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Extinction with multiple excitors

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Abstract

Four conditioned suppression experiments with rats, using an ABC renewal design, investigated the effects of compounding the target conditioned excitator with additional, nontarget conditioned excitors during extinction. Experiment 1 showed stronger extinction, as evidenced by less renewal, when the target excitator was extinguished in compound with a second excitator, relative to when it was extinguished with associatively neutral stimuli. Critically, this deepened extinction effect was attenuated (i.e., more renewal occurred) when a third excitator was added during extinction training. This novel demonstration contradicts the predictions of associative learning models based on total error reduction, but it is explicable in terms of a counteraction effect within the framework of the extended comparator hypothesis. The attenuated deepened extinction effect was replicated in Experiments 2a and 3, which also showed that pretraining consisting of weakening the association between the two additional excitors (Experiments 2a and 2b) or weakening the association between one of the additional excitors and the unconditioned stimulus (Experiment 3) attenuated the counteraction effect, thereby resulting in a decrease in responding to the target excitator. These results suggest that more than simple total error reduction determines responding after extinction.

Experimental extinction refers to the repeated presentation of a conditioned excitator in the absence of any explicit outcome. This treatment ordinarily results in less conditioned responding to the stimulus, relative to an otherwise comparable conditioned excitator that was not extinguished (Pavlov, 1927). Associative learning models based on total error reduction (e.g., Rescorla & Wagner, 1972) explain this effect by assuming that, during extinction, the conditioned excitator created an expectation of the occurrence of the outcome, which was not fulfilled. Thus, there was a discrepancy between the outcome that was predicted on the basis of the associative status of all of the cues present on that trial (i.e., the conditioned excitator) and the outcome that actually occurred. According to a total error reduction approach, this results in a negative change in the cue's associative status that reduces the amount of predictive error on the following trials. At the end of extinction, weak or no responding should be observed to the extinguished cue because its associative status should be near zero (i.e., erasure). The total error reduction approach further predicts that extinguishing an excitator in compound with another excitator should yield deeper extinction (i.e., less responding at test) than when comparable extinction occurs with the stimulus presented alone. This is because both excitors should contribute to the total expectation of the unconditioned stimulus (US), resulting in a larger amount of predictive error during extinction than when only one excitator is extinguished. Importantly, according to the total error reduction rule and data from Rescorla (2006), it is the total predictive error, not the magnitude of the response that is shown, that is critical in reducing the associative strength

of a conditioned stimulus (CS). Thus, a greater change in the target cue's associative status should occur following extinction with two excitors in compound, relative to one excitor elementally. This prediction has been confirmed in multiple types of preparations with both rats and pigeons (e.g., Rescorla, 2000, 2006) and is considered supportive of a total error reduction's explanation of extinction.

In the present study, we wished to extend this question by asking what the effect is of extinguishing the target CS in compound with two additional conditioned excitors. According to the total error reduction approach, three compound excitors should create an even greater expectancy of the US, which should result in more extinction, relative to when only two conditioned excitors are compounded. Thus, the total error reduction approach predicts that the number of excitors present during extinction should monotonically correspond to the amount of predictive error experienced and that increasing the number of excitors present during extinction should result in more error and, thus, decreased levels of responding to the target CS at test.

