Psicológica (2007), 28, 193-214.

Overshadowing and potentiation of illness-based context conditioning

Joan Sansa[1♦], Antonio A. Artigas[1] & Jose Prados[2]

[1] *Universitat de Barcelona, Spain*
[2] *University of Leicester, UK*

In five experiments using rats, we investigated compound context-flavor conditioning. The subjects were allowed to spend time in the target context, where they had access to a flavored solution (either citric acid or saccharine) before receiving an injection of LiCl. Context aversion was then assessed by using a blocking procedure. When the flavor accompanying the context was a non-palatable one, citric acid, impaired learning about the context was observed, an instance of overshadowing. However, when we presented saccharine in the novel environment enhanced learning about the context was found, an instance of context potentiation. The role of the motivational properties of the flavor that accompanies the target context during conditioning is discussed.

In standard classical conditioning experiments, pairing a single stimulus with a reinforcer typically establishes that stimulus as an effective conditioned stimulus (CS), which reliably elicits a conditioned response. It is also well established that the presentation of the CS in conjunction with a second stimulus forming a compound often results in poorer conditioning than that observed after simple conditioning, an instance of overshadowing (e.g., Pavlov, 1927). Standard accounts of associative learning (e.g., Rescorla & Wagner, 1972) assert that the added stimulus competes with the target CS for a limited amount of associative strength conditionable by a given reinforcer. However, compound conditioning not always results in overshadowing. Sometimes, presentation of a CS accompanied by a second stimulus results in stronger conditioning. This effect, which has been called potentiation (e.g., Durlach & Rescorla, 1980), constitutes a challenge for standard associative theory and has been therefore the focus of extensive research and theoretical debate (see, e.g., LoLordo & Droungas, 1989). The

---

♦ Acknowledgements: This work was supported by a grant from the Spanish *Ministerio de Educación y Ciencia* to the authors. Correspondence concerning this article should be addressed to Jose Prados, School of Psychology, University of Leicester, Lancaster Road, Leicester LE1 9HN, United Kingdom. E-mail: jpg19@le.ac.uk

present study addresses the differential outcomes of compound conditioning by using a context conditioning preparation with rats.

Rats subjected to a nausea-inducing treatment during or immediately following exposure to a novel context develop an aversion to that context (see, e.g., Best, Best, & Hanggeler, 1977; Symonds & Hall, 1997). Traditionally, context conditioning experiments consisted in allowing rats to drink water in a novel context before being injected with lithium; the aversion acquired by the context was then tested by allowing rats to drink a novel flavored fluid in that context. The usual result was that rats given context conditioning consumed less of the test flavor than control rats (e.g., Boakes, Westbrook, & Barnes, 1992; Mitchell & Heyes, 1996). However, it has been repeatedly shown that allowing rats to drink a novel flavor (typically saccharine or sucrose) instead of water results in potentiation of context conditioning.

The consumption test traditionally employed in context conditioning experiments has been recently criticized because it cannot provide unequivocal evidence of context aversion nor potentiation, given that suppression of consumption of the test fluid can also be explained as a result of generalized aversion to the fluid presented during training (Symonds & Hall, 1997, 1999). Symonds and Hall (1999) concluded that "the consumption test might be an unreliable measure of the aversive strength of a context and that the potentiation effect it reveals might be artifactual" (p. 381).

Symonds and Hall (1997; see also Prados & Sansa, 2002; Rudy, Iwens, & Best, 1977; Willner, 1978; Westbrook & Brookes, 1988) reported a different demonstration of context aversion conditioning that avoids this methodological problem. This procedure made use of a less direct measure of the context associative strength provided by assessing its ability to block the acquisition of an aversion to a novel flavor. After context aversion conditioning has been established, rats receive a new trial in which a novel flavor and the contextual cues are conditioned as a compound. In this way, evidence for context aversion is provided by a failure in the conditioning of the novel flavor. Direct generalization from the aversion formed to the fluid present during the initial phase of context conditioning cannot explain the result.

Using the blocking test procedure, Symonds and Hall (1999) assessed the effect of compound context-flavor conditioning. A group of rats was allowed to drink a novel flavor—a solution of HCl—in a novel context before being injected with lithium, whereas control rats drank water. Symonds and Hall's design controls for generalization from the conditioning to the test flavor by equating rats' experience with tastes, contexts and the illness-US. This was done by conditioning a non-target context in which control rats drank HCl while the experimental animals drank water. The strength of context aversion was then measured by assessing the ability of the target context to block the acquisition of an aversion to sucrose in a further phase of training. Symonds and Hall 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.

Though Symonds and Hall's results constitute a clear demonstration of overshadowing, their conclusion that the potentiation effect is artifactual can be questioned. The experiments in which a potentiation effect was observed had always presented a sweet palatable taste (saccharine or sucrose) in the context during conditioning, but Symonds and Hall (1999) had used a sour taste (HCl) in theirs. In fact, they had introduced two changes: the test procedure—blocking instead of consumption—and the palatability of the taste that accompanied the context during conditioning—sour instead of a palatable taste. However, the latter variable had not been accounted for in their conclusions. The present study investigates whether the presence of taste stimuli that differ in their palatability produces differential context conditioning using a blocking procedure.

EXPERIMENT 1

In Experiment 1 a preference test was carried out in which rats were given a choice between a saccharine solution and plain water or between citric acid and plain water in the experimental contexts. The aim of the experiment was to see whether, in the particular contexts to be used as the target CS in our context conditioning experiments, these flavored solutions—saccharine and citric acid—elicit reliable differential responses.

METHOD

Subjects and apparatus. The subjects were 32 male Long Evans rats (*Rattus Norvegicus*), with a mean free-feeding body weight of 344,62 g (range: 302-426 g). The animals were housed individually in home cages made of transparent white plastic, 25x25x20 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.

