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Effects of an extinguished CS on competition with another CS

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Abstract

Three experiments were conducted using a conditioned taste aversion procedure with rats to examine the effect of nonreinforced presentations of a conditioned stimulus (CS) on its ability to compete with a target stimulus for manifest conditioned responding. Two CSs (A and B) were presented in a serial compound and then paired with the unconditioned stimulus. CS A was first paired with the US and then presented without the US (i.e., extinction) prior to reinforced presentation of the AB compound. Experiment 1 showed that A was poor at competing with B for conditioned responding when given conditioning and extinction prior to reinforcement of AB relative to a group that received both A and B for the first time during compound conditioning. That is, an extinguished A stimulus allowed greater manifest acquisition to B. Experiment 2 found that extinction treatment produced a poor CR to the pretrained and extinguished CS itself following compound conditioning. Experiment 3 found that interposing a retention interval after extinction of A and prior to compound conditioning enhanced A's ability to compete with B. The results of these experiments are discussed with regard to different theories of extinction and associative competition.
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1. Introduction

A large number of recent studies have examined treatments influencing extinction of conditioned responding to a conditioned stimulus (CS) during classical conditioning. Extinction refers to the decrease in conditioned responding (CR) elicited by a CS due to its repeated presentation without the unconditioned stimulus (US) following CS–US pairings. Studies have revealed that an extinguished CR can be recovered by performing different manipulations, such as interpolating a retention interval before testing (i.e., spontaneous recovery, Pavlov, 1927), testing the CS in a context different from the extinction context (i.e., renewal of the CR, Bouton and King, 1983; Chelonis et al., 1999), or presenting the US in the absence of the CS before testing (i.e., US reinstatement, Rescorla and Heth, 1975; Schachtman et al., 1985). Consistent with Pavlov's (1927) original view, these findings of recovery of the CR show that extinction cannot be viewed as unlearning of the excitatory association

between a CS and a US formed during conditioning (see also Bouton, 1993; Delamater, 1996).

Traditional associative theories of learning (e.g., Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972) cannot readily accommodate these recovery effects. These theories either explain extinction as *unlearning* of the excitatory CS–US association (e.g., Mackintosh, 1975; Rescorla and Wagner, 1972), making such recovery effects implausible, or as the *learning* of an interfering CS–US inhibitory association (e.g., Pearce and Hall, 1980) which offsets excitatory associations; and such processes do not allow for such CR recovery effects. However, these findings have encouraged the development of alternative theories that focus on the formation of inhibitory CS–US associations that produce interference with retrieval of the intact CS–US association when the CS is tested (e.g., Bouton, 1993), while other theories focus on an impaired CR due to the formation of an inhibitory CS-response association (e.g., Delamater, 1996; Rescorla, 1993). The retrieval-interference theories state that the CS–US association is retained (but poorly retrieved/expressed) after extinction treatment, and that CR recovery is caused by facilitated retrieval/expression of the excitatory CS–US association at the time of testing (Miller et al., 1986). Thus, according to Miller et al., the manipulations

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described above are claimed to enhance the retrievability of the CS–US association by reducing interference from the information acquired during the extinction phase. Clearly there are many views of extinction; some of which can address these recovery effects and some cannot. While these effects involve postconditioning changes in the CR to an extinguished CS, little work has been done examining the effect of such a CS on associative competition.

The predictions that retrieval-interference theories make regarding the potential for associative competition by an extinguished CS are not immediately clear. Associative competition typically occurs when two CSs are presented together as a stimulus compound and paired with reinforcement. Often less learning occurs for such CSs than if either CS had been paired with reinforcement in the absence of the other stimulus (i.e., overshadowing). Because retrieval-interference theories claim that the CS–US association is retained despite the CS-alone extinction trials, such theories do not readily predict that an extinguished CS will be at a disadvantage (compared with a nonextinguished CS) at competing with another stimulus during compound conditioning. That is, if a CS (A) is paired with the US and then given extinction trials prior to its pairings with the US in the presence of a novel CS (B)–retrieval theory can claim that A should be very effective at competing for conditioning with B because the A-US association is retained. However, retrieval-interference theories could assert that the processing that occurs during extinction somehow renders the CS–US association poor at competition (see McPhee et al., 2001; Schachtman et al., 1992, for discussions of this view). For example, extinction could result in the formation of an inhibitory association (A-noUS association) and this association could limit A's ability to compete with B.

Rescorla's (1993) more recent view of extinction (see also Rescorla, 1996a, 1996b) denies that an extinguished CS would be at a disadvantage when competing with another CS on compound conditioning trials. This theory states that, during extinction, an inhibitory CS–CR association is formed and this association is not expected to influence associative competition with another CS. According to Rescorla's view, CS–US associations remain functional throughout extinction training, although the CS no longer evokes a strong CR due to its inhibitory association with the CR.