This prediction was investigated by comparing responding to the target CS following extinction in compound with two associatively neutral stimuli, in compound with one additional conditioned excitor and one associatively neutral stimulus, or in compound with two additional conditioned excitors. Thus, all groups received extinction of the target CS in compound with two additional stimuli, but the groups differed in whether the additional stimuli were conditioned excitors or associatively neutral stimuli. This treatment allowed us to equate generalization decrement across all groups changing between elemental acquisition and extinction treatment and between extinction treatment and elemental testing (see Urcelay, Lipatova, & Miller, 2009, for a discussion about generalization decrement during compound extinction treatment). Additionally, all subjects received training, extinction, and testing in different contexts (i.e., ABC renewal design; Bouton & Bolles, 1979) in order to provoke a recovery of responding. Thus, the effect of compounded excitors during extinction treatment was indexed by different levels of recovery of responding. Using a renewal design increased sensitivity to observing the effects of extinction with an additional excitor, which might otherwise have been masked by a floor effect. Also, it minimized the influence of nonassociative factors created by the extinction trials on final responding (Rescorla, 2004). Lastly, extinguishing the target excitor outside of the acquisition context limited the role of the acquisition context as another comparator stimulus (see Witnauer & Miller, 2012, for a demonstration of compound extinction in an excitatory context). While there is no direct evidence that levels of extinction correspond exactly to levels of recovery, it is a reasonable assumption, and there are data that provide indirect support of this idea. For example, Denniston, Chang, and Miler (2003) showed that massive extinction, which presumably resulted in a deeper level of extinction than moderate extinction, reduced the level of renewal that was observed. Perhaps even more compelling, Graham and Richardson (2010) administered fibroblast growth factor-2, a mitogen that is known to facilitate extinction, and showed less renewal, relative to control rats. This occurred even after the vehicle rats received twice the amount of extinction as the experimental rats, thus adding support to the view that extinction does translate to differing levels of recovery. However, because we were not interested in studying renewal per se, we did not include the standard group renewal control (i.e., an ABB group), and thus the degree of renewal cannot be assessed directly. Importantly, all groups received the same renewal manipulation; hence, it could not have contributed to any differences observed among groups. Previous renewal studies have shown that conducting acquisition, extinction, and testing in different contexts ordinarily provokes a recovery of responding, and presumably this recovery of responding should be less if extinction is somehow made more effective (e.g., by extinguishing the target with an additional excitor).

Experiment 1

In Experiment 1, three groups were conditioned with three separate CSs, target CS X, and additional excitors D and E in context 1 (see Table 1). All groups received extinction treatment in context 2. Group E0 received extinction of X in compound with two associatively neutral stimuli (0 refers to the number of additional conditioned excitors presented during extinction treatment). Group E1 received extinction of X in compound with one neutral stimulus and one conditioned excitor (D), and Group E2 received extinction of X in compound with two conditioned excitors (D and E). Thus, all groups received extinction of a three-stimulus compound consisting of the target CS X and two nontarget stimuli. This treatment was intended to equate generalization decrement among the three groups between acquisition and extinction and between extinction and testing. All groups were then tested on X alone in a neutral context (context 3). According to the total error reduction approach, strong responding should be observed in Group E0 due to ABC renewal. Less responding should be observed in Group E1 due to the compound extinction treatment creating greater predictive error in Group E1, which should drive a larger negative change in X's associative strength. This approach predicts even weaker responding in Group E2, relative to Group E1, as a result of an even greater amount of error being produced by the three excitors all predicting the US during extinction.

Method

Subjects—Subjects were 18 male and 18 female experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Average body weights were 276 g for males (range: 218–375 g) and 206 g for females (range: 185–236 g). Subjects were randomly assigned to one of three groups ($n_s = 12$), counterbalanced within groups for sex. The animals were individually housed in standard hanging stainless steel wire-mesh cages in a vivarium maintained on a 16:8-hr light:dark cycle. Experimental manipulations occurred near the middle portion of the light phase. The animals received free access to Purina Lab Chow, whereas water availability was limited to 30 min per day following a progressive deprivation schedule initiated 1 week prior to the start of the study. From the time of weaning until the start of the study, all animals were handled for 30 s, three times per week.

Apparatus—Twelve identical chambers, each measuring $30 \times 25 \times 32$ cm ($l \times w \times h$), were used. Two of the walls of each chamber were made of Plexiglas, and the other two were made of stainless steel. The floor was constructed of 0.5 cm diameter rods, spaced 2 cm center-to-center and connected by NE-2 neon bulbs that allowed a 0.7-mA, 0.5-s constant-current footshock to be delivered by means of a high voltage AC circuit in series with a 1.0-M Ω resistor. Each chamber was housed in an environmental isolation chest and was dimly illuminated by a houselight (#1820 incandescent bulb) mounted on the ceiling of the experimental chamber. This light was turned off for the entire duration of the experiment, except for when it was used as a 10-s cue. On one metal wall of each chamber, there was an operant lever and, adjacent to it, a niche ($4.5 \times 4.0 \times 4.5$ cm) centered 3.3 cm above the floor, through the bottom of which a 0.04-cc cup could deliver water. A 45- Ω speaker mounted on the interior back side of each environmental chest could deliver a low-frequency complex tone stimulus (600 and 670 Hz). A second 45- Ω speaker mounted on the ceiling of the experimental chamber was used to deliver a click train stimulus (6/s). A third 45- Ω speaker mounted on the sidewall of the chamber was used to deliver a white noise stimulus. Additionally, a SonAlert mounted in each environmental chest was able to deliver a high frequency tone (1900 Hz). All auditory cues were 6 dB (C scale) above background, which was a constant 72-dB background noise provided by ventilation fans in each enclosure. A flashing light stimulus (0.25 s on/0.25 s off) was provided by a 75-W incandescent bulb, nominal at 120 VAC but driven at 60 VAC. The bulbs were mounted on