Two sets of cages, both distinctively different from home cages, served as the experimental contexts. The first set was located in a separated room in semi-darkness only illuminated by a single 25-W bulb located in a corner far away from the cages. These cages measured 50x25x20 cm. The walls and floors of the cages were made of opaque plastic and the wire mesh roofs included a section through which a drinking spout could be inserted. The floors of the cages were covered with wood shavings. We will refer to this as the Dark context. The second set of cages were smaller, measuring 25x12.5x20 cm, and were located in a room in a separated part of the laboratory, which was highly illuminated by one window in one of the walls and two fluorescent lamps. The walls and floors of these cages were made of black plastic and the roofs of wire mesh. The floor was covered with commercially obtained cat litter. We will refer to this as the Light context. Different fluids were made available from inverted 50 ml bottles equipped with stainless steal spouts. The fluids used were plain water, a 0.1% w/v solution of citric acid, and a 0.1 % w/v solution of saccharine. Fluid consumption was recorded by weighing the bottles.

Procedure. The experiment started with a water deprivation schedule. The standard water bottles were first removed overnight. On the following three days, access to water was restricted to two daily sessions of 30 min initiated at 1100 and 1600 h. Presentations of fluids continued to be given at this time throughout the experiment. Two further sessions took place in which the animals were given plain water in two bottles at 1100h and water intakes were measured. Subjects were assigned to two groups matched by levels of water consumption.

During the next 4 days the preference test took place in the experimental contexts at 1100h. Half the rats were tested in the Dark and the other half in the Light context. Each day the animals were put in the context for 30 min where they had access to two bottles containing fluids: one bottle contained a flavored solution (saccharine for half the subjects and citric acid for the other half) whereas the other one contained plain water. The relative location of the bottles containing saccharine/acid and water was counterbalanced and changed every day. Consumption of fluids was recorded, and a preference ratio was obtained by applying the formula: flavored fluid / (flavored fluid + water).

RESULTS AND DISCUSSION

The results of the preference test are shown in the Figure 1. During the four test sessions rats that were given a choice between saccharine and water did show an increased preference for the sweet solution. On the other hand, rats that were given the acid-water choice showed a marked preference for plain water during the four test sessions. An ANOVA with flavor and test sessions as factors showed an effect of flavor, $F(1,39)=23.06$, and a significant interaction Flavor x Test. The analysis of the Flavor x Test interaction showed that there were differences between the two flavors in the tests 2, 3 and 4, Fs(1,30)>4.55. Otherwise, the preference for saccharine increased during the four test sessions, F(3,90)=4.26, whereas the preference for water over citric acid remained unchanged. (Here and elsewhere a significance level of $p < .05$ was adopted.)

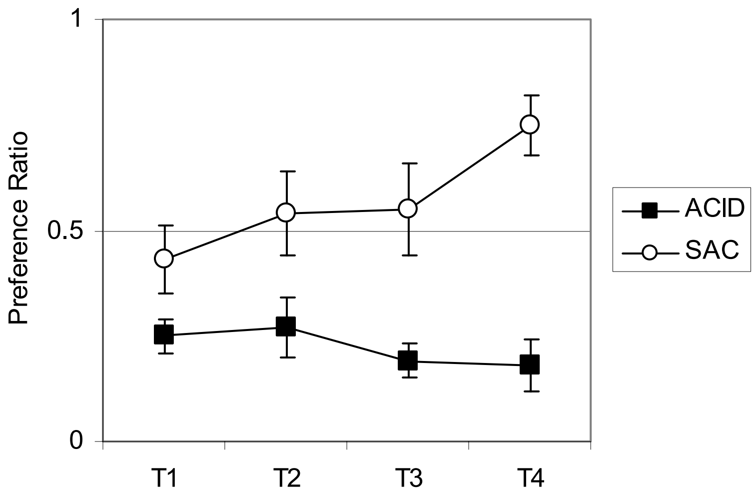

Figure1. Experiment 1. Group mean preference ratio (± *SEs*) for Citric Acid vs Water and Saccharine vs Water presented in a novel context.

The present results suggest that saccharine and acid elicit opposite motivational reactions. The observed preference for saccharine may imply that this stimulus elicits a positive motivational reaction, whereas rejection of acid can be taken to be evidence for its slightly aversive properties. Whether the presence of stimuli that elicit opposite motivational reactions may produce differential results in context conditioning was assessed in Experiments 2 and 3.

EXPERIMENT 2

Experiment 2 intends to replicate the overshadowing effect reported by Symonds and Hall (1999, Experiment 2) using a blocking procedure to assess the strength of context aversion. However, the present experiment was carried out under slightly different conditions to that observed in Symonds and Hall's original experiment. In particular, we used a somewhat different sour flavored solution during context conditioning, citric acid instead of HCl, and a salt solution instead of sucrose during the blocking-test phases of the experiment.

METHOD

Subjects and Apparatus. The subjects were 32 Long Evans rats (20 males and 12 females), with a mean free-feeding body weight of 428.4 g (range: 371-475 g) for males and 260.75 g (range: 224-283 g) for females. They were maintained in the same way as the subjects of experiment 1. The two sets of cages described for the previous experiment were used. The flavors used were plain water, a 0.1% w/v solution of citric acid and a 0.9% w/v solution of saline. The US for the conditioning trials was an intra-peritoneal injection of 0.15 M LiCl administered at 10 ml/kg of body weight.

Procedure. The experiment started with a water deprivation schedule. The standard water bottles were first removed overnight. On the following three days, access to water was restricted to two daily sessions of 30 min initiated at 1100 and 1600 h. Presentations of fluids continued to be given at this time throughout the experiment. On the last day of this cycle, water intakes were measured, and subjects were assigned to two groups matched by sex and levels of water consumption.

The next five days constituted the conditioning phase (see Table 1). On the first Day 1, all the animals were put in the target context T for 30 min at 1100 h, where they had access to 10 ml of fluid. Animals in group ACID had access to citric acid whereas animals in group WATER had access to tap water. After drinking, all the rats were removed from the experimental cages and given an injection of LiCl before being returned to their home cages. All the subjects were allowed 30 min of free access to water from the standard bottles in their home cages at 1600 h. The next day (Day 2) constituted a recovery day, in which rats received two 30-min sessions of free access to tap water in the colony room at 1100 and 1600 h. On day 3, the animals were moved to the non-target context NT for 30 min at 1100 h. Animals in groups ACID were given 10 ml of tap water whereas rats in group WATER were given access to 10 ml of citric acid solution. Again, the rats were injected upon removal from the context 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 1600 h. Days 4 and 5 were recovery days. The two contexts were counterbalanced.

