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Failure of serial taste–taste compound presentations to produce overshadowing of extinction of conditioned taste aversion

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ABSTRACT

Two experiments were conducted to study overshadowing of extinction in a conditioned taste aversion preparation. In both experiments, aversive conditioning with sucrose was followed by extinction treatment with either sucrose alone or in compound with another taste, citric acid. Experiment 1 employed a simultaneous compound extinction treatment and found results indicative of overshadowing of extinction. By contrast, Experiment 2, in which extinction treatment involved serial compound presentations, failed to obtain evidence of overshadowing of extinction. The results of Experiment 2 indicate that the serial presentation of two tastes was processed as equivalent to the separate presentation of the tastes. The results are discussed in relation to: (1) Convergent evidence from research on latent inhibition, (2) competing theories of learning and, (3) their possible adaptive value in food-selection learning.

Nonreinforced exposure to a previously conditioned stimulus results in a reduction of the conditioned response, an effect known as *extinction* (Pavlov, 1927). Extinction of conditioned responding is a robust effect that has been observed in multiple classical (and operant) conditioning preparations. One such preparation involves the pairing of a novel taste with a noxious consequence, such as illness caused by the injection of an emetic, which produces the development of aversive responding to the taste (e.g., Garcia, Kimeldorf, & Koelling, 1955; Garcia & Koelling, 1966). Following a taste-illness pairing, taste-alone presentations result in the gradual extinction of conditioned aversion to the taste, as indicated by a progressive increase in its consumption.

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A number of studies have found that extinction of taste aversion can be impaired by the concurrent presentation of a second taste during nonreinforced exposure – an effect known as *protection from extinction*. In these studies, a conditioning treatment consisting of the pairing of a target taste (X) with an emetic (i.e., lithium chloride or LiCl, an X → LiCl pairing) is followed by an extinction treatment, consisting of exposure to the target taste in the absence of any noxious consequence (i.e., X → no LiCl trials). For the critical condition, however, target taste X is accompanied by a second taste (A) during the extinction treatment (i.e., AX → no LiCl trials). Protection from extinction of the aversive response elicited by taste X has been obtained when, prior to its compound nonreinforced exposure with taste X, taste A had also been paired with LiCl (i.e., when tastes A and X were both excitors of illness prior to their compound extinction treatment; e.g., Pineño, 2007; Pineño, Zilski, & Schachtman, 2007), as well as when taste A's conditioned aversion had been extensively extinguished (i.e., when taste A was a putative inhibitor of illness prior to its compound extinction treatment with X; e.g., Calton, Mitchell, & Schachtman, 1996; Pineño, 2007). Thus, in these studies the addition of taste A during nonreinforced presentations of taste X resulted in protection from extinction of aversion to taste X, regardless of taste A's associative status (i.e., excitatory or inhibitory).

A third kind of treatment that is able to yield protection of extinction comprises the concurrent presentation of a novel stimulus (i.e., with a neutral associative status) during extinction treatment – an effect known as *overshadowing of extinction* due to its procedurally mirroring the overshadowing effect, typically studied in the acquisition of a conditioned response (Pavlov, 1927). In a typical overshadowing treatment, a target conditioned stimulus, CS X, is paired with the unconditioned stimulus (US) in the presence of a second CS, A (i.e., AX → US pairings). When presented alone at test, CS X elicits a weak response compared to a control condition in which its pairings with the US occurred without the concurrent presence of CS A (i.e., X → US pairings). Analogously, in an overshadowing of extinction treatment, compound AX → no US presentations hindered extinction of conditioned responding to X, relative to a condition given X → no US presentations.

To date, very few studies have reported evidence of overshadowing of extinction. The first of these studies was conducted by Kamin (1968) using a conditioned suppression preparation with rats. More recently, Rescorla (2003) also reported this effect in an autoshaping preparation with pigeons (Experiment 3) and a magazine approach preparation with rats (Experiment 4). This effect was also found by Calton et al. (1996, see comparison between Groups Neut and X-alone in Experiment 4) in a conditioned taste aversion preparation. Unfortunately, this phenomenon was not systematically investigated in the previous studies, especially in those of Rescorla and Calton et al., in which this treatment merely provided a control condition. However, this phenomenon was central to a series of experiments performed by Taylor and Boakes (2002, Experiments 3 and 4), who showed that the presentation of saline during extinction treatment with sucrose impaired extinction of an aversion to sucrose. In their Experiment 3, overshadowing of extinction of aversion to sucrose (i.e., 1% concentration) was detected with a relatively high concentration (1%), but not a lower concentration (0.2%) of saline. Thus, the relative intensity or salience of the stimuli in compound determined the occurrence of overshadowing, a result in line with research on overshadowing of acquisition (e.g., Mackintosh, 1976). Furthermore, in their Experiment 4, Taylor and Boakes compared the effectiveness of one vs. two compound extinction trials in yielding overshadowing of extinction. This comparison was made in an attempt to contrast different families of learning theories, which disagreed regarding the effectiveness of a single compound extinction trial in producing detectable overshadowing of extinction. Single-trial overshadowing (both in acquisition and in extinction) is a possibility within the framework of comparator theory (e.g., Denniston, Savastano, & Miller, 2001) and configural theories (e.g., Pearce, 1987, 1994), whereas at least two compound trials are required in the framework of most traditional associative theories (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981) for the occurrence of overshadowing. Taylor and Boakes (Experiment 4) found overshadowing of extinction following two, but not one, compound extinction trials, thereby lending support to the latter class of theories.