the interior backside of the environmental chest. This composed context 1, the acquisition context. A second context (context 2 [extinction context]) was created by placing Plexiglas on the grid floor, using 2 drops of Wintergreen odor cue placed on a wooden block in each chamber, and placing subjects in a different instance of the context. This context was the extinction and preexposure context for all groups. A third context (context 3 [testing context]) was created by placing 1.25 cm stainless steel wire mesh on the grid floor, applying 2 drops of a banana odor to a wooden block in each chamber, and placing subjects in a different instance of the context. The white noise, houselight on, low tone, and flashing light served as stimuli D, E, F, and G, counterbalanced within groups, with the rule that the nontarget cues during extinction had to be one visual and one auditory cue. The click train served as CS X for all groups. During all training and preexposure, the target X was 15 s in duration, and CSs D, E, F, and G were 10 s in duration. During compound extinction treatment, the cues were initiated at the same time, but X was terminated 5 s after the termination of the other cues. This was done to encourage elemental, as opposed to configural, processing of the cues and followed the same strategy as Urcelay, Lipatova, and Miller (2009). The SonAlert served as a signal for water delivery during shaping and testing. It was 0.5 s in duration. During testing, X was presented for 30 s per trial.

Procedure

Acclimation and shaping: On days 1–5, all subjects were acclimated to context 1 and shaped to leverpress for water during daily 48-min sessions. To facilitate magazine training, the onset of the water delivery was accompanied by a 0.5-s SonAlert (1900 Hz). On days 1 and 2, a fixed-time 2-min schedule of SonAlert plus water delivery occurred concurrently with a continuous reinforcement schedule. On day 3, the noncontingent water delivery was discontinued, and subjects were trained on the continuous reinforcement schedule alone. All subjects that emitted fewer than 50 responses on this day were later placed back in the chambers and hand-shaped through successive approximation for 30 min. Three subjects were given additional training on day 3. On days 4 and 5, water was provided on a variable interval 20-s (VI-20) schedule. After shaping, the operant lever remained present, but water reinforcement was discontinued until reacclimation, at which time it was resumed on a VI-20 schedule.

Preexposure: On days 6 and 7, all subjects received daily 120-min sessions in context 2. Subjects received interspersed trials consisting of two nonreinforced presentations of each nontarget CS each day. This was done to minimize any configural processing during compound extinction. The order of stimulus presentations for all subjects was white noise, houselight on, low tone, flashing light, houselight on, white noise, flashing light, and low tone. The mean intertrial interval (ITI) was 15 min (range: 7–24 min), with ITIs measured from CS onset to CS onset.

Phase 1: Acquisition: On days 8–11, all subjects received daily 48-min acquisition training sessions in context 1. Subjects received interspersed trials consisting of one daily reinforced presentation each of X, D, and E. The order of presentation was scrambled across days. The mean ITI was 16 min (range: 7–20 min). The CS and US coterminated.

Phase 2: Extinction: On days 12–17, all subjects received daily 90-min extinction sessions in context 2. Subjects in Group E0 received six daily nonreinforced presentations of compound XFG; subjects in Group E1 received six daily nonreinforced presentations of compound XDF; subjects in Group E2 received six daily nonreinforced presentations of compound XDE. All groups also received one daily nonreinforced presentation each of X, D, E, F, and G, interspersed with the compound presentations. These additional elemental trials were intended to reduce configural processing of the compound. This technique has

been used previously for the same purpose both in our laboratory (e.g., McConnell & Miller, 2010) and in other laboratories (e.g., Rescorla, 2000). The mean ITI was 8.81 min (range: 5–11 min).