Table 1. Design: Experiments 2-5.

	Group	Context Conditioning	Blocking	Test
EXP 2	ACID	NT W + / T Acid +	Salt →T +	Salt
	WATER	NT Acid + / T W +	Salt →T +	Salt
EXP 3	SACCH	NT W + / T Sac +	Salt →T +	Salt
	WATER	NT Sac + / T W +	Salt →T +	Salt
EXP 4	SACCH	NT W Ø / T Sac Ø	Salt →T +	Salt
	WATER	NT Sac Ø / T W Ø	Salt →T +	Salt
EXP 5	ACID	NT Sac + / T Acid +	Salt →T +	Salt
	SACCH	NT Acid + / T Sac +	Salt →T +	Salt

Acid, citric acid solution; Sac, saccharine solution; W, plain water; Salt, salt solution; NT, non-target context; T, target context; +, LiCl, 0.15M, 10 ml/kg; Ø, non-reinforcement.

The next phase of training consisted of two blocking trials. On the first of this trials, all the animals received a 10 ml presentation of salt for 15 min in the home cage at 1100 h. The animals were then transferred to the target context T, where they remained for 30 min (no fluids being available). Rats were then removed and injected with LiCl before being returned to their home cage, where they were given free access to tap water at 1600 h. The next day was a recovery day, in which rats received free access to water in the home cage at 1100 and 1600h. This 2-day cycle was then repeated. A further recovery day was given after this second cycle. Finally the subjects received 3 non-reinforced tests trials in which free access to salt solution was given in the home cage for 30 min at 1100 h.

RESULTS AND DISCUSSION

Context conditioning. On the context conditioning trial in which the subjects were placed in the target context T, Group ACID consumed 4.16 ml of citric acid whereas subjects in group WATER consumed 4.85 ml of plain water. On the conditioning trial in which the rats were placed in the non-target context NT, Group ACID consumed 5.23 ml of water whereas subjects in group WATER consumed 3.43 ml of citric acid. The data of central interest are those from the two blocking trials and the three non-reinforced tests trials in which a salt solution was presented.

Blocking. The results of the blocking phase, in which subjects were allowed to drink a salt solution in the home cage before their placement in the target context, are displayed in Figure 2. Rats in group ACID showed lower consumption of salt during the blocking trials than animals in group WATER. An ANOVA with flavor and day as factors confirmed these impressions. There were significant effects of flavor, $F(1,30)=6.1$, and day, $F(1,30)=19.6$. The interaction Flavor x Day was not significant.

Test. The test phase results are also shown in Figure 2. During the three nonreinforced test trials, rats in group ACID showed a greater aversion to the salted fluid than those in group WATER. An ANOVA with flavor and day as factors showed a marginally significant effect of flavor, $F(1,30)=3.92$ ($p=0.05$) and a significant effect of day, $F(2,60)=47.61$. The interaction Flavor x Day was not significant.

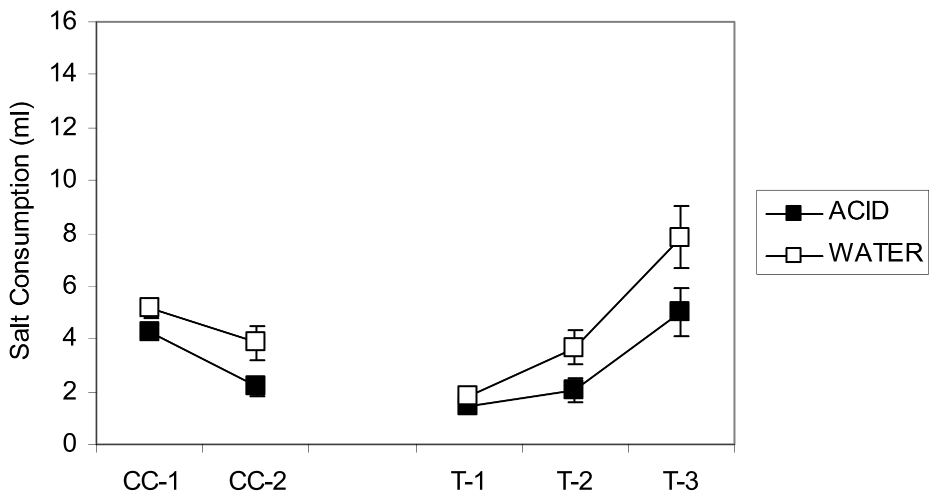

Figure 2. Experiment 2. Group mean quantities (± *SEs*) of saline solution consumed in each of two compound conditioning trials and on each of three non-reinforced test trials.

Taken together, the results of the blocking and the test phases provide evidence that the target context was less effective as a blocking cue in the group ACID. The animals that consumed a sour taste during context conditioning showed less aversion to the target context than those animals given plain water. These results replicate Symonds and Hall’s (1999) previous experiments in which the presence of a sour taste overshadowed rather than potentiated the acquisition of aversive properties by a novel context.

As argued above, the use of a sweet instead of a sour taste accompanying the context during conditioning may produce a different outcome to that observed in the present experiment. Experiment 3 was designed to test this hypothesis.

EXPERIMENT 3

Experiment 3 replicated any procedural detail of Experiment 2 employing a different taste during the context conditioning phase—saccharine was used instead of citric acid. The aim of the experiment was to assess whether the hedonic value of the novel taste that accompanies the context during conditioning plays any role in determining the outcome of compound conditioning.

METHOD

Subjects and apparatus. The subjects were 28 Long Evans rats, 16 males and 12 females, with a mean free-feeding body weight of 478 g (males, range: 430-535 g) and 278 g (females, range: 240-305 g). They were maintained in the same way as the subjects of previous experiments. The two sets of cages described for the previous experiments as the experimental contexts were used. The fluids used were plain water, a 0.1 % w/v solution of saccharine and a 0.9 % w/v solution of saline.