The lack of evidence of one-trial overshadowing of extinction in the study of Taylor and Boakes (2002) is important because it rules out the possibility that their results were caused by generalization decrement – a basic learning phenomenon consisting of a decrease in responding that occurs

when the stimulus presented in an experimental phase does not completely match the stimulus previously presented in another phase. A generalization decrement process is formally incorporated in the framework of configural theories (e.g., Pearce, 1987, 1994; for models able to account for a series of effects typically viewed as configural/perceptual phenomena from a purely elemental perspective, see Rescorla, 1973; Wagner & Brandon, 2001). From this viewpoint, simultaneous compound presentations of two stimuli, A and X, promote processing of the AX compound as a configural unit or perceptual whole, that is, as a new stimulus that resembles both A and X, but that is fundamentally different from the mere addition of its constituents. Overshadowing then results from a generalization decrement, or a decrease in responding due to the partial similarity between the stimuli presented in training (the AX configuration) and testing (the X configuration). A configural account for the results of Taylor and Boakes (2002; see also Calton et al., 1996), was especially relevant when considering that these studies were performed using a conditioned taste aversion preparation. In this preparation, the simultaneous presentation of two tastes not only implies receiving two tastes at the same time, but also in the same bottle, mixed in a single solution – a solution that could easily be processed as a brand new perceptual whole. (This is not to say that the constituent elements in a cocktail containing two or more tastes cannot possibly be identified and processed separately. Rather, this means that, among the all possible stimulus compounds, those involving tastes are prime candidates for configural processing.)

Taylor and Boakes (2002) rejection of the contribution of a generalization decrement based on a failure to obtain single-trial overshadowing of extinction has even deeper implications, given that a single conditioning trial has been reported to suffice in overshadowing of acquisition (e.g., Cole, Oberling, & Miller, 1999; James & Wagner, 1980; Mackintosh & Reese, 1979; Revusky, 1971). This discrepancy thus suggests that these two phenomena rely on different processes, with generalization decrement possibly playing a role in overshadowing of acquisition, but not in overshadowing of extinction. Nevertheless, converging evidence from different sources is necessary before we can definitely rule out the role of generalization decrement in overshadowing of extinction. An alternative strategy to evaluate this possibility consists of trying to preclude the occurrence of a generalization decrement altogether. This approach has been typically followed in studies of overshadowing of acquisition of a taste aversion, by employing serial, instead of simultaneous, taste–taste compound presentations during a conditioning treatment (e.g., Kaye, Gambini, & Mackintosh, 1988; Nakajima, Ka, & Imada, 1999; Schachtman, Kasprow, Meyer, Bourne, & Hart, 1992). In a serial compound treatment, taste X is presented alone (although preceded or followed by taste A) and, therefore, it should perfectly match the presentation of taste X at test, thereby rendering the role of a generalization decrement in the results highly unlikely. Unfortunately, no study has yet been conducted to ascertain if overshadowing of extinction can also be observed with serial taste–taste compound presentations during extinction treatment. The present experiments were carried out in an attempt to fill this gap. In the present experiments, animals received aversive conditioning with a sucrose solution followed by an extinction treatment with sucrose, either alone or together with the presentation of a citric acid solution. Experiment 1 used a simultaneous compound presentation during extinction, whereas Experiment 2 used a serial compound presentation. If overshadowing of extinction was found in these experiments, low consumption of sucrose (i.e., indicative of strong aversion) should be observed at test in the conditions given compound presentations of citric acid and sucrose during extinction, relative to the conditions given sucrose-alone presentations.

Experiment 1

Before attempting to determine whether overshadowing of extinction can be obtained with the serial presentation of two tastes during an extinction treatment, it must be first established that such an effect can be detected with simultaneous compound presentations with our experimental parameters (e.g., nature and concentration of the tastes). Towards this purpose, Experiment 1 compared extinction of conditioned aversion to sucrose in a condition given sucrose-alone presentations (i.e., Group Suc)

with that of a condition given simultaneous presentations of citric acid[1] and sucrose during the extinction treatment (i.e., Group Cit + Suc).

Methods

Subjects

The subjects were 16 Wistar, naïve, young adult rats (8 males and 8 females), born in our laboratory. Rats were 94 days old at the beginning of the experiment, and their body weights ranged from 400 to 462 g (M = 438.50, SEM = 7.16) for males and from 231 to 288 g (M = 248.00, SEM = 6.39) for females. The animals were housed individually in 48.26 × 26.67 × 20.32 cm Plexiglas cages on a 12:12-h light:dark cycle (from 10:00 to 22:00 h), with all the experimental sessions occurring during the light period. Subjects had free access to food in the home cage. Prior to initiation of the experiment, water availability was progressively reduced to 30 min per day, provided approximately 1 h after any scheduled treatment. For 2 weeks prior to initiation of the experiment and until its termination, subjects were handled for 30 s 2–3 times a week. All procedures were approved by the Hofstra University Institutional Animal Care and Use Committee.

Apparatus

All the experimental manipulations were conducted in the Plexiglas home cages. The animals were maintained in the laboratory since their birth until termination of the experiment with no interruption. Daily access to water was provided in 500-ml plastic bottles fitted with stainless steel spouts, attached to the front of each cage. In the experimental sessions, liquid rations were provided in 8 oz (i.e., approximately 236.5 ml) glass bottles fitted with stainless steel spouts containing ball bearings, also attached to the front of each cage. The amount of liquid intake was assessed by the difference between bottle weight before and after the liquid presentations (in all our reports, it was assumed that 1 g = 1 ml).