Reacclimation: On days 18–21, all subjects were reacclimated to the VI-20 schedule in context 3 during daily 60-min sessions. No nominal stimuli were programmed to occur. The purpose of these sessions was to reestablish a stable rate of leverpressing behavior, which might have been differentially disrupted by the footshock US, thereby providing similar baseline behavior across the three groups upon which conditioned leverpress suppression was to be assessed.

Testing: On day 22, all subjects were tested for conditioned suppression to X in context 3. Each subject received four nonreinforced 30-s presentations of CS X during a 30-min session initiated at 8, 13, 18, and 24 min into the session. The response rates (per minute) during the 120-s periods preceding each CS exposure (pre-CS score) and that during the 30-s CS exposure (CS score) were recorded. Subjects continued to be reinforced on a VI-20 schedule throughout the test session.

A suppression ratio (Annau & Kamin, 1961) for each subject was calculated by the formula $P/(P + Q)$ for day 22, where P is the rate of leverpressing during all four 30-s CS presentations and Q is the rate of leverpressing during the 120-s period preceding the first CS test presentation. A longer pre-CS period relative to the CS presentation was adopted in order to reduce the variability in baseline response rate. A suppression ratio of 0.5 indicates no conditioned suppression, indicative of no fear to the CS, and that of 0 indicates complete suppression, indicative of strong fear to the CS.

Results and discussion

The predictions of the total error reduction approach were not supported. There was a curvilinear relationship between the number of excitors extinguished in compound and conditioned suppression to the target CS at test. Less conditioned suppression (i.e., more extinction, less renewal) was observed following extinction of the target with one additional excitor and one neutral stimulus, relative to either extinction of the target in compound with two neutral stimuli or extinction of the target in compound with two conditioned excitors (see Fig. 1). This pattern of results is not consistent with predictions of an associative model based on total error reduction, which predicts increasingly deeper extinction and, therefore, less recovery of responding, with more excitors during extinction. These conclusions are supported by the following statistics.

A one-way analysis of variance (ANOVA) was conducted on leverpressing during the 120 s preceding the first CS presentation. There was no difference in baseline leverpressing among groups, $p = .58$. A similar ANOVA was conducted on the suppression ratios. This detected a significant difference between groups, $F(2, 33) = 28.74$, $MSE = .19$, $p < .01$, Cohen's $f = .87$. Planned comparisons were conducted to identify the source of this variance. We report the comparisons using the error term from the ANOVA, as is our custom, because it generally provides a more accurate measure of within-group variance, but we additionally report the results from t -tests because of the large differences in variances among groups. Both analyses showed the same differences to be significant. Specifically, Group E0 showed more suppression of leverpressing, relative to Group E1, $F(1, 33) = 54.42$, $p < .01$, $t(22) = 8.91$, $p < .01$, indicating that extinction with an additional excitor resulted in less fear to the CS at test (i.e., the deepened extinction effect). Importantly, Group E2 suppressed more than Group E1, $F(1, 33) = 27.10$, $p < .01$, $t(22) = 4.42$, $p < .01$, demonstrating that compound extinction with two additional excitors left the target CS with more behavioral control than

extinction with only one additional excitator. The pattern of results that we observed does not support the monotonic predictions of a total error reduction approach. Deepened extinction was observed, as indicated by less recovery of suppression in Group E1 relative to Group E0, which is consistent with the total error reduction approach's predictions. But despite a greater degree of predictive error present in Group E2 relative to Group E1, evidence of less extinction was observed in Group E2. The results are also not explicable in terms of differential second-order conditioning. Second-order conditioning refers to increased responding to a neutral stimulus as a result of being paired with an excitatory stimulus (e.g., Anderson, Plant, Johnson, & Vandever, 1967; Holland & Rescorla, 1975). Pineño, Zilski, and Schachtman (2007) demonstrated that a CS with a prior associative value is sensitive to second-order conditioning. Thus, one might argue (e.g., Pineño, 2007b) that the increased suppression to X in Group E2 is the result of second-order conditioning of excitation mediated by D and E to X, whereas in Group E1, X received second-order excitation only from one stimulus, D. However, if this were correct, suppression to X in Group E0 should have been weakest. Thus, a second-order conditioning explanation predicts a monotonic relationship between the number of added excitors present during extinction and suppression at test, such that increasing the number of excitors compounded during extinction should result in increasing levels of behavioral control. This is not consistent with what we observed. Additionally, our results are consistent with those of Witnauer and Miller (2012), who showed attenuated deepened extinction following extinction of the target CS in compound with a discrete excitator and an excitatory context, and they provided evidence that second-order conditioning did not likely play a major role in determining suppression.