Procedure. The procedure of this experiment replicated the procedural details of Experiment 2. Therefore, the only change introduced was the fluid presented during the context conditioning—saccharine instead of citric acid. After context conditioning and blocking, there where nine non-reinforced test trials in which a salt solution was presented at the home cage.

RESULTS AND DISCUSSION

Context conditioning. On the context conditioning trial in which the subjects were placed in the target context, group SACCH consumed 5.00 ml of saccharine whereas subjects in group WATER consumed 5.64 ml of plain water. On the conditioning trial in which the rats were placed in the non-target context, Group SACCH consumed 5.79 ml of water whereas subjects in group WATER consumed 3.44 ml of saccharine.

Blocking. The results of the compound conditioning phase, in which subjects were allowed to drink a salt solution in the home cages before their placement in the target context, are displayed in Figure3. An ANOVA with flavor and day as factors showed a marginal effect of day, $F(1,26)=4.01$ ($p=0.05$), but the remaining factors and interactions were all not significant.

Test. The test phase results are also shown in Figure 3. During the not reinforced test trials, rats in group SACCH showed a lower aversion to salted fluid than those in group WATER. An ANOVA with flavor and blocks of three test trials as factors showed a significant effect of blocks, $F(2,52)=89.72$, and a significant interaction Flavor x Blocks, $F(2,52)=3.75$. The analysis of this interaction (simple main effects) showed that there was a flavor effect in the third block of three test trials, $F(1,26)=4.51$.

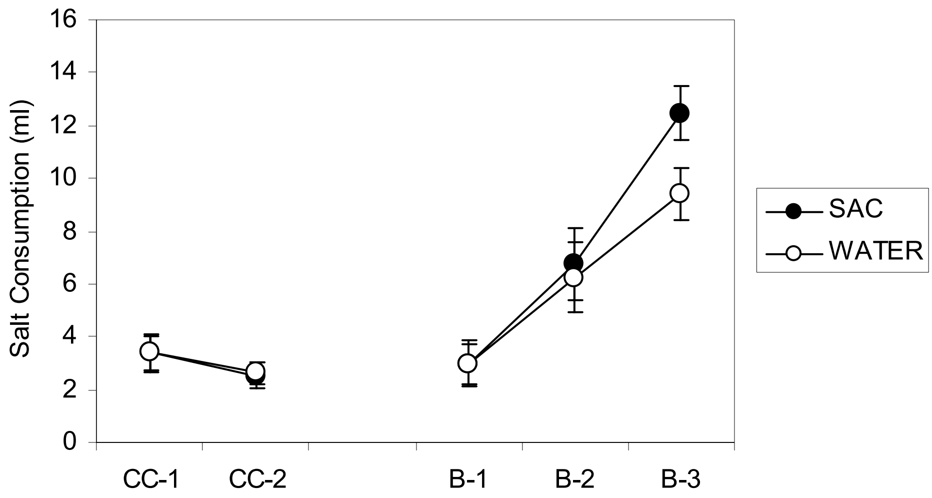

Figure 3. Experiment 3. Group mean quantities (± *SEs*) of saline solution consumed in each of two compound conditioning trials and on each block of three non-reinforced test trials.

With the particular contexts and stimuli that we have employed, the subjects given the opportunity to consume a novel sweet flavored solution—saccharine—during pairings between a context and LiCl showed more evidence of aversion to the context than did those that received plain water on the conditioning trials. The presence of a sweet flavor potentiated rather than overshadowed the acquisition of aversive properties by the context. In the present experiment, the differences between the groups emerged only after prolonged extinction during the test phase—in contrast with Experiment 2, where aversion to salt extinguished after a few test trials. The usage of saccharine instead of acid in the first phase of the experiment accounts for these differences: an aversion conditioned to saccharine is more likely to generalize to the—relatively similar—salt element employed in the test phase than an aversion established to acid (see, for example, Symonds & Hall, 1999).

Increased salt consumption in group SACCH has been interpreted here in terms of blocking: the presence of saccharine is assumed to favor the establishment of a context-illness association which then blocks the formation of a saline-illness association in the blocking trials. However, another interpretation is possible. Experience of saccharin in the target context in group SACCH could establish a direct saccharine-context association, perhaps endowing the context with a positive value (see Symonds & Hall, 1999, for a similar discussion of this hypothesis as applied to overshadowing). In the blocking phase of the experiment, presentation of salt and context in a serial compound could result in the establishment of a context-salt association. At the time of testing, the associative chain saccharine-context-salt could make the salt solution more attractive in the SACCH than in the WATER group. According to that view, the results of the experiment could have been observed even if the context was not an effective blocking cue during the second phase of the experiment in group SACCH—that is, even if there was no context conditioning during the first phase of the experiment. Experiment 4, in which the contexts were not paired with LiCl during the first phase of the experiment, examined this hypothesis.

EXPERIMENT 4

Two groups of rats were given exposure to the contexts and flavors used in Experiment 3. As in Experiment 3, animals in group SACCH were allowed to drink saccharine in the target context and water in the non-target context, whereas animals in group WATER were allowed to drink water in the target and saccharine in the non-target contexts. No lithium injections were given to the rats during this phase of the experiment. In the second phase of the experiment, a conditioning trial took place in which animals were given conditioning with the salt-context compound paired with LiCl. This conditioning trial is not essential to check the hypothesis that the saccharine-context-saline associative chain can increase the levels of consumption of saline. However, given that saline is a palatable flavour for rats, we decided to give a conditioning trial with the illness-US to avoid a ceiling effect concealing any effect of the saccharine-context-saline associative chain. Also, to avoid any floor effect in the levels of consumption of saline, we decided to restrict the conditioning trials to just one. Finally, all the animals were given three test trials with saline in their home cages. If the increased consumption of salt observed in group SACCH of Experiment 3 was due to the establishment of a saccharine-context-salt associative chain, we should observe a higher level of saline consumption in group SACCH than in group WATER.

METHOD

Subjects and Apparatus. The subjects were 16 Long Evans rats, (8 males and 8 females) with a mean free-feeding body weight of 358.75 g (range: 320-400 g) for males and 210 g (range: 190-220 g) for females. They were maintained in the same way as the subjects of previous experiments. After a schedule of water deprivation had been established they were assigned to one of two groups, Group SACCH or Group WATER. The two sets of cages and the flavors described for Experiment 3 were used.