Two distinct tastes were employed in this study, a 5% (wt/vol, 0.14 M) sucrose solution, and a 1% (wt/vol, 0.05 M) citric acid solution (for a parametric study employing these solutions, see Miller & Holzman, 1981). All solutions were made using tap water at room temperature (20 °C/68 °F). Gastrointestinal illness was induced by a 15 ml/kg of body weight intraperitoneal (i.p.) injection of 0.12 M lithium chloride (LiCl). All solutes were obtained from Sigma–Aldrich Chemie GmbH (Steinheim, Germany).

Procedure

The design of Experiment 1 is summarized in Table 1. Prior to the start of the experiment, subjects were assigned to one of two experimental groups, matched for body weight (n = 8, each group containing 4 males and 4 females). Unless explicitly stated otherwise, all subjects were given a single 10-min experimental session per day, which started at approximately 12:00. Also, all subjects received additional 20-min access to tap water soon after the session. Consumption during each session was recorded.

Pretraining. On Days 1–4, tap water was presented with the glass bottle. This treatment acclimated subjects to drinking from the lick tubes at the daily treatment time. Also, intake during pretraining served to ensure that previous assignment of animals to the experimental groups based on matching for body weight led to matching intake; if necessary, some animals could be reassigned to a different group.

[1] Citric acid was chosen as the nontarget taste due to its inherently aversive motivational value, which ensured low consumption of this solution (e.g., Miller & Holzman, 1981). This was not necessary in Experiment 1, but it was critical in Experiment 2, in which the tastes were presented in a serial compound (i.e., citric acid followed by sucrose) and, hence, it was required that the animals consumed low volumes of the first solution in the compound (i.e., citric acid) in order to remain relatively thirsty prior to the presentation of the second solution in the compound (i.e., sucrose).

Table 1
Design of the experiments.

Group	Conditioning (Day 5)	Extinction (Days 7–9)	Test 1 (Day 10)	Test 2 (Day 11)
Experiment 1				
Suc	1S → LiCl	3 S	1S	1C
Cit + Suc	1S → LiCl	3 C + S	1S	1C
Experiment 2				
Suc	1S → LiCl	9 S	1S	1C
Cit	1S → LiCl	9 C	1S	1C
Cit–Suc	1S → LiCl	9 C → S	1S	1C

Notes: S = sucrose solution; C = citric acid solution; LiCl = lithium chloride i.p. injection. ' → ' means 'immediately followed by' and '+' means 'mixed with' (i.e., simultaneous compound). The numbers denote the number of presentations of each trial type in each phase. See text for further details.

Conditioning. Conditioning treatment took place on Day 5. On this day, all subjects received presentation of the sucrose solution, followed immediately by an i.p. injection of LiCl, after which the animals were immediately returned to the Plexiglas home cage. Day 6 consisted of a recovery day, on which tap water was presented with the glass bottle, while allowing the subjects to recover from the impact of the LiCl injection.

Extinction. Extinction treatment took place on Days 7–9, on which Groups Suc and Cit + Suc received a 10-min presentation of the sucrose solution, either alone (Group Suc) or in simultaneous compound with citric acid (Group Cit + Suc), both followed by no LiCl injection.

Test. Testing took place on Days 10 and 11. On these days, all subjects received a 10-min presentation of sucrose (Day 10) or citric acid (Day 11). An alpha level of $p < .05$ was adopted for all statistical analyses.

Results and discussion

Conditioning and extinction treatments

The results from conditioning and extinction phases are depicted in the top panel of Fig. 1. Groups Suc and Cit + Suc consumed sucrose in comparable amounts during conditioning, as shown by a *t*-test, $p > .67$. On the first extinction day, consumption of sucrose (Group Suc) and the solution containing citric acid and sucrose (Group Cit + Suc) was lower than consumption of sucrose on the conditioning day, as shown by a 2 (Group) × 2 (Day) analysis of variance (ANOVA), which yielded a main effect of day, $F(1, 14) = 165.88$, $p < .01$, but no main effect of group, $p > .55$, nor an interaction, $p > .82$. On Extinction Days 1 and 2, Groups Suc and Cit + Suc consumed their corresponding solutions in comparable amounts. However, on Extinction Day 3, consumption was appreciably higher in Group Suc than in Group Cit + Suc. A 2 (Group) × 3 (Day) ANOVA on the consumption during extinction treatment showed main effects of group, $F(1, 14) = 6.47$, $p < .05$, and day, $F(2, 28) = 70.20$, $p < .01$, as well as a Group × Day interaction, $F(2, 28) = 20.89$, $p < .01$. Pairwise comparisons confirmed that the source of this interaction was the higher consumption of Group Suc than of Group Cit + Suc on Extinction Day 3, $F(1, 14) = 14.50$, $p < .01$, along with the comparable consumption on Extinction Days 1 and 2, $ps > .20$.

Test

The bottom panel of Fig. 1 depicts the results of test of sucrose and citric acid. Separate analyses were conducted on each test of sucrose and citric acid, showing that Group Suc consumed more sucrose, $t(14) = 5.38$, $p < .01$, but less citric acid, $t(14) = 4.35$, $p < .01$, than Group Cit + Suc. These results therefore show that extinction of conditioned aversion to sucrose was impaired in Group Cit + Suc relative to Group Suc, presumably due to the concurrent presentation of citric acid during extinction trials in Group Cit + Suc. That is, Experiment 1 found evidence indicative of overshadowing of extinction.