These results are important because, currently, there is wide acceptance of the view that more excitatory associative strength present during extinction makes extinction treatment more effective. The present results show that this is not necessarily true. We extinguished the target CS in compound with two other excitatory CSs, which should have made the net associative strength of the extinction compound more positive than when it was extinguished in compound with only one other excitator, which therefore should have made extinction even more effective. Instead, we observed less effective extinction. This suggests that some other mechanism might also be working during extinction, as opposed to or in addition to a total error reduction process. One such mechanism has been proposed by the extended comparator hypothesis (ECH; Denniston, Savastano, & Miller, 2001; see also Stout & Miller, 2007), which does not use a total error reduction learning rule. According to this model, responding to the target CS is a function of the strength of the target CS-US association (link 1; see Fig. 2, inset), relative to the product of the strength of the association between the target CS and any other stimulus with which the target CS has been paired (i.e., the comparator stimulus; link 2) and the association between the comparator stimulus and the US (i.e., link 3). Responding is directly related to the strength of link 1 and inversely related to the strength of the product of links 2 and 3, which is called the comparator term.

The original comparator hypothesis (Miller & Matzel, 1988; see Fig. 2, inset) was expanded to allow the target CS to have multiple comparator stimuli (Denniston et al., 2001; see Fig. 2, main figure). Moreover, it was assumed that each comparator stimulus is regulated in its ability to down-modulate responding to the target by its own comparator process (i.e., higher-order comparator processes involving second-order comparators to the target CS). Thus, strong second-order comparator processes reduce the potential for first-order comparator stimuli to activate a representation of the US, which would normally decrease responding to the target CS. Importantly, stimuli that are strongly associated with the target CS and that share a within-compound association with each other simultaneously act as both first- and second-order comparator stimuli to the target CS. This results in a counteraction effect in which the two comparator stimuli simultaneously down-modulate each other. This should leave the target CS with only weakly effective comparator stimuli to activate an

alternative representation of the US (for other demonstrations of counteraction effects, see Blaisdell, Bristol, Gunther, & Miller, 1998; Sissons & Miller, 2009; Urcelay & Miller, 2006, 2008; Urushihara & Miller, 2006; Witnauer, Urcelay, & Miller, 2008; see also Wheeler & Miller, 2008, for a review).

According to the SOCR model (Stout & Miller, 2007, the mathematical implementation of the ECH), during elemental extinction, the context assumes the role of the target CS's primary comparator stimulus. Extinction is due to both a weakening of the target-CS-US association (link 1) and down-modulation of the target CS's behavioral control by the comparator term, which is determined by the product of the CS-context association (link 2), which gets stronger during extinction, and the context-US association (link 3), which gets weaker during extinction. Of note, the weakening of link 1 is similar to the mechanism of extinction assumed by the total error reduction approach, but according to the ECH, this process is driven by local error reduction (i.e., based only on the predictive value of the stimulus being revalued). Moreover, down-modulation by the comparator term does not affect the strength of link 1; rather, it attenuates responding based on link 1.