While there are different views of the effects of using an extinguished CS in an associative competition procedure, previously published work on such effects is limited. Kamin (1969, pp. 18–19) assessed whether an extinguished CS could effectively compete with another CS for manifest learning. Using a fear conditioning procedure and apparently relying on cross-experimental comparisons, Kamin administered noise-footshock trials to rats prior to noise-light compound trials and tested for responding to the light and observed a poor CR (i.e., blocking occurred). Extinction of the noise prior to the compound trials caused a significantly greater CR to the light relative to a condition given no extinction.

The present experiments sought to further examine the effects of extinction of a CS on associative competition by examining the effectiveness of an extinguished CS as a competitor for associative strength when it is paired with the US in compound with a novel, target CS. Using a conditioned taste aversion (CTA) procedure, Experiment 1 explored whether extinction treatments that occur prior to compound conditioning trials with a previously conditioned CS limit or enhance the CR to an added target CS when compared with a group that receives both CSs for the first time during compound conditioning. As mentioned earlier, we know from the occurrence of spontaneous recovery following extinction that a retention interval can cause the CR to re-emerge. The present experiments also examined whether a retention interval would enhance the competing ability of an extinguished CS.

2. Experiment 1

Experiment 1 explored whether a CS given pairings with a US and then CS-alone extinction can reduce conditioning to an added, target CS when the two CSs are presented as a stimulus compound and paired with the US. Initially, rats were given either conditioning with a control solution (a coffee flavor) or a sucrose solution (the pretrained flavor) paired with LiCl and then given three extinction trials with the same flavor received during initial conditioning. Then all rats received compound conditioning with the sucrose solution and an added vinegar flavor (the target CS) paired with LiCl. Then consumption of vinegar was assessed to determine whether the extinguished flavor reduced or enhanced the acquisition of conditioned responding to the vinegar flavor relative to the CR for the control condition given initial training with coffee.

2.1. Method

2.1.1. Subjects
A total of 20 female and male, Sprague–Dawley-derived rats served as subjects. The rats were obtained from the University of Missouri-Columbia breeding colony and were approximately 4–6 months of age at the start of the study. Each rat was individually-housed in hanging, stainless-steel, wire-mesh cages that measured 24 cm × 17.7 cm × 18.2 cm (l × w × h) with ad lib. access to lab chow. Subjects were handled a few times prior to the start of the experiment. The rats were also water-deprived prior to the start of the experiment using a graded water-deprivation schedule that culminated in 10-min of water access each day. Water access occurred in the home cage after each day's treatments, approximately 23.5 h prior to the experimental manipulations of the next day. The room housing the animals was on a 16-h/8-h light/dark cycle and treatments occurred during the middle of the light portion of the cycle.

2.1.2. Apparatus
Flavored solutions were presented in plastic drinking tubes with a metal lick tube attached. All conditioning treatments and testing occurred in the home cage. LiCl was administered using a 25-ga, 1.59-cm hypodermic needle. A 12% (w/v) sucrose solution (Suc) (Sigma Co., St. Louis, MO), a 1.5% (w/v) decaffeinated coffee solution (Coff) (Sanka, General Foods, White Plains, NY), and a 3% (v/v) vinegar solution (Vin) (Heinz apple cider vinegar, Pittsburgh, PA) were used as drinking solutions.

Table 1
Design of Experiment 1

Group	Conditioning	Extinction	Compound conditioning	Test
Ext	Suc+	Suc−	VinSuc+	Vin−
Control	Coff+	Coff−	VinSuc+	Vin−

Note: Suc = Sucrose Solution; Vin = Vinegar; Coff = Coffee; "+" = LiCl; "−" = no LiCl.

2.1.3. Procedure

Table 1 summarizes the design of Experiment 1. The groups were counterbalanced for body weight and sex to the extent possible. As can be seen in the table, during the initial conditioning phase all rats received a single conditioning trial with one flavor. On Day 1, Group Ext (Extinction, $n = 10$) consumed Suc for 15 min, followed immediately by an i.p. injection of 2% (w/v) LiCl (Sigma, St. Louis, MO) at 10 ml/kg body weight. On each of Days 3–5, the rats in Group Ext received 15-min Suc-alone extinction trials. Group Control ($n = 10$) consumed Coff during the conditioning phase on Day 1 and were given 15-min extinction trials with Coff on each of Days 3–5. No treatment occurred on Day 2 for any of the rats to allow for recovery from LiCl-induced illness.