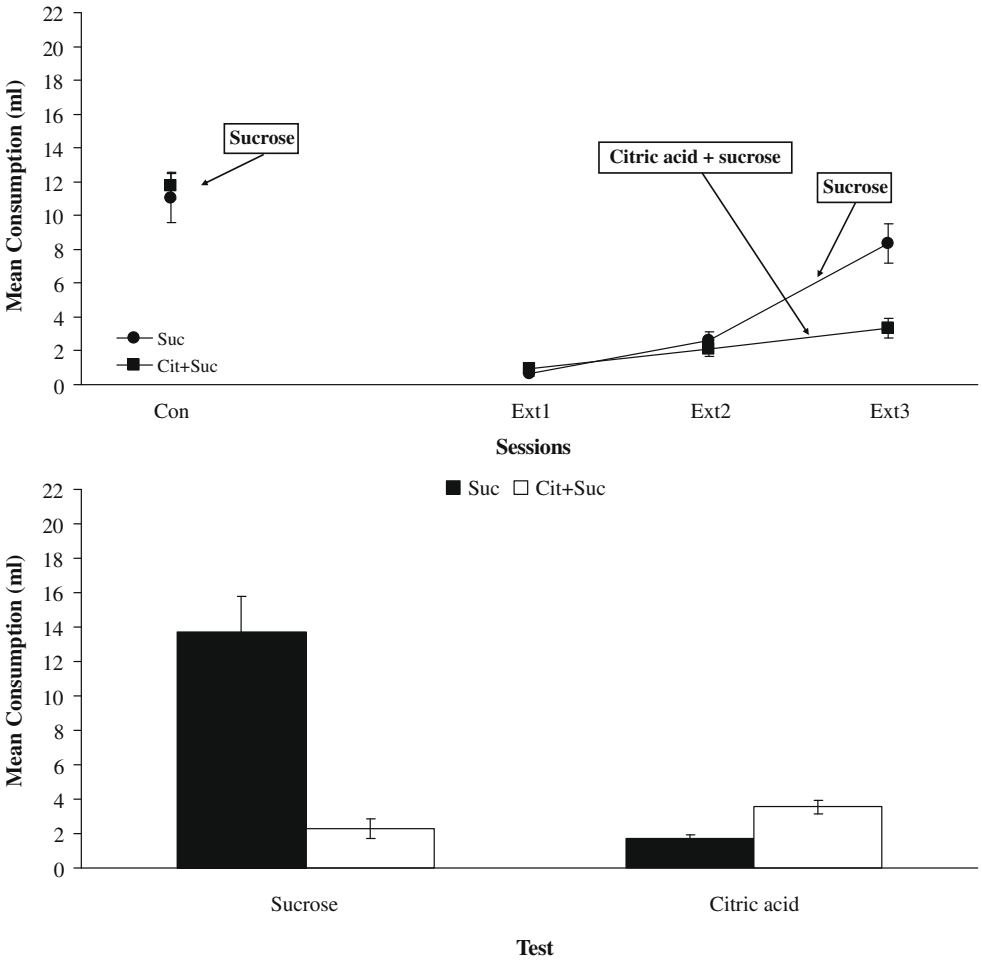

Fig. 1. Experiment 1. Top panel: mean consumption of the sucrose solution and the solution containing a mix of citric acid with sucrose during conditioning and extinction. Bottom panel: mean consumption at test of sucrose and citric acid. Error bars depict standard error of the means.

The results of the test of citric acid merely reflect differences in familiarity with this taste at test: While Group Cit + Suc was already familiar with citric acid, Group Suc was being exposed to this taste for the first time and, hence, presumably displayed a neophobic reaction (see Miller & Holzman, 1981).

The results of the test of sucrose are open to an alternative interpretation involving differential consumption on the last extinction day. On this day, Group Suc drank more of the sucrose solution than Group Cit + Suc drank of the citric acid and sucrose compound solution. This difference might simply be due to the presence of citric acid, an inherently aversive taste, during extinction of sucrose for Group Cit + Suc. Prior research showed that a conditioned taste aversion is strongly determined by the amount of solution consumed during conditioning (e.g., Bond & Di Giusto, 1975; Bond & Harland, 1975; see also De la Casa and Lubow (1995), for a symmetrical effect of the amount of solution consumed during nonreinforced exposure to a taste prior to conditioning). Consequently, because Group Cit + Suc consumed less sucrose during extinction treatment than Group Suc, it can also be assumed that Group Cit + Suc underwent less extinction of the aversion to sucrose. An implication of this account is that, if the amount of sucrose consumed during extinction determined the amount of sucrose consumed at test, a positive correlation (Spearman R) should be found between the sucrose

consumption scores of extinction and test within each group. The averaged cumulative sucrose consumption was 11.59 ml (*SEM* = 1.68) and 6.40 ml (*SEM* = 1.14) for Groups Suc and Cit + Suc, respectively. This correlation was significant for Group Suc, $R = 0.78$, $p < .05$, but not for Group Cit + Suc, $R = 0.61$, $p > .10$. Thus, these results indicate that, if anything, the amount of sucrose consumed during the extinction treatment influenced sucrose consumption at test for Group Suc, but not for Group Cit + Suc. However, because a nonsignificant correlation was also found in the latter group, there is no strong basis for ruling out this possibility with the present data. This issue will be further discussed in the analysis of the results of Experiment 2.