Procedure. On the first phase of the experiment, all the animals were exposed to the context-flavor combinations described for Experiment 3. The first day of the phase all the animals were put in the non-target context NT for 30 min at 1100 h, where they had access to 10 ml of fluid. Animals in group SACCH had access to tap water whereas animals in group WATER had access to saccharine. After drinking, all the rats were removed from the experimental cages and returned to their home cages. All the subjects were allowed 30 min of free access to water from the standard bottles in their home cages at 1600 h. The next day (Day 2) rats received two 30-min sessions of free access to tap water in the colony room at 1100 and 1600 h. On day 3, the animals were moved to the target context T for 30 min at 1100 h. Animals in group SACCH were given 10 ml of saccharine whereas rats in group WATER were given access to 10 ml of tap water. All the subjects were allowed 30 min of free access to water from the standard bottles in their home cages at 1600 h. During days 4 and 5 rats received two 30-min sessions of free access to tap water in the colony room at 1100 and 1600 h. The two contexts were counterbalanced.

The next phase of training consisted of one blocking trial. All the animals received a 10 ml presentation of salt for 15 min in the home cage at 1100 h. The animals were then transferred to the target context T, where they remained for 30 min (no fluids being available). Rats were then removed and injected with LiCl before being returned to their home cage, where they were given free access to tap water at 1600 h. The next day was a recovery day, in which rats received free access to water in the home cage at 1100 and 1600h. Finally the subjects received three non-reinforced tests trials in which free access to saline was given in the home cage for 30 min at 1100 h.

RESULTS AND DISCUSSION

Context conditioning. On the trial in which the subjects were placed in the non-target context NT, Group SACCH consumed 3.86 ml of plain water whereas subjects in group WATER consumed 3.10 ml of saccharine. On the trial in which the rats were placed in the target context T, Group SACCH consumed 4.14 ml of saccharine whereas subjects in group WATER consumed 4.36 ml of water. The data of central interest are those from the blocking and tests trials in which a salt solution was presented.

Blocking and Test. The results of the compound conditioning phase, in which subjects were allowed to drink a salt solution in the home cages before their placement in the target context, are displayed in Figure 4. A one-way ANOVA performed on this data showed that groups did not differ, $F<1$. Group means for consumption of salt during the first test trials are also shown in Figure 3. The consumption of saline decreased from the blocking to the first test trial. An ANOVA with groups and trials (blocking and test 1) showed a significant effect of trial, $F(1,14)=5.15$, but the group factor and the interaction Group x Trial were not significant (Maximum $F(1,14)=1.19$). Finally, an analysis of variance (ANOVA) conducted on the data from the three test trials, with group and trials as the variables, showed a significant effect of trial, $F(2,28)=7.49$, but the group factor and the interaction Group x Trial were not significant (Maximum $F(2,28)=1.23$).

The results of Experiment 4 show that pairing the target context with saccharine does not result in increased consumption of saline at the time of testing. The associative chain saccharine-context-saline could only have been established in the SACCH group, thus increasing the motivational value of the saline solution (compared to the control group, in which the target context was paired with plain water). We cannot reject the idea that such an associative chain was actually established, but it seems clear that it does not significantly affect the motivational properties of the saline solution at the time of test. Accordingly, the results observed in Experiment 3, higher consumption of saline in group SACCH than in group WATER, can be taken to be evidence that the target context was a more effective blocking cue in the former group, an instance of potentiation.

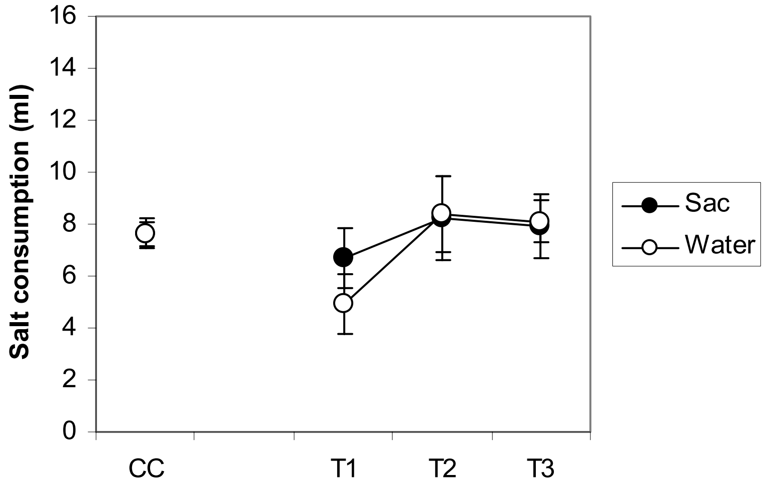

Figure 4. Experiment 4. Group mean quantities (± *SEs*) of saline solution consumed in the compound conditioning trial and on each of three non-reinforced test trials.

EXPERIMENT 5

Experiments 2 and 3 assessed the effects of presenting a sour or a sweet taste in the target context during conditioning. The results suggest that the presence of a sour taste overshadows context conditioning, whereas the presence of a sweet taste potentiates it. However, we have not compared the effect of those flavours directly. The reason for that is that their differential properties make them difficult to compare using the standard overshadowing-potentiation design. Using this design, a novel flavor, salt, is presented in the blocking phase of the experiment in a serial compound with the target context. If the context is a good predictor of the illness-US, it can block the acquisition of aversion by the new flavour. However, the aversion conditioned to saccharine and acid during the first phase of the experiment is likely to differentially generalise to the salt element. Accordingly, comparison of two groups given conditioning trials with saccharine or acid at the onset of the experiment can be expected to produce differences in salt consumption attributable to differential generalisation—making the capacity of the target context to block the new added cue irrelevant.

