure to injections of LiCl has been shown to retard the subsequent development of a conditioned taste aversion—the *US preexposure effect* (e.g., Gamzu, 1977). One interpretation of this effect is that preexposure to LiCl allows the conditioning of aversions to the environment in which the injection is given or to handling and other cues associated with the injection itself. These associations then interfere with subsequent flavor conditioning (see, e.g., Best, Best, & Henggeler, 1977; Randich & Ross, 1985). Our procedure differs in a number of ways from that usually employed in studies of the US preexposure effect (e.g., in using a distinctive context different from the home cage for the US preexposure stage; in testing the flavor aversion outside the pretrained context.) Nonetheless, our demonstration of blocking (i.e., of retarded acquisition of the aversion to sucrose) in these circumstances lends strong support to the plausibility of blocking by pretrained cues as an (partial) explanation of the US preexposure effect.

Second, the training paradigm developed here should prove useful in further study of the phenomenon of potentiation in flavor aversion learning. As was noted in the introduction, it is commonly supposed that rats will form an aversion to contextual cues only when this learning is potentiated by the presence of a (usually novel) flavor cue. As we also noted, the possibility of direct generalization from the potentiating cue to the test cue complicates interpretation of a number of previous studies of the phenomenon. The blocking procedure provides a sensitive measure of learning about the context that is free from this complication and thus could be usefully employed to assess the effects of having a potentiating cue present in the first stage of training. In this respect it is interesting to note that Best *et al.* (1984, Experiment 3) found a blocking effect only in subjects that were given novel saccharin to drink during context conditioning; animals given water during this stage showed no more learning about the context than did subjects given no pairings of context and illness. Our studies, on the other hand, have provided good evidence of context conditioning in subjects that received only water during context conditioning. The source of this discrepancy remains to be investigated.

Finally, an understanding of the processes involved in contextual conditioning with an illness US may have considerable clinical relevance. In particular, the development of anticipatory nausea and vomiting (ANV) in cancer patients undergoing chemotherapy has been thought to reflect a classical conditioning process, in which the cues that constitute the clinical setting enter into an association with illness produced by the therapeutic drug (see Morrow, Lindke, & Black, 1991). The obvious candidate for an animal learning model of ANV is contextual conditioning with an illness US (see Mitchell & Heyes, 1996). The procedure employed in the present studies (particularly that of Experiment 2) appears to allow a sensitive assessment of aversions formed to contextual cues analogous in some ways to those of the clinic. Investigation of techniques that restrict the formation of such aversions could prove a useful first step in the development of potential intervention strategies for the control of ANV in the clinical population.

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