Experiment 2

Experiment 2 aimed to ascertain if the results of Experiment 1, namely, overshadowing of extinction of a conditioned taste aversion, could also be obtained with serial, instead of simultaneous, compound presentation of the tastes during the extinction treatment. The design of Experiment 2 is summarized in Table 1. In this experiment, two groups received treatment comparable to that of Groups Suc and Cit + Suc in Experiment 1: Group Suc was given sucrose-alone presentations during extinction, whereas Group Cit–Suc received serial presentations of citric acid followed by sucrose.[2] A third group was included that received citric acid-alone presentations (Group Cit). Because this group received no extinction treatment with sucrose, it provided a control condition to assess the amount of extinction undergone by sucrose in both Groups Suc and Cit–Suc. Also, a comparison between Groups Cit and Cit–Suc regarding their consumption of citric acid could render interesting information. For example, if consumption of citric acid at test was only determined by familiarity with this taste, Groups Cit and Cit–Suc should consume comparable amounts of this solution, given that these two groups received identical exposure to citric acid during treatment. By contrast, if citric acid became an inhibitor of illness due to its serial presentation with sucrose during extinction (e.g., a possibility predicted by traditional associative theories; e.g., Rescorla & Wagner, 1972; see also Rescorla, 1999), one could expect to observe higher consumption of citric acid in Group Cit–Suc than in Group Cit (Best, 1975; but see Delamater, Kruse, Marlin, & LoLordo, 1986).

Additionally, in Experiment 2 the extinction treatment comprised a larger number of extinction trials than that in Experiment 1 (i.e., 9 vs. 3 trials). Prior research (Brooks, Bowker, Anderson, & Palmatier, 2003; Calton et al., 1996; Pineño, 2007) showed that, although extinction of a taste aversion can be achieved with a moderate number of extinction trials (i.e., 3 or 5 trials, in these studies), extensive extinction treatment (i.e., 9 or 10 trials, in these studies) can endow the extinguished taste with properties similar to those of a conditioned inhibitor (but see Brooks et al., 2003, for an alternative viewpoint). Extending the extinction treatment is relevant to the present study according to traditional associative models of learning (e.g., Rescorla & Wagner, 1972), which expect compound extinction treatment (either simultaneous or serial) to result in overshadowing of extinction due to the competitive nature of the learning mechanisms they posit. Specifically, as previously mentioned, overshadowing of extinction is proposed to take place due to the added stimulus (i.e., citric acid, in our experiments) acquiring part of the negative or inhibitory associative strength that would otherwise be fully available to the target stimulus (i.e., sucrose, in our experiments). Therefore, according to these models, extending the compound extinction treatment could endow citric acid with detectable inhibitory value, while yielding evidence of impaired extinction of the aversion to sucrose, that is, overshadowing of extinction.

Methods

Subjects and apparatus

The subjects were 24 Wistar, naïve, young adult rats (12 males and 12 females), obtained from Charles River, Inc. (Raleigh, NC). Rats were 75 days old at the beginning of the experiment, and their

[2] Serial compound presentations exclusively consisted of citric acid followed by sucrose. The order in the presentation of the citric acid and sucrose solutions was not counterbalanced because, while it was assumed that the animals would consume (albeit in small amounts) citric acid when given prior to sucrose, consumption of citric acid was expected to be significantly lower following the presentation of sucrose.

body weights ranged from 315 to 387 g (M = 366.41, SEM = 7.24) for males and from 192 to 227 g (M = 206.83, SEM = 2.93) for females. The animals were maintained as in Experiment 1. The apparatus was identical to that of Experiment 1.

Procedure

Pretraining (Days 1–4), conditioning (Day 5), and recovery (Day 6) treatments were identical to those of Experiment 1. Extinction treatment took place on Days 7–15, on which Groups Suc and Cit–Suc received a 10-min presentation of the sucrose solution, followed by no LiCl injection. For Group Cit–Suc, the sucrose solution was immediately preceded by a 10-min presentation of the citric acid solution, whereas for Group Suc, the sucrose solution was presented alone. A third condition, Group Cit, received a daily 10-min presentation of the citric acid solution, followed by no LiCl injection. Testing was conducted on Days 16 and 17. On Day 16, all subjects received a 10-min presentation of sucrose. On Day 17, half of the subjects in each group[3] received a 10-min presentation of citric acid.

Results and discussion

Conditioning and extinction treatments

The top panel of Fig. 2 depicts the results from conditioning and extinction. No appreciable difference was found in the consumption of sucrose during conditioning, an impression that was confirmed by a one-way ANOVA, $p > .91$. Sucrose elicited aversive responding following the conditioning treatment, as shown by a 2 (Group: Suc vs. Cit–Suc) $\times$ 2 (Day) ANOVA comparing sucrose consumption on conditioning day and on the first extinction day, which yielded a main effect of day, $F(1, 14) = 104.93$, $p < .01$, but no main effect of group, $p > .76$, nor an interaction, $p > .73$. More importantly, consumption of sucrose increased during extinction treatment in both Groups Suc and Cit–Suc, although such an increase was more marked in the former group than in the latter. This impression was corroborated by a 2 (Group: Suc vs. Cit–Suc) $\times$ 9 (Day) ANOVA comparing sucrose consumption during extinction, which yielded main effects of group, $F(1, 14) = 5.00$, $p < .05$, and day, $F(8, 112) = 35.74$, $p < .01$, but no significant interaction, $p > .37$. An analogous 2 (Group: Cit vs. Cit–Suc) $\times$ 9 (Day) ANOVA comparing citric acid consumption during extinction yielded a main effect of day, $F(8, 112) = 35.74$, $p < .01$, but no main effect of group, $p > .35$. However, this ANOVA detected a marginally significant interaction, $p > .05$, which was caused by the tendency of Group Cit to increase its consumption of citric acid more rapidly than Group Cit–Suc.