During the compound conditioning phase (Days 6 and 8), all rats received 7.5 min access to Vin followed immediately by 7.5 min access to Suc. Following exposure to the two flavors, the rats were then immediately injected with an i.p. injection of 2% (w/v) LiCl at 1% body weight. A serial conditioning procedure was used rather than a simultaneous compound because prior work has found reliable stimulus competition effects with CTA using a serial compound (Revusky et al., 1977). Also, serial conditioning likely reduces problems of stimulus generalization decrement (and, especially, differential stimulus generalization decrement across groups) from the compound conditioning trials to the test trials. No treatments occurred on Days 7 and 9 to allow the rats to recover from illness. Testing occurred on Days 10–15 in the home cage with 15 min of access to Suc. Flavored solutions given during all of the experimental treatments were recorded by weighing the drinking tubes before and after treatment.

2.2. Results and discussion

Two rats were removed from the control condition due to illness or procedural error. Also, consumption scores during the training phases of the experiment were not available due to experimenter error. Previous work in our laboratory has obtained significant conditioning for the Suc and Coff flavors by rats given such treatments and three extinction trials have been found to produce adequate and often comparable extinction. Moreover, few differences have been detected by such similarly treated groups during compound conditioning suggesting, for example, that neophobia to Suc (for rats in Group Control on Day 6) is not substantial. Earlier work in our laboratory using very similar parameters to those used in the early phases of this experiment found that rats consumed group means of 12.5 ml of Suc on the conditioning trial and 4.0, 8.6 and 10.7 ml on the three Suc
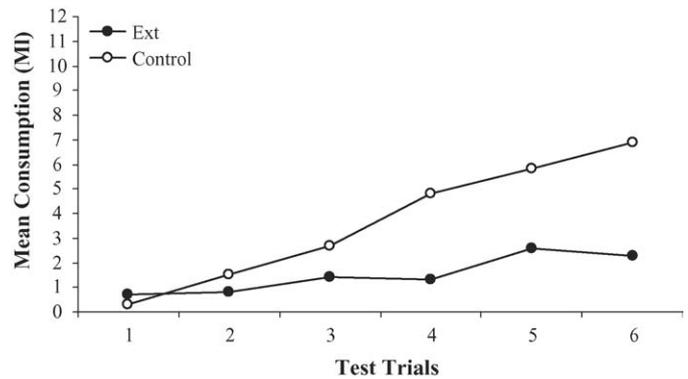

Fig. 1. Mean intake on the test trials of Experiment 1.

extinction trials. Consumption of 1.5% Coff is described in subsequent experiments of this report.

The test data are shown in Fig. 1. As can be seen, the rats in Group Ext drank significantly less Vin than the rats in Group Control over the course of testing, indicating that the aversion to Vin extinguished more quickly for Group Control than for Group Ext during testing. This finding was confirmed by an analysis of variance (ANOVA) as revealed by a main effect of Group, $F(1,16) = 4.64$, $p < 0.05$. There was also a main effect of Days, $F(4,64) = 12.13$, $p < 0.0001$; and a Group × Day interaction, $F(4,64) = 4.91$, $p < 0.002$.

The results of Experiment 1 found that conditioning and extinction of sucrose, which was then paired with LiCl in compound with an added, target vinegar solution (Group Ext), resulted in a greater CR to the added CS compared to that of a group that received no pretraining with Suc. In other words, an extinguished CS was poor at competing with another CS for manifest conditioned responding. These results are not expected based on associative conditioning models that predict that (assuming a sufficient number of extinction trials such that extinction is complete) CS-alone trials following conditioning will eliminate (or negate) excitatory associative strength and produce a CS that is effectively neutral with respect to influencing conditioned responding to another CS (Rescorla and Wagner, 1972). These models are challenged by the present results. Of course, an extinguished CS can become inhibitory (e.g., stemming from the influence of excitatory contextual cues producing inhibition to the CS), thereby causing "superconditioning" to another cue or causing "protecting from extinction" (see Calton et al., 1996, Exp. 4). The present results are consistent with this view. The results of this experiment are also quite consistent with views that predict that CS-alone exposures during extinction can produce a loss of CS associability that allow greater manifest learning to a concurrent, added element during compound conditioning (Mackintosh, 1975; Pearce and Hall, 1980).

A retrieval-interference view, which claims that extinction does not eliminate the CS–US association (and assumes that the CS–noUS association potentially learned during extinction does not influence a CS's competitive potential), posits that this association is intact following extinction and thus predicts that an extinguished CS should effectively compete for associative strength. However, evidence of good competitive ability of an

extinguished CS was not seen. In fact, the extinguished CS (Suc), rather than competing well for the acquisition of associative strength, allowed for the added CS (Vin) to reveal a particularly strong CR.

Nonetheless, a variation on the retrieval-interference view of extinction (see McPhee et al., 2001; Schachtman et al., 1992) that is applied to address compound conditioning procedures can predict the present effect by stating that the retrievability of the competing CS–US association is impacted by the putative CS–noUS association acquired during extinction. That is, if the CS–noUS association learned during extinction is well retrieved and interferes with retrieval of the CS–US association, then the CS will be poor at associative competition (see also McPhee et al., 2001 for a discussion). That is, retrievability of an association influences its ability to associatively compete.