Experiment 5 was designed to directly compare the effect of the presence of a relatively palatable or unpalatable flavor (saccharine or acid respectively) in the target context at the time of conditioning. Context aversion was assessed by using the blocking procedure used in Experiments 2 and 3. The experimental design employed controls for generalization from conditioning to test by equating rats' experience with tastes (saccharine and acid), contexts and the illness-US. All the animals were given two context conditioning trials: animals in group SACCH drank saccharine in the target and acid in a distinctive non-target context during the conditioning trials, whereas animals in group ACID drank acid in the target and saccharine in the non-target contexts. According to the results observed in Experiments 2 and 3, group ACID can be expected to show relatively low conditioning of the target context. That being the case, the target context will not acquire the properties of an effective blocking cue. On the contrary, the presence of saccharine should potentiate context conditioning, making the target context an effective blocking cue.

METHOD

Subjects and Apparatus. The subjects were 16 male Long Evans rats, with a mean free-feeding body weight of 342.8 g (range: 308-369 g). They were maintained in the same way as the subjects of previous experiments. After a schedule of water deprivation had been established they were assigned to one of two groups, Group ACID or Group SACCH. The two sets of cages described for the previous experiments were used. The flavors used were plain water, a 0.1% w/v solution of citric acid, a 0.1 % w/v solution of saccharine and a 0.9% w/v solution of saline.

Procedure. On the first day of the context conditioning phase, all the animals were put in the non target context NT for 30 min at 1100 h, where they had access to 10 ml of fluid. Animals in group ACID had access to saccharine whereas animals in group SACCH had access to a citric acid solution. After drinking, all the rats were removed from the experimental cages and given an injection of LiCl before being returned to their home cages. All the subjects were allowed 30 min of free access to water from the standard bottles in their home cages at 1600 h. The next day (Day 2) constituted a recovery day, in which rats received two 30-min sessions of free access to tap water in the colony room at 1100 and 1600 h. On Day 3, the animals were moved to the target context T for 30 min at 1100 h. Animals in groups ACID were given 10 ml of citric acid solution whereas rats in group SACCH were given access to 10 ml of saccharine solution. Again, the rats were injected upon removal from the context 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 1600 h. Days 4 and 5 were recovery days. The two contexts were counterbalanced.

The next phase of training consisted of two blocking trials. On the first of these trials, all the animals received a 10 ml presentation of salt for 15 min in the home cage at 1100 h. The animals were then transferred to the target context T, where they remained for 30 min (no fluids being available). Rats were then removed and injected with LiCl before being returned to their home cage, where they were given free access to tap water at 1600 h. The next day was a recovery day, in which rats received free access to water in the home cage at 1100 and 1600 h. This 2-day cycle was then repeated. A further recovery day was given after this second cycle. Finally the subjects received 5 non-reinforced tests trials in which free access to salt solution was given in the home cage for 30 min at 1100 h.

RESULTS AND DISCUSSION

Context conditioning. On the context conditioning trial in which the subjects were placed in the non-target context NT, Group ACID consumed 4.67 ml of saccharine whereas subjects in group SACCH consumed 3.19 ml of citric acid. On the conditioning trial in which the rats were placed in the target context T, Group ACID consumed 2.46 ml of citric acid whereas subjects in group SACCH consumed 1.79 ml of saccharine. The data of central interest are those from the two blocking trials and the three non-reinforced tests trials in which a salt solution was presented.

Blocking. The results of the blocking phase, in which subjects were allowed to drink a salt solution in the home cage before their placement in the target context, are displayed in Figure 5 (left hand). An ANOVA carried out on these data with flavor (ACID *vs* SACCH) and day as factors showed that there was no significant effect of flavor, day, and the interaction Flavor x Day was also not significant (Maximum $F(1,14)=1.61$).

Test. The test phase results are also shown in Figure 5 (right hand). During the five non-reinforced test trials, rats in group ACID showed more aversion to the salted fluid than those in group SACCH. An ANOVA with flavor and day as factors showed a significant effect of flavor, $F(1,14)=5.14$, of day, $F(4,56)=6.60$, and also a significant interaction Flavor x Day, $F(4,56)=5.41$. The analysis of this interaction, simple main effects, showed that groups SACCH and ACID did differ in sessions 4 and 5, $Fs(1,14)>4.38$, and there was a significant effect of session in group SACCH, $F(4,56)=11.96$.

The present results seem to confirm the hypothesis that flavor palatability modulates the acquisition of aversion by a context when that flavor is presented in a compound with the context. The presence of a sour taste—which could be said to elicit a motivational response similar to the one elicited by the illness-US—results in relatively poor context conditioning. On the contrary, the presence of a more palatable flavor, saccharine, results in relatively higher context conditioning. These results seem to confirm that the results observed in Experiments 2 and 3 correspond to instances of overshadowing and potentiation respectively.

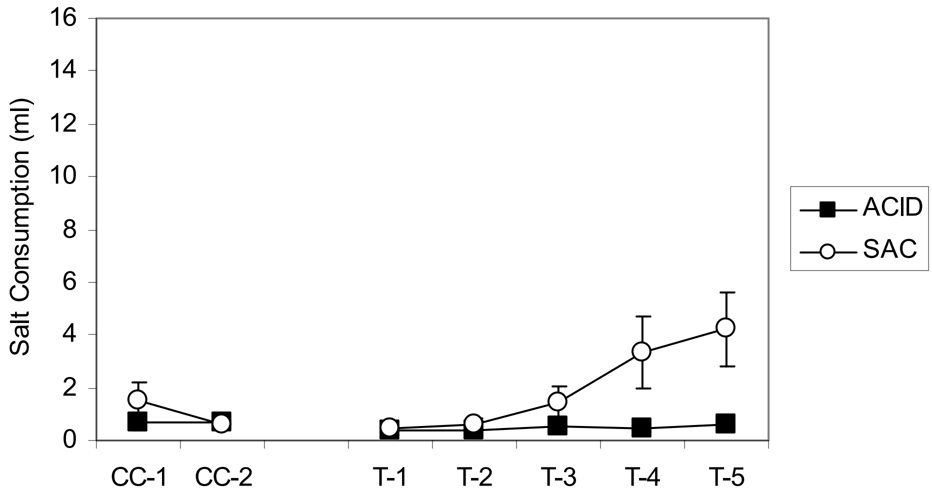

Figure 5. Experiment 5. Group mean quantities (± *SEs*) of saline solution consumed in each of two compound conditioning trials and on each of five non-reinforced test trials.