Test

The bottom panel of Fig. 2 depicts the results of the test of sucrose and citric acid. A one-way ANOVA on the consumption of sucrose yielded significant differences, $F(2, 21) = 29.20$, $p < .01$. Pairwise comparisons showed that Groups Suc and Cit–Suc consumed sucrose in similar amounts, $p > .91$, and in amounts higher than Group Cit, $Fs(1, 21) > 43.12$, $ps < .01$. The present results, thus, found comparable consumption in a group given sucrose-alone presentations during extinction (i.e., Group Suc) and a group given serial compound presentations of citric acid and sucrose (i.e., Group Cit–Suc), thereby failing to obtain evidence of overshadowing of extinction. The test of citric acid also found differences among groups, as confirmed by a one-way ANOVA, $F(2, 9) = 4.75$, $p < .05$. Pairwise comparisons showed that these differences were only due to the higher consumption of citric acid by Group Cit relative to Group Suc, $F(1, 9) = 9.42$, $p < .05$. No difference was found between Groups Cit and Cit–Suc in their consumption of citric acid, $p > .22$. Also, the expected difference between Groups Suc and Cit–Suc fell short of significance, $p > .10$.

An additional experiment was conducted in our laboratory, in which compound treatment comprised serial taste–taste presentations (i.e., as in Experiment 2), but with only three extinction trials being given (i.e., as in Experiment 1). This experiment roughly replicated the test results of Experiment 2: Groups Suc and Cit–Suc consumed comparable amounts of sucrose at test (and more than Group

[3] The other half of the subjects were not given citric acid in order to test a hypothesis, secondary to the present study (not described here).

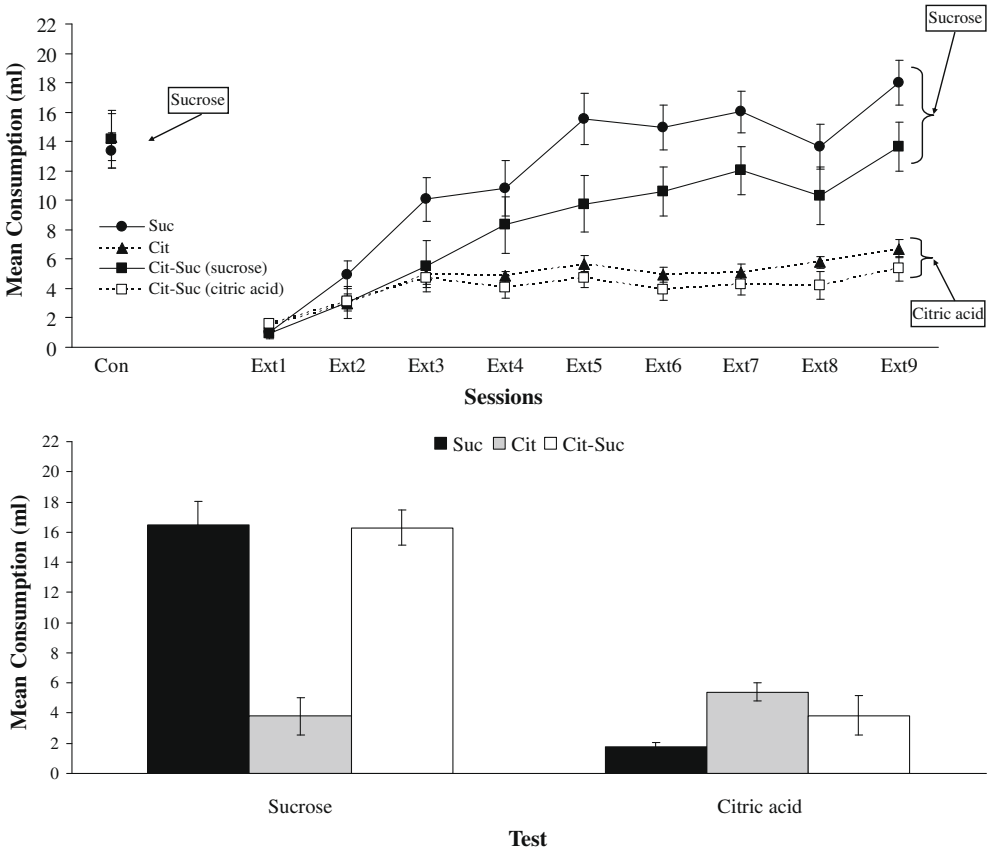

Fig. 2. Experiment 2. Top panel: mean consumption of the sucrose and citric acid solutions during conditioning and extinction. Bottom panel: mean consumption at test of sucrose and citric acid. Error bars depict standard error of the means.

Cit), thereby showing a failure to detect overshadowing of extinction. Thus, the lack of overshadowing of extinction in Experiment 2 cannot be attributed to its use of a larger number of extinction trials, but to its use of a serial taste–taste compound extinction treatment.