3. Experiment 2

Experiment 1 found that an extinguished CS allowed for a greater CR to an added CS during the compound conditioning phase than when both CSs were novel during compound conditioning. Some models, such as those of Pearce and Hall (1980) and Mackintosh (1975) as well as retrieval-interference models as described above, make the prediction that the extinguished CS can allow an added, target CS on the compound conditioning trial to acquire relatively more excitatory associative strength presumably at the expense of reconditioning for the pretrained CS. Therefore, we sought to confirm this possibility by examining whether an *extinguished CS* is at a particular disadvantage in acquiring associative strength on the compound trials. That is, if an extinguished CS allows for the added CS to be more learned about, then this greater learning should be at the expense of the extinguished CS. Towards this end, we conducted a similar experiment to that of Experiment 1 except that the extinguished CS was tested for its associative strength. Moreover, we reversed the role of the flavors in Experiment 2. A vinegar flavor was used as the pretrained CS and a sucrose solution was used as the blocked CS such that both Experiments 1 and 2 tested on the vinegar flavor.

3.1. Method

3.1.1. Subjects

Seven female and thirteen male, Sprague–Dawley-derived rats served as subjects. Ten rats, representing the first replication, were obtained from the University of Missouri breeding colony while 10 (the second replication) were purchased from Sasco Co. (Indianapolis, IN). At the start of the study, the ranges of the body weights were 208–443 g and 276–305 g for the male and female rats, respectively. The rats were maintained identically to those in Experiment 1.

3.1.2. Apparatus and procedure

The apparatus was identical to that of Experiment 1. Table 2 summarizes the design of Experiment 2. The groups were counterbalanced for body weight and sex to the extent possible. During the conditioning phase (Day 1) all rats received a condi-

Table 2
Design of Experiment 2

Group	Conditioning	Extinction	Compound conditioning	Test
Ext	Vin+	Vin−	SucVin+	Vin−
Control	Coff+	Coff−	SucVin+	Vin−

Note: Suc = Sucrose Solution; Vin = Vinegar; Coff = Coffee; "+" = LiCl; "−" = no LiCl.

tioning trial with a flavored solution. Half of the subjects (Group Ext, $n = 10$) consumed Vin for 15 min whereas the remaining subjects (Group Control, $n = 10$) drank Coff. The flavor was followed by an injection of 2% LiCl. During the extinction phase (Days 3–5), the rats in Group Ext received a Vin-alone exposure while rats in Group Control received a Coff-alone exposure on each day.

During the compound conditioning phase (Days 6 and 8), all rats received 7.5 min of access to Suc followed immediately by 7.5 min of access to Vin. The rats were then immediately injected with an i.p. injection of 2% LiCl at 1% body weight.

Testing occurred in the home cage. All rats were tested for consumption of Vin during 15-min access to the flavor on Days 10–14. All unspecified procedural details were identical to those of Experiment 1.

3.2. Results and discussion

Four rats were eliminated from the study (two from each of Groups Ext and Control) for failing to consume at least 1.5 ml of solution upon its initial presentation (i.e., Vin or Coff on Day 1 or Suc on Day 6). Groups Control and Ext consumed 7.1 ($\pm$1.1) and 7.2 ($\pm$1.5) ml, respectively, on Day 1 and there was no difference between these means, $F < 1$. Group Control consumed 1.8 ($\pm$0.5), 4.0 ($\pm$1.4), and 7.6 ($\pm$2.6) ml on the three extinction trials; while Group Ext consumed 2.4 ($\pm$0.5), 6.2 ($\pm$1.5), and 10.3 ($\pm$2.4) ml on these trials. An ANOVA conducted on the three extinction trials found no main effect of Group, $F < 1$, nor a Group × Days interaction, $F < 1$, although an increase across days occurred, $F(2,28) = 20.17$, $p < 0.0001$. Group Ext consumed 11.9 ($\pm$2.6) and 1.0 ($\pm$0.2) ml of Suc on the first and second compound conditioning trial, respectively. Group Control consumed 11.8 ($\pm$1.7) and 1.2 ($\pm$0.5) ml of Suc on these trials. There were no differences between groups on these scores ($Fs < 1$), although subjects consumed less Suc on the second conditioning trial than on the first conditioning trial, $F(1,14) = 55.25$. Group Ext consumed 4.3 ($\pm$1.3) and 4.4 ($\pm$1.4) ml of Vin on the first and second compound conditioning trial, respectively; whereas Group Control consumed 2.7 ($\pm$0.7) and 0.9 ($\pm$0.3) ml of Vin on the first and second compound conditioning trial, respectively. An analysis of these scores found that there was a strong tendency for Group Ext to consume more Vin than Group Control, $F(2,24) = 3.63$, $p = 0.08$. The groups did not differ in consumption of Vin on the first compound trial, $F(1,14) = 1.19$, $p > 0.25$; but there was a difference on the second compound trial, $F(1,14) = 5.50$, $p < 0.05$. Vinegar produced a poorer conditioned taste aversion for Group Ext as a result of
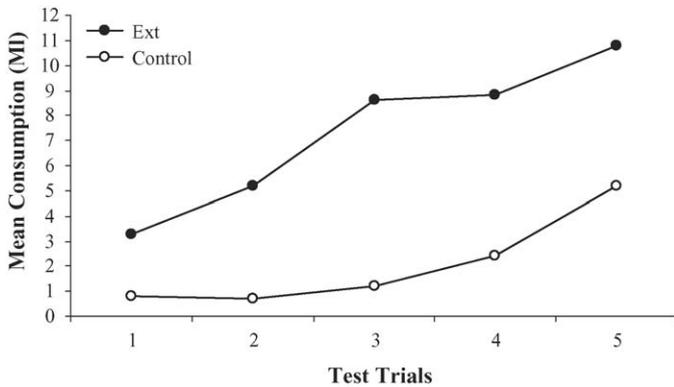
Fig. 2. Mean intake on the test trials of Experiment 2.