In the present experiment, the acquisition and extinction contexts acted as comparator stimuli for X in all groups, but because they are diffuse, they were presumably of lower salience than the discrete CSs. The acquisition trials were widely spaced to minimize strong context-US associations. Moreover, all groups had equal experience with the contexts. Therefore, the two nontarget stimuli compounded with X were the comparator stimuli of interest. Because they were presented in compound, they should also act as comparator stimuli for each other. In Group E0, the comparator stimuli (F and G) did not influence behavioral control by X, presumably because they did not have an association with the US (i.e., there was not an effective link 3 between the comparator CSs and the US; Fig. 3a). In Group E1, only one of the comparator CSs had an effective link 3 (i.e., D; link 3.2 in Fig. 3b); the other comparator CS (F) was associatively neutral and, therefore, effectively null (link 3.3 in Fig. 3b). Therefore, F had no effect on D's link 3, thereby allowing the excitatory comparator CS D to down-modulate the behavioral control of the target CS. This, in turn, reduced suppression to X in Group E1 relative to Group E0, thus producing the deepened extinction effect. However, in Group E2, the two comparator CSs (D and E) were both conditioned exciters; therefore, they both had effective link 3s (i.e., associations with the US; Fig. 3c). Because the two exciters also shared a within-compound association with each other (link 3.2 in Fig. 3c), they counteracted each other in their potential to activate an effective representation of the US. That is, D acted as a second-order comparator stimulus to X and down-modulated X's first-order comparator stimulus E's potential to activate an indirect US representation. Simultaneously, E acted as a second-order comparator stimulus to X and down-modulated D's potential to produce an effective link 3. Therefore, responding to X was moderately strong because X was essentially left without any effective stimuli to provide an alternative expectation of the US.

Thus, the ECH can account for the pattern of responding we observed. This model predicts that extinguishing two exciters in compound should result in less responding than elemental extinction or extinction of three exciters in compound. It should be noted that Group E0 suppressed more than Group E2, $F(1, 33) = 4.72$, $p < .05$, $t(22) = 2.25$, $p < .05$, which is indicative of the counteraction effect that is predicted by the ECH being incomplete. This is consistent with other demonstrations of incomplete counteraction effects (e.g., Sissons & Miller, 2009; Witnauer et al., 2008). Critically, both of these groups showed more suppression than did Group E1.

Experiment 2a

The results of Experiment 1 are not consistent with the predictions of a total error correction approach, but they are compatible with the ECH. To further investigate the ECH's account, we conducted two experiments that tried to isolate the contributing mechanisms proposed by the ECH. According to this model, two associative links other than that between the target CS and the US (i.e., link 1) determine overall conditioned responding. Link 2 refers to the association between the target CS and its comparator stimuli, and link 3 refers to the association between the comparator stimuli and the US (see Fig. 2). The product of links 2 and 3 produce the comparator term, which is then compared with link 1. A strong comparator term reduces responding to the target CS. The effectiveness of a first-order comparator stimulus is modulated by similar associations within a higher-order comparator process. For example, the product of link 3.2, which refers to the within-compound association between the first- and second-order comparator stimuli, and link 3.3, which refers to the association between the second-order comparator stimulus and the US, produces the second-order comparator term that is compared with the strength of link 3.1, the association between the first-order comparator stimulus and the US. Strong second-order comparator terms reduce the effectiveness of first-order comparator stimuli.

What we call the attenuated deepened extinction effect, which describes stronger responding to the target following extinction of the target with two additional conditioned excitors, relative to one additional excitor, presumably was the result of links 3.2 (i.e., the D–E and E–D associations) and 3.3 (the D–US and E–US associations) both being relatively strong, which caused the comparator stimuli to counteract each other. In the following experiments, we further investigated this counteraction effect by manipulating the links of the comparator term. Presumably, weakening either of these links should attenuate the counteraction effect, thereby allowing each of the comparator stimuli to more effectively reduce conditioned suppression to X. Experiment 2a focused on the influence on the counteraction effect of weakening link 3.2, and Experiment 3 focused on the influence on the counteraction effect of weakening link 3.3. Manipulating the strength of either of these associations should have the same result of reduced conditioned suppression to X.

Experiment 2a weakened the association between comparator stimuli D and E, using a procedure that establishes an inhibitory association between them (e.g., Mackintosh, Kaye, & Bennett, 1991; see Table 2). This involves interspersed presentations of two compounds with a common element, which, based on the theory of McLaren et al. (1989) and supported by data from several studies (e.g., Bennett, Scatill, Griffiths, & Mackintosh, 1999; Dwyer, Bennett, & Mackintosh, 2001; Dwyer & Mackintosh, 2002; Leonard & Hall, 1999; Mundy, Dwyer, & Honey, 2006), causes the unique elements to produce inhibitory behavior with respect to each other. This same manipulation was used by Witnauer et al. (2008) to retard the development of the within-compound association between two comparator stimuli in a blocking design. It should be noted that the ECH cannot explain this effect itself, but it does assume that weakening the association between D and E (through any means) should attenuate the counteraction effect, thereby reducing the amount of conditioned suppression to X at test (see Amundson, Witnauer, Pineño, & Miller, 2008, for a demonstration of this training establishing an inhibitory-like relationship between two cues that resulted in reduced cue competition between them). Thus, the perceptual learning procedure used here is simply a tool we employed to weaken the within-compound association between D and E, which should leave each comparator stimulus less able to down-modulate the other, thus allowing each comparator stimulus to have a greater effect on conditioned suppression to X. This manipulation was compared with an E1 condition, which should not be affected by the inhibitory training, according to the ECH. This is because, in Condition E1, only D was the target's effective comparator stimulus (F was associatively neutral). Making D inhibitory to