Finally, as in Experiment 1, correlations were computed to ascertain if consumption of sucrose at test was determined by the amount of sucrose previously consumed during extinction. In this experiment, the averaged cumulative sucrose consumption was 105.03 ml (*SEM* = 8.52) and 74.17 ml (*SEM* = 10.84), for Groups Suc and Cit–Suc, respectively. As in Experiment 1, a positive correlation was found for Group Suc, $R = 0.85$, $p < .01$, whereas no significant correlation was found for Group Cit–Suc, $R = 0.57$, $p > .13$. Based on the results of both Experiments 1 and 2, it is not clear how the differential consumption of sucrose during extinction could be held accountable for the observed differences in the consumption of sucrose at test in these experiments. While this contribution cannot be discarded based on the present analyses,[4] it is appropriate to state that, even if the differential con-

[4] Experiments 1 and 2 showed comparable differences regarding the consumption of sucrose during extinction, and yet, different results were found at test. This suggests that the amount of sucrose consumed during extinction was not a factor in determining the test results. Nevertheless, this comparison might be flawed due to the large differences in the overall consumption of sucrose during extinction between Experiments 1 and 2. For instance, it could be claimed that, in Experiment 2 (but not in Experiment 1), both groups had consumed enough sucrose during extinction treatment to guarantee maximal consumption during testing (i.e., a ceiling effect).

sumption of sucrose during extinction was a necessary condition for the observation of overshadowing of extinction, it cannot be given the status of a sufficient condition for its occurrence: a simultaneous compound extinction treatment appears to be necessary in order for this effect to occur.

General discussion

The two experiments in this report studied protection from extinction of aversion to a target taste, sucrose, achieved by the compound presentation of a second taste, citric acid, during extinction treatment – an effect typically known as overshadowing of extinction (Taylor & Boakes, 2002). In Experiment 1, the citric acid and sucrose presentations were given in a simultaneous compound, whereas in Experiment 2 the tastes were presented in a serial compound, with citric acid being immediately followed by sucrose. Results indicative of overshadowing of extinction were found in Experiment 1, in which consumption at test of sucrose was lower in the group that had been given simultaneous presentations of citric acid and sucrose (Group Cit + Suc) during extinction compared to the group given sucrose-alone presentations (Group Suc). These results were not obtained in Experiment 2, in which comparable sucrose consumption at test was found in the groups given extinction with sucrose, either alone (Group Suc) or in a serial compound with citric acid (Group Cit–Suc). Also, the results of Experiment 2 found that consumption of citric acid at test was not affected by its having been presented in a serial compound with sucrose (Group Cit–Suc), as indicated by the similar consumption in a group that received citric acid-alone presentations during the extinction treatment (Group Cit).

As mentioned in the Introduction, evidence of overshadowing of extinction is scarce in the literature, being reported only in a few studies (i.e., Calton et al., 1996; Kamin, 1968; Rescorla, 2003; Taylor & Boakes, 2002), and being systematically examined in only one of them (i.e., Taylor & Boakes). By contrast, protection from extinction has been more widely reported in studies in which the extinction treatment comprised the concurrent presentation of a stimulus with prior associative history. For example, protection from extinction has been revealed by the concurrent presentation of a conditioned inhibitor (e.g., Chorazyna, 1962; Lovibond, Davis, & O'Flaherty, 2000; Rescorla, 2003; Soltysik, Wolfe, Nicholas, Wilson, & Garcia-Sanchez, 1983), as well as by the concurrent presentation of a previously extinguished stimulus (e.g., Calton et al., 1996; Pineño, 2007), or even another previously conditioned stimulus (e.g., Lovibond, Davis, & O'Flaherty, 2000; Pearce & Wilson, 1991; Pineño, 2007; Pineño et al., 2007). Interestingly, the studies of Calton et al. and Taylor and Boakes used a conditioned taste aversion preparation, and employed a simultaneous presentation of the tastes during the extinction treatment. That is, these studies were comparable to our Experiment 1, which also found results indicative of overshadowing of extinction. However, no sign of overshadowing of extinction was found in the results of Experiment 2, in which the tastes were presented in a serial compound. Of course, it would be erroneous to categorically conclude from the results of Experiment 2 that overshadowing of extinction cannot be found with a serial taste–taste compound extinction treatment. After all, overshadowing of acquisition of a taste aversion has been reported with serial taste–taste compound presentations (e.g., Kaye et al., 1988; Nakajima et al., 1999; Schachtman et al., 1992). However, the fact remains that an effect (i.e., overshadowing of extinction), which can be easily reproduced with simultaneous compound training, becomes more elusive when the tastes are presented in a serial compound.

The results of Experiment 2 did not find any evidence of overshadowing of extinction with serial taste–taste compound presentations during extinction. As a matter of fact, they did not detect any kind of interaction between the tastes: The presence of citric acid failed to overshadow extinction of the aversion to sucrose and the presence of sucrose failed to endow citric acid with inhibitory value. In other words, the tastes in the serial compound were processed as if they were presented separately; or, alternatively put, they were perceived as being presented independently from each other, instead of as part of a compound. Interestingly, this is not the first study leading to this observation. In a conditioned taste aversion study on the latent inhibition effect (i.e., impaired conditioned response to a stimulus following repeated nonreinforced preexposure; Lubow (1973) and López and Aguado (1992) found that the effectiveness of conditioning of a simultaneous compound of two flavors (i.e., coffee and vinegar) with illness was impaired following preexposure to the simultaneous compound, but not as much following elemental preexposure to the flavors (see also Baker, Haskins, & Hall, 1990,

but see Holland & Forbes, 1980; Lubow, Wagner, & Weiner, 1982). More important for our purposes, López and Aguado also found that the conditioning of a serial compound involving these flavors (i.e., coffee followed by vinegar, or *vice versa*) was similarly disrupted by preexposure to the serial compound and by elemental preexposure to the flavors. López and Aguado summarized their findings with words that could perfectly describe our own findings (i.e., ignoring their reference to the latent inhibition effect, instead of extinction): "From this, it may be inferred that although the animals discriminate between a simultaneous flavor compound and its elements, they treat a serial compound as functionally equivalent to its separate elements. At least in relation to the processes that underlie the latent inhibition effect, serial compounds of flavors do not seem to have properties different from those of their elements, and there is no need to appeal to any feature that emerges as a result of the sequential pairing of these stimuli." (p. 280).