the first compound conditioning trial, thereby revealing a slow reacquisition effect for an extinguished CS (see Bouton, 1986).

The test data are shown in Fig. 2. During the test on Vin, Group Ext consumed significantly more Vin than those in Group Control. This was confirmed by an ANOVA which produced a main effect of Group, $F(1, 14) = 6.27$, $p < 0.03$. There was also a main effect of Days, $F(4,56) = 9.49$, $p < 0.0001$; but no significant Group × Days interaction, $F(4,56) = 1.56$, $p > 0.15$.

These results show that a CS given three extinction trials following conditioning and prior to compound conditioning is relatively poor at acquiring manifest associative strength on the compound conditioning trials. Because it can be assumed that the two elements of the stimulus compound compete for manifest associative strength on the compound trial (but see Barnet et al., 1993, for an alternative interpretation as to the type of competition that occurs on such trials), the poor acquisition of learning for the pretrained CS presumably allows for more acquisition to the added CS. Hence, the results of Experiment 2 are compatible with those of Experiment 1 in viewing an extinguished CS as poor at competing for manifest learning.

4. Experiment 3

The occurrence of spontaneous recovery following extinction reveals that a retention interval can cause a CR to re-emerge (Pavlov, 1927). It is also known that a retention interval after extensive extinction treatment can cause the CR to re-emerge quickly if the CS is again paired with the US. That is, the slow reacquisition effect ordinarily observed following extensive extinction (Bouton, 1986) can be reversed by the placement of a retention interval between extinction and reacquisition (Calton et al., 1996; Schachtman et al., 2000). Experiment 3 examined whether a retention interval would enhance the competing ability of an extinguished CS given that such a treatment increases the CR (i.e., spontaneous recovery) as well as facilitates reacquisition to the CS.

Experiment 3 differed from Experiments 1 and 2 in that six extinction trials were employed rather than three in order to augment the influence of the presumed CS–noUS learning that occurs during the extinction phase. Also, saccharin was used as the initially conditioned and extinguished flavor for Ext groups while vinegar served as the target CS since saccharin has been used in earlier work conducted in our laboratory which examined the effects of a retention interval on reacquisition of an extinguished CS (Calton et al., 1996; Schachtman et al., 2000). Finally control conditions consumed tap water instead of Coff in the initial phases of the study because earlier studies have found differential generalization effects among flavors when a retention interval is manipulated (e.g., Kraemer and Roberts, 1984).

4.1. Method

4.1.1. Subjects

Twenty-two naive, male, Sprague–Dawley served as subjects. At the start of the study, the range of the body weights was 265–337 g. The rats were obtained from Sasco and maintained as in Experiments 1 and 2.

4.1.2. Apparatus and procedure

The apparatus was similar to that of Experiments 1 and 2 except where noted. A 0.1% (w/v) saccharin solution (Sac) (Sigma Co.) and Vin were used in this experiment. The design of Experiment 3 is summarized in Table 3. Rats in Group Ext-RI ($n = 6$) received conditioning on Day 1 with a 15-min exposure to Sac followed by an i.p. injection of a 0.3 M LiCl solution at 13 ml/kg body weight (i.e., the dose used in our previous work on extinction and retention interval effects) and then followed by extinction with this flavor on Days 3–8. Group Control-RI ($n = 5$) received identical treatment on these days except that they received tap water from the drinking tubes during conditioning and extinction. The rats in these groups then received a 21-day retention interval on Days 9–29.