GENERAL DISCUSSION

The present study aimed to assess whether the presence of flavors that differ in their palatability differentially affect context conditioning. In Experiment 1, a preference test was carried out in the particular contexts to be used in our context conditioning experiments. The results showed a clear preference for a saccharine solution over water, whereas a citric acid solution was rejected in favor of plain water. These results suggest that sweet solutions elicit a positive response whereas acid solutions may be said to induce an aversive reaction. Experiment 2 successfully replicated the overshadowing effect reported by Symonds & Hall (1999): allowing rats to drink a sour taste solution during context conditioning interfered with its acquisition of aversive properties. Experiment 3 replicated every procedural detail of Experiment 2 presenting a sweet instead of a sour taste at the time of context conditioning; the results showed that the presence of a sweet taste potentiates context conditioning. Experiment 4 allows us to discard an alternative explanation for Experiment 3 in terms of the establishment of an associative chain saccharine-context-salt that could increase the value of the salt solution at the time of test even if the context was not an effective blocking cue. Accordingly, with the procedure employed in the Experiment 3, the context became an effective blocking cue. Finally, Experiment 5 shows the differential effect of the presence of a sour and a sweet flavor in the target context at the time of conditioning in a single experiment using an appropriate design that controls for generalization. The results showed that the presence of acid impairs context conditioning whereas saccharine favors the development of the context-illness association.

The potentiation effect observed in Experiment 3 constitutes a challenge for standard associative learning theory. Compound conditioning is thought to provoke a competition between the two CSs to gain a part of the associative strength available from a given US (e.g., Rescorla & Wagner, 1972). This account predicts that compound conditioning should always result in overshadowing rather than potentiation.

There have been, however, some attempts to account for potentiation within an associative framework. Durlach and Rescorla (1980), for example, argued that whenever two stimuli are presented as a compound, three associations would develop: one from each of the CSs to the US, and a third within-compound association. Accordingly, when testing one of the elements of the compound, the CS1, the US is activated via the CS1—US and also via the CS1—CS2—US associations. In that way the CS1 elicits a stronger conditioned response than if it had been reinforced in isolation. According to this hypothesis, presentation of a compound taste-context stimulus before the lithium injection would enable the establishment of an association between the taste and the US and between the context and the US, as well as an association between the taste and the context. Subsequent presentations of the context would then activate a representation of the taste stimulus and its associate, the illness-US. This additional source of activation may account for the potentiation effect observed in Experiment 3 when the taste employed was a sweet solution. However, it fails to explain why this additional source of activation does not produce the expected potentiation effect when the taste employed is a sour one. The within-compound association hypothesis needs to incorporate additional assumptions to make clear why using tastes that differ in their palatability would result in different outcomes.

We have been arguing that the taste stimuli employed in this experimental series differed in their palatability or hedonic value. It could be argued, however, that these stimuli differ also in other aspects that could account for the pattern of results observed. One such factor could be salience. Differential salience between saccharine and acid might account for the results observed in Experiment 5: assuming that acid is more salient than saccharine, the presence of a relatively salient acid element could better interfere with the processing of the target context in group ACID, which would prevent context conditioning. On the other hand, a less salient saccharine element could be expected not to interfere with context processing, and the target context could then acquire the properties of an effective blocking cue. However, this explanation cannot account for the pattern of results observed in Experiments 2 and 3. Certainly, both acid and saccharine can be argued to be more salient than plain water. If the salience of the stimulus accompanying the target context was the relevant factor, saccharine should better interfere with context processing than water, thus resulting in context overshadowing. Experiment 3 showed, however, that the presence of saccharine potentiates rather than overshadows context conditioning. (We have assumed acid to be more salient than saccharine taking into account the results of Experiment 1, where animals that were given a choice between acid and water showed a clear preference for water since the first test trial; animals given a choice between saccharine and water did not show such a clear preference for saccharine during the first trials. However, even assuming that saccharine was more salient than acid would not solve the problems outlined above.)

A better explanation for the whole pattern of results reported here takes into account the motivational properties of the stimuli employed, more particularly the contrasting palatability of acid and saccharine. The question that arises is why taste stimuli with different palatability should differentially affect context conditioning. It has been suggested that every stimulus elicits innate, unconditioned motivational and behavioral responses (e.g., Konorski, 1967). Sour and sweet flavors may be said to produce contrasting motivational responses; sour tastes such as the HCl solution employed by Symonds and Hall (1999) may elicit a gloomy motivational response, whereas sweet tastes such as sucrose or saccharine may be said to elicit a cheerful reaction. These innate responses elicited by sour and sweet tastes may differentially affect processing of the lithium-induced illness employed as the US in context conditioning experiments. According to many theories of learning, conditioning depends on the discrepancy between the anticipated and experienced US (e.g., Rescorla & Wagner, 1972; Wagner, 1981). The presence of a sour taste in the target context may induce an aversive motivational reaction. This reaction might serve to prime the animal for aversive events, thus weakening the associative impact of the illness-US. Lattal and Abel (2001) have reported some evidence that seems to support this using an immediate-shock freezing deficit preparation. Animals that were placed in a novel context and immediately given a shock (within 2 sec after placement on the conditioning floor) showed less context conditioning than animals that were given a delayed shock (148 sec after placement in the context). According to Lattal and Abel, placement in a novel context induces an aversive reaction that primes the animal for aversive events, thus reducing the effectiveness of the shock-US. However, for animals in the delayed-shock group, the aversive reaction initially elicited by the context weakens facilitating US processing. Taking this hypothesis a bit further, we could expect that the presence of a sweet taste in the target context would induce a positive reaction, thus increasing the discrepancy between the anticipated and experienced illness-US.

In the present experiments, the presence of a sour taste, acid, could have primed the animals for aversive events, thus weakening the impact of the illness-US. Impaired processing of the US may account for the poor conditioning of the context presented in a compound with a sour taste (Experiment 2). On the other hand, assuming that sweet tastes elicit positive emotional responses, presentation of the saccharine-context compound before conditioning should result in an increased impact of the illness-US. In that way enhanced processing of the US could result in better context conditioning than in the control condition (Experiment 3). Similarly, the presence of saccharine in the target context in group SACCH of Experiment 5 could have enhanced processing of the US, resulting in better context conditioning than in group ACID, in which the presence of acid, by priming the animals for aversive events, could have impaired US processing.