The convergence of the present results with those of López and Aguado (1992) is not surprising given the important similarities between extinction and latent inhibition phenomena. The similarity is obvious, not only at a procedural level (i.e., both treatments comprise CS–US pairings and CS-alone presentations, only in different orders), but also at an explanatory one (i.e., a series of theories have proposed that common mechanisms underlie both phenomena; e.g., Bouton, 1993; Brooks et al., 2003; Kraemer & Spear, 1992). In this vein, the generalization decrement account offered by López and Aguado for their results could also be applied to the present results. In the study of López and Aguado, generalization decrement seemingly occurred from preexposure to conditioning, due to the partial similarity between the separate elements and the simultaneous (but not the serial) compound. In our Experiment 1, a generalization decrement presumably occurred from extinction treatment to test. That is, the extinguished aversion did not fully transfer from the citric acid and sucrose simultaneous compound to the elemental presentation of sucrose. (In Experiment 1, a generalization decrement could have also occurred between conditioning and extinction. However, such decrement was not detectable in the animals' consumption of the compound solution.) In Experiment 2, a generalization decrement was not appreciably detected between the serial presentation of citric acid and sucrose during extinction and the presentation of sucrose at test, presumably because the animals processed the serial compound as the separate presentation of two tastes.

Generalization decrement is not the only available explanation for our results. For example, these results can be readily explained by comparator theory (Denniston et al., 2001), according to which simultaneous compound presentations of A and X enhance the formation of an A–X bidirectional association (i.e., a within-compound association). This association plays a critical role in the observation of overshadowing by allowing the presentation of stimulus X at test to activate the representation of stimulus A, thereby triggering a comparison of the relative strengths of X–US and A–US associations which, in turn, determines the observation of overshadowing. As with configural theory (discussed in the Introduction), it follows from the premises of comparator theory that a treatment involving serial compound presentation should impair overshadowing of extinction. Although this theory does not formally incorporate temporal mechanisms, it could be assumed that the serial presentation of stimulus A followed by stimulus X should produce a weak within-compound association relative to the simultaneous presentation of A and X, merely due to the poor temporal contiguity, or partial/null overlap in the presentation of the stimuli with the serial compound treatment.

Traditional theories of learning (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981) can also explain overshadowing of extinction. According to these theories, the presence of stimulus A limits the loss of associative strength undergone by stimulus X during extinction (i.e., Mackintosh, 1975; Rescorla & Wagner, 1972) or, alternatively, the acquisition of inhibitory strength by X during extinction (i.e., Pearce & Hall, 1980; Wagner, 1981), by absorbing part of the associative change undergone by X. Interestingly, these theories not only posit that A should protect, at least partially, X from extinction, but also that A should become a conditioned inhibitor due to its gaining negative associative strength or inhibitory value (e.g., Rescorla, 1999). As with the comparator model, most of these theories (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) do not incorporate any explicit temporal mechanism (but see Wagner, 1981 SOP model, for a precise real-time theory able to explain the present results). Nevertheless, these models could perfectly account for the failure to observe overshadowing of extinction with serial presentations of the stimuli by merely positing that these presentations were processed by the animals as belonging

to two separate trials (i.e., A-alone trial followed by X-alone trial), instead of a single compound trial (i.e., AX-alone trial). In this case, not only would A be unable to overshadow the extinction undergone by X, but it would also fail to acquire inhibitory strength throughout the serial compound treatment.

In sum, the present results can be explained by various theories of learning, which comprise mechanisms capable of explaining why a taste–taste compound extinction treatment could fail to produce overshadowing of extinction with the serial, but not the simultaneous, presentation of the tastes. However, these theories are silent about the failure of serially presented tastes to interact with each other during an extinction treatment. Although speculative at this point, a possible answer might lay in the rat's evolutionary history. Consider that, in their varied diet (typical of an omnivorous animal), a rat might consume dozens of different foods, usually without any noxious consequence. A food-selection learning mechanism constraining or, more correctly put, filtering the acquisition of information regarding these foods would be of great adaptive value. One such constraint might involve the source of the tastes in taste–taste learning. While it might be worth remembering the compound presentation of different tastes (e.g., sour and sweet tastes) when *simultaneously* consumed in the same food due to their natural connection (e.g., they both were produced by the same fruit), it might not be relevant to do so when these same tastes are *serially* consumed in separate foods, even if both foods were consumed in the same meal. In the latter case, their co-occurrence could be perfectly coincidental (e.g., the animal just happened to encounter a sour fruit first, immediately followed by a sweet fruit), and remembering such co-occurrences would result in storing a tremendous amount of spurious information. The function of the processes involved in this "learning failure" would be, thus, comparable to that of many other learning phenomena, such as latent inhibition (e.g., Lubow, 1973) or blocking (e.g., Kamin, 1968): To filter information from the environment in an attempt to detect lawful regularities, while setting apart information that might be redundant and/or irrelevant.

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