Group Ext-noRI ($n = 6$) received its initial conditioning treatment on Day 22 when they received Sac followed by an injection of LiCl just as Group Ext-RI received on Day 1 and this treatment was followed by extinction with this flavor on Days 24–29 as Group Ext-RI experienced on Days 3–8. Group Control-noRI ($n = 5$) drank tap water from drinking tubes during the conditioning trial on Day 22 and were then given tap water for six days on Days 24–29 just as Group Control-RI had received earlier.

During the compound conditioning phase on Day 30, all rats received 7.5 min access to Vin followed immediately by 7.5 min access to Sac. Rats were then received an i.p. injection of 0.3 M LiCl at 1.33% body weight. Testing occurred on each of Days 32–36 in the home cage. All rats received 15 min access to Vin during this phase. No treatments occurred on Days 2, 23, and

Table 3
Design of Experiment 3

Group	Conditioning	Extinction	Retention interval	Compound conditioning	Test
Ext-RI	Sac+	Sac−	21 days	VinSac+	Vin−
Ext-noRI	Sac+	Sac−	0 days	VinSac+	Vin−
Control-RI	W+	W−	21 days	VinSac+	Vin−
Control-noRI	W+	W−	0 days	VinSac+	Vin−

Note: Sac = Saccharin; Vin = Vinegar; W = Water; "+" = LiCl; "−" = no LiCl; Retention interval = number of days lacking experimental treatments.

31 to allow rats receiving injections to recover. All unspecified details were the same as those in earlier experiments.

4.2. Results and discussion

Two rats (one from Group Ext-noRI and one from Group Cont-noRI) were removed from the study due to illness. Groups Ext-noRI and Ext-RI consumed 12.5 ($\pm$1.8) and 9.7 ($\pm$0.8) ml, respectively, of Sac on their initial conditioning trial, and there were no differences in consumption, $F(1,16) = 2.20$, $p > 0.15$.

Groups Ext-noRI and Ext-RI consumed 1.1 ($\pm$0.6) and 0.8 ($\pm$0.1) ml, respectively, on the first extinction trial and there were no differences in these group means, $F(1,9) = 2.09$, $p > 0.15$. Groups Ext-noRI and Ext-RI consumed 5.4 ($\pm$2.0) and 9.7 ($\pm$2.1) ml, respectively, on the final extinction trial. When comparing Sac consumption on the first trial of the extinction phase to the sixth and final extinction trial, there was no significant main effect comparing the two groups given Sac, $F(1,9) = 1.57$, $p > 0.20$, although a significant effect of Day did occur, $F(1,9) = 22.23$, $p < 0.001$, and the Group × Day interaction was not significant, $F(1,9) = 2.77$, $p > 0.05$. This indicates that the two groups given Sac consumed a comparable amount of Sac.

Groups Ext-RI, Ext-NoRI, Control-RI, and Control-noRI consumed 5.5 ($\pm$0.4), 5.0 ($\pm$0.7), 5.4 ($\pm$0.4), and 4.7 ($\pm$0.6) ml of Vin, respectively, on the compound conditioning trial; and 7.0 ($\pm$0.4), 4.1 ($\pm$0.0), 4.0 ($\pm$1.0), and 2.7 ($\pm$0.9) ml, respectively, of Sac on this trial. Analysis of Vin (the target CS) consumption on the compound conditioning trials found no significant differences among groups, $F < 1$. A similar analysis conducted on Sac consumption on compound conditioning trials obtained a main effect of the solution experienced during Phases 1 and 2 (Ext versus Control) [$F(1,16) = 5.51$, $p < 0.05$] and a main effect of retention interval [$F(1,16) = 5.03$, $p < 0.05$], but no Flavor × Retention Interval interaction, $F < 1$. Rats in the control conditions likely consumed less Sac on this trial because it had not undergone six CS-alone exposures (i.e., more neophobia). A specific comparison showed that Group Ext-noRI consumed less Sac than Group Ext-RI, $F(1,9) = 5.36$, $p < 0.05$. This effect is surprising given that the latter group received Sac extinction much more recently.