E should not affect D's potential to activate an alternative representation of the US to reduce responding to the target. Thus, the ECH predicts no effect of the pretraining on responding in Condition E1; thus, there should be weak responding in both groups of the E1 condition. The ECH predicts that inhibitory pretraining should weaken responding in Condition E2 and, consequently, result in weak responding in Group E2-Inhib, relative to moderately strong responding in Group E2-Ctrl.

Lastly, it should be noted that this treatment does not always produce inhibition. In fact, with fewer trials, the same procedure has been shown to establish an excitatory association between the unique elements (e.g., Espinet, Iraola, Bennett, & Mackintosh, 1995, Experiment 4). Thus, we performed a check of our manipulation in Experiment 2b to ensure that our procedure did establish inhibition between Stimuli D and E.

Method

Subjects—Subjects were 24 male and 24 female experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Average body weights were 303 g for males (range: 226–381 g) and 199 g for females (range: 180–265 g). Subjects were randomly assigned to one of four groups ($n = 12$), counterbalanced within groups for sex. The animals were housed and maintained using the same procedures as those in Experiment 1.

Apparatus—The apparatuses and stimuli were the same as those in Experiment 1.

Procedure

Acclimation and shaping and preexposure: On days 1–7, acclimation and shaping and preexposure were conducted in the same manner as described in Experiment 1.

Phase 1: Inhibitory training: On days 8–15, all subjects received daily 60-min sessions in context 2. All subjects received four daily nonreinforced presentations of DG that were interspersed with four daily nonreinforced presentations of EF in Groups E1-Ctrl and E2-Ctrl or four daily nonreinforced presentations of EG in Groups E1-Inhib and E2-Inhib. Two different training schedules were used on alternate days. For both schedules, the mean ITI was 7.5 min (range: 4–15 min). For Groups E1-Ctrl, E1-Inhib, and E2-Ctrl, all of the compounds were composed of stimuli of different modalities (auditory and visual). But because of the nature of the design and the limitation of stimulus modalities, in Group E2-Inhib, half of the subjects received DG with stimuli of the same modality, and half received EG with stimuli of the same modality. This confound was allowed in order to ensure that the nontarget stimuli present during target extinction treatment were of different modalities. Importantly, making the stimulus compounds of the same modality in Group E2-Inhib should, if anything, weaken the perceptual learning effect and, thus, weaken our manipulation, because this effect requires elemental processing of the unique components during extinction treatment.

Phase 2: Acquisition: On days 16–19, subjects received acquisition training in the same manner as described in Experiment 1.

Phase 3: Extinction: On days 20–25, subjects received extinction training. Condition E1 was extinguished in the same manner as Group E1 in Experiment 1. Condition E2 was extinguished in the same manner as Group E2 in Experiment 1.

Reacclimation and testing: On days 26 and 27, all subjects were reacclimated in context 3 in the same manner as described in Experiment 1. On day 28, all subjects were tested on X

alone in the same manner as described in Experiment 1. Suppression ratios were similarly calculated.

Results and discussion

We successfully replicated the main effect from Experiment 1 of attenuated deepened extinction, as indexed by more recovery of suppression, when extinction of the target occurred in the presence of two independently trained conditioned excitors, relative to when extinction occurred in compound with only one additional excitor. Additionally, we showed that making the two added excitors inhibitory with respect to each other prior to any other training decreased suppression to X, presumably because this reduced the counteraction effect (see Fig. 4). No significant effect of inhibitory pretraining was observed in the E1 condition. Thus, the results are consistent with the ECH's predictions. The following statistics support these conclusions.