Finally, it may be worth mentioning the possible clinical applicability of our findings. Cancer patients can associate the cues (sights, smells…) of the clinical context where they are given chemotherapy with the pharmacological side effects of the treatment, thus developing anticipatory nausea and vomiting (ANV) (e.g., Burish & Carey, 1986; Hall, 1997; Morrow, Lindke, & Black, 1991; Stockhorst, Klosterhalfen, & Steingrüber, 1998). Assuming that the mechanism responsible for the ANV syndrome is similar to that responsible for the development of the context aversion in rats, ANV could be attenuated, as Symonds and Hall (1999) suggested, by giving chemotherapy in a context presented in a compound with ingestion of a non-palatable substance, which could overshadow context acquisition of aversion. However, it should be avoided presenting palatable substances such as candy or sweet potions, which may potentiate context conditioning thus increasing the likelihood of ANV to develop.

RESUMEN

Ensombrecimiento y potenciación del condicionamiento de aversión al contexto. En cinco experimentos, se investigó el condicionamiento compuesto sabor-contexto empleando ratas como sujetos. Los animales fueron expuestos a un contexto novedoso en el que tenían acceso a una solución de ácido cítrico ó de sacarina antes de ser inyectados con LiCl. A continuación medimos la aversión condicionada al contexto empleando un procedimiento de bloqueo. Cuando el sabor que acompañaba al contexto durante el condicionamiento era relativamente aversivo (ácido cítrico) observamos un nivel relativamente bajo de condicionamiento contextual; de acuerdo con nuestra interpretación, el sabor ácido ensombreció al contexto. Por el contrario, cuando el sabor era agradable (solución de sacarina) se observó una potenciación del condicionamiento contextual. Nuestra discusión de los resultados toma en consideración las propiedades motivacionales del sabor que acompaña a contexto en el momento del condicionamiento.

REFERENCES

Best, P.J., Best, M.R., & Hanggeler, S. (1977). The contribution of environmental non-ingestive cues in conditioning taste aversive internal consequences. In L.M. Barker and M. Domjan (Eds.), *Learning mechanisms in food selection* (pp. 371-393). Waco, TX: Baylor Univ. Press.

Boakes, R.A., Westbrook, R.F., & Barnes, B.W. (1992). Potentiation by a taste of toxicosis-based context conditioning: Effects of varying the test fluid. *Quarterly Journal of Experimental Psychology*, 45B, 303-325.

Burish, T.G., & Carey, M.P. (1986). Conditioned aversion responses in cancer chemotherapy patients: Theoretical and developmental analysis. *Journal of Consultive and Clinical Psychology, 54*, 593-600.

Durlach, P.D., & Rescorla, R.A. (1980). Potentiation rather than overshadowing in flavor aversion learning: An analysis in terms of within-compound associations. *Journal of Experimental Psychology: Animal Behavior Processes, 6*, 175-187.

Hall, G. (1997). Context aversion, Pavlovian conditioning and the psychological side effects of chemotherapy. *European Psychologist, 2*, 118-124.

Konorski, J. (1967). *Integrative activity of the brain*. Chicago: University of Chicago Press.

Lattal, K.M., & Abel, T. (2001). An immediate-shock freezing deficit with discrete cues: A possible role for unconditioned stimulus processing mechanisms. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 394-406.

LoLordo, V.M., & Droungas, A. (1989). Selective associations and adaptative specializations: Taste aversions and phobias. In S.B. Klein & R.R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 145-179). Hillsdale, NJ: Erlbaum.

Mitchell, C., & Heyes, C. (1996). Simultaneous overshadowing and potentiation of taste and contextual cues by a second taste in toxicosis conditioning. *Learning and Motivation, 27*, 58-72.

Morrow, G.R., Lindke, J., & Black, P.M. (1991). Anticipatory nausea development in cancer patients: Replication and extension of the learning model. *British Journal of Psychology, 82*, 61-72.

Pavlov, I.P. (1927). *Conditioned reflexes*. London: Oxford University Press.

Prados, J., & Sansa, J. (2002). Differential acquisition of aversion by two distinctive contexts paired with lithium-induced illness. *Learning and Motivation, 33*, 253-268.

Rescorla, R.A., & Wagner, A.R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and non-reinforcement. In A.H. Black & W.F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64-99). New York: Appleton-Century-Crofts.

Rudy, J.W., Iwens, J., & Best, P.J. (1977). Pairing novel exteroceptive cues and illness reduces illness-induced taste aversions. *Journal of Experimental Psychology: Animal Behavior Processes, 3*, 14-25.

Stockhorst, U., Klosterhalfen, S., & Steingrüber, H.J. (1998). Conditioned nausea and the side-effects in cancer chemotherapy: A review. *Journal of Psychophysiology, 12* (Suppl.), 14-33.

Symonds, M., & Hall, G. (1997). Contextual conditioning with lithium-induced nausea as the US: Evidence from a blocking procedure. *Learning and Motivation, 28*, 200-215.

Symonds, M., & Hall, G. (1999). Overshadowing not potentiation of illness-based contextual conditioning by a novel taste. *Animal Learning and Behavior, 27*, 379-390.

Wagner, A.R. (1981). SOP: A model of automatic memory processing in animal behavior. In N.E. Spear & R.R. Miller (Eds.), *Information processing in animals: Memory mechanisms* (pp. 5-47). Hillsdale, NJ: Erlbaum.

Westbrook, R.F., & Brookes, N. (1988). Potentiation and blocking of conditioned flavour and context aversions. *Quarterly Journal of Experimental Psychology, 40B*, 3-30.

Willner, J.A. (1978). Blocking of a taste aversion by prior pairings of exteroceptive stimuli with illness. *Learning and Motivation, 9*, 125-140.

(Manuscript received: 25 September 2006; accepted: 22 December 2006)