The data from the five test trials are shown in Fig. 3. An overall ANOVA showed a main effect of retention interval [$F(1,16) = 6.14$, $p < 0.025$], but no main effect of Flavor [$F(1,16) = 1.18$, $p > 0.25$] nor any significant interactions, $F < 1$. It is clear from the figure that the groups consumed little of the Vin solution on the initial test trial and group differences emerged over the course of testing. A simple factorial analysis comparing Groups Ext-noRI and Control-noRI was conducted and showed that Group Ext-noRI consumed significantly less Vin than Group Control-noRI [$F(1,7) = 7.47$, $p < 0.03$] during the test trials. These differences occurred on Test Trials 3–5 as revealed by pairwise comparisons [$Fs(1,30) > 4.18$, $ps < 0.05$], but not Test Trials 1 or 2 [$Fs(1,30) < 1.46$, $ps > 0.20$]. A similar comparison of the two control conditions yielded no main effect of Group [$F(1,7) = 1.38$, $p > 0.25$] nor a Group × Day interaction [$F(4,28) = 1.09$, $p > 0.35$]. These results confirm the finding
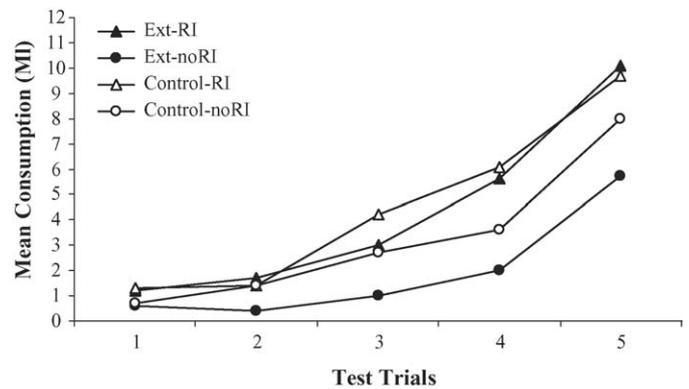

Fig. 3. Mean intake on the test trials of Experiment 3.

obtained in Experiment 1 such that a group given extinction to an element of the compound (and no retention interval) allowed for greater manifest learning to the added element relative to a control condition for which both CSs were novel at the time of compound conditioning.

A comparison of the two conditions given conditioning and extinction with Sac (Groups Ext-noRI and Ext-RI) showed that Group Ext-noRI drank significantly less Vin than Group Ext-RI, $F(1,9) = 5.67$, $p < 0.05$. These differences occurred on Test Trials 4 and 5 as revealed by pairwise comparisons [$Fs(1,22) > 7.90$, $ps < 0.02$], but not on the Trials 1–3 [$Fs(1,22) < 2.40$, $ps > 0.10$]. Hence, recent extinction of Sac in Group Ext-noRI allowed for good manifest learning about Vin for Group Ext-noRI relative to Ext-RI–the latter group having received a retention interval prior to compound conditioning. A comparison between Groups Ext-RI and Control-RI showed no significant difference between the groups, $F < 1$. The greater consumption of Vin by Group Ext-RI than by Group Ext-noRI is consistent with facilitated retrieval of the Sac–US association, presumably by hindered retrieval of the Sac–noUS association acquired during extinction in Group Ext-RI, which would allow Sac to better compete with Vin for manifest learning. It is known that a retention interval causes recovery of the CR (spontaneous recovery, Pavlov, 1927) and reverses the slow reacquisition effect (Calton et al., 1996; Schachtman et al., 2000). The current results demonstrate that a retention interval can also enhances the competitive ability of an extinguished CS.

5. General discussion

Classical conditioning effects involving competition between conditioned stimuli have been critical in influencing associative learning theory (e.g., Barnet et al., 1993; Dickinson and Burke, 1996; Miller and Matute, 1996; Rescorla and Wagner, 1972; Van Hamme and Wasserman, 1994). Examination of the effect of an extinguished CS on associative competition has been lacking. This may be due in part because the associative processes underlying extinction of conditioned responding have not been completely delineated and so its effect on stimulus competition has not been clear. We know from phenomena such as spontaneous recovery, disinhibition, reinstatement effects, and renewal effects that extinction does not result in a complete loss of the

CS–US association, but the effects of an extinguished CS on competition with another CS has not been established.

The present experiments show that a CS that has undergone conditioning and extinction is subsequently impaired in its ability to compete with another CS (see also Kamin, 1969) and that such impairment can be improved with a retention interval. These results are difficult for current learning theories to accommodate. Theories of learning that explain extinction as unlearning of the CS–US excitatory association (e.g., Rescorla and Wagner, 1972) are challenged in explaining these results.

According to these theories, a CS that has previously undergone conditioning and complete extinction has no associative strength and should be at no advantage or disadvantage with respect to acquisition during compound conditioning relative to a condition for which both CSs are novel at the time of compound conditioning. Also, according to these models, because extinction produces unlearning of the CS–US association, a retention interval after extinction should be irrelevant with respect to the competing ability of the extinguished CS and conditioned responding to it.

As mentioned above, Rescorla's (1993) more recent view of extinction (see also Rescorla, 1996a, 1996b) denies that an extinguished CS is at a disadvantage when competing with another CS on compound conditioning trials. This theory states that, during extinction, an inhibitory CS–CR association is formed and this association should not influence associative competition with another CS. According to Rescorla's view, CS–US associations remain functional throughout extinction training, although the CS no longer evokes a strong CR due to its inhibitory association with the CR. Clearly, the present results are not consistent with this view of extinction.

These results can be explained, at least in part, by attentional theories, such as those proposed by Mackintosh (1975) and Pearce and Hall (1980). According to these theories, extinction produces a decrease in the associability of the CS or, in other words, a decrease in the attentional processing received by the CS. Therefore, an extinguished CS will be slow in reacquiring an association with the US and should be therefore poor at competing with another CS during compound training (since stimulus competition for associative strength is assumed). However, these attentional theories must explain why interposing a retention interval after extinction should recover the competing ability of the extinguished CS. A retention interval could be viewed as enhancing associability to a CS (Robbins, 1990).

Retrieval models (Miller et al., 1986) claim that extinction results in the formation of a CS–noUS association and this association prevents retrieval of the CS–US association formed during original conditioning, which results in the poor CR seen during extinction. With respect to CS competition, retrieval-interference theories could assert (described below) that the processing that occurs during extinction somehow renders the CS–US association poor at competition (see McPhee et al., 2001; Schachtman et al., 1992 for discussions of this view). Such theories could allow for CS–noUS associations to hinder the competitive ability of a CS. Within this view, an explanation of the results of Experiments 3 and 4 requires that the processing that causes this poor competitive ability to be reversed by

a retention interval. If the formation of a CS–noUS association formed during extinction renders the CS–US less retrievable (and hence poor competitive ability occurs), then the retention interval might allow the CS–US association to become accessible again and return a CS's competitive ability.

The results from Experiment 3, in showing the effects of a retention interval on conditioning, are not an isolated case with respect to the effects of such intervals. The increase in associative competition by the pretrained CS after a retention interval is consistent with other phenomena in which the behavioral impact of the CS–US association is enhanced, including spontaneous recovery (Brooks et al., 1999; Rosas and Bouton, 1996) and renewal (Chelonis et al., 1999). Also, it is quite likely that—to the extent that associative competition mirrors spontaneous recovery—we would have seen poorer associative competition by an extinguished CS if a longer interval had been used between the conditioning trial on Day 1 and the Phase 2 extinction phase (see Rescorla, 2004).

Schachtman et al. (1992) found that US reinstatement following extinction of a preconditioned CS improved the CS's competitive ability. Hence, the present retention interval potentially served much like the US reinstatement treatment in the Schachtman et al. study by enhancing retrieval of the CS–US association and thereby increasing the competitive potential of the CS. That is, while it can be presumed that a US reinstatement treatment acts to enhance the retrievability of the CS–US association and, thus, improve competitive potential (Gustavson et al., 1992; Schachtman et al., 1992), the present results showed that a retention interval may have produced a similar effect.

The retention interval administered for Group Ext-RI in the present Experiment 3 may have made the CS–noUS association less accessible, thereby mirroring Kraemer's (e.g., Kraemer et al., 1991; Kraemer and Spear, 1992) effect on performance to a CS given latent inhibition treatment followed by a retention interval. McPhee et al. (2001), using a fear conditioning procedure, administered CS-alone exposures, followed by CS–US pairings, then compound conditioning with that CS and an added CS, and finally tested on the CS added during compound conditioning. A group given a retention interval just prior to compound conditioning did not differ from those not given such an interval. Hence, that report found no effect of a retention interval on the competitive ability of a CS that received the same treatment as the present experiments except that the CS-alone phase preceded (rather than followed) the CS–US pairings. Consequently, dissimilar effects obtained by McPhee et al. and the present ones are surprising for those that have suggested that latent inhibition and extinction may have similar underlying mechanisms (Kraemer and Spear, 1992; Miller et al., 1986). However, similar to the present effects using an extinguished CS, Carr (1974) reported that a latent inhibitor (a group given CS-alone presentations prior to compound conditioning) is poor at associative competition (see also Revusky et al., 1977).

One other mechanism that can explain the present results should be noted. The pretrained CS A in Experiments 1 and 2 may have been capable of supporting second-order conditioning to CS B and this process could have contributed to the relatively stronger CR observed for such conditions compared to

the control conditions. However, this mechanism does not readily account for the retention interval effect of Experiment 3.

Regardless of the theoretical implications of the present set of results, they add further knowledge to the growing evidence showing the impaired competitive ability of an extinguished CS (Kamin, 1969). Many interactions among CSs (such as blocking, overshadowing and second-order conditioning) have been found to involve retained but poorly expressed associations (Barnet et al., 1997; Kasprow et al., 1982; Schachtman et al., 1983). The present findings are consistent with other findings regarding the poor ability of unexpressed associations (with respect to showing a CR) at limiting associative strength to other CSs. For instance, an association that has been "blocked" by another CS is poor itself at blocking another CS or supporting second-order conditioning to another CS (McPhee et al., 2001; Rauhut et al., 1999; Williams, 1996; see also Denniston et al., 2003). The results of the present experiments bid for additional empirical efforts in order to better understand the mechanisms that mediate the interaction between conditioned stimuli and the role of retention on such interactions.

Acknowledgements

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