A 2 (phase 1: Ctrl vs. Inhib) $\times$ 2 (phase 3: E1 vs. E2) ANOVA was conducted on leverpressing during the 120 s prior to the first CS presentation to assess for baseline differences. There were no significant main effects or interactions, smallest $p = .49$. A similar ANOVA was conducted on the suppression ratios calculated from the CS data. This detected a main effect of phase 3 training, $F(1, 44) = 7.65$, $p < .01$, $MSE = .10$, Cohen's $f = .37$, and more important, an interaction between the phase 1 and phase 3 training, $F(1, 44) = 17.17$, $p < .01$, $MSE = .23$, Cohen's $f = .58$. Planned comparisons were then conducted to identify the source of this variance. There was a difference between Groups E2-Ctrl and E2-Inhib, $F(1, 44) = 15.51$, $p < .01$, indicating that making the two excitatory nontarget stimuli (D and E) inhibitory with respect to each other weakened the counteraction they otherwise would have produced. This resulted in less suppression to X (i.e., less renewal) in Group E2-Inhib than what was observed when the counteraction was strong, such as in Group E2-Ctrl. Notably, the level of conditioned suppression was of similar magnitude to the level of conditioned suppression produced by a single added excitor. That is, extinction with two added excitors did appear to reduce recovery of suppression, presumably by enhancing extinction, when a counteraction effect was minimized. However, any conclusions drawn from this observation must be made with caution, given that it is unclear how much of an influence the counteraction effect had, relative to the inhibitory training. Nevertheless, it is notable that when these two treatments were combined, the size of the recovery effect was no larger than when extinction occurred with only one added excitor, which is contrary to the predictions of an associative model based on total error reduction.

There was a marginally significant effect of the inhibitory pretraining in Condition E1 (i.e., Group E1-Ctrl vs. Group E1-Inhib), $p = .06$. The ECH has no principled reason for why these groups should have differed based on the inhibitory pretraining, and thus we attribute this difference to experimental noise. Importantly, the effect was in the opposite direction than in the E2 condition (i.e., inhibitory pretraining resulted in more suppression in Condition E1). Moreover, we note that the interaction was significant, and that is the critical finding. Lastly, there was a difference between Groups E1-Ctrl and E2-Ctrl, $F(1, 44) = 23.88$, $p < .01$, which replicates the effect of Experiment 1. These data are consistent with the ECH's prediction that weakening the counteraction effect by attenuating the association between the two added conditioned excitors should result in less suppression to the target CS than when the two added excitors are not inhibitory with respect to each other.

These results are congruent with those of Witnauer et al. (2008), in which they demonstrated a counteraction effect between two discrete cues and an attenuation of the counteraction effect by retarding the expression of an excitatory association between the two comparator stimuli, using the perceptual-learning procedure. Thus, the present experiment adds a second demonstration of a counteraction effect in which the context is not one of the interacting

comparator stimuli. Moreover, it provides further support to the view that within-compound associations are important in determining response potential.

Experiment 2b

Experiment 2b was a manipulation check of the inhibitory pretraining that we used in Experiment 2a. We assessed whether our alternated preexposure produced inhibitory tendencies between D and E, using a retardation test (see Table 3). Two groups, Inhib and Ctrl, received the same preexposure treatments as those in Experiment 2a. Then both groups were presented with D and E in compound three times without reinforcement. This was intended to establish a within-compound association between D and E. In phase 3, D was made excitatory in both groups, and then all subjects were tested on E alone. Through sensory preconditioning, E should have acquired moderate behavioral control, but this should be reduced if the within-compound association was retarded in being formed due to the pretraining treatment received by Group Inhib.

Method

Subjects—Subjects were 12 male and 12 female experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Body-weight ranges were 208 g for males (range: 198–217 g) and 183 g for females (range: 172–203 g). Subjects were randomly assigned to one of two groups ($n = 12$), counterbalanced within groups for sex. The animals were housed and maintained in the same manner as described in Experiment 1.

Apparatus—The apparatus and stimuli were the same as those in context 1 described in Experiment 1. The white noise, houselight on, low tone, and flashing light served as stimuli D, E, F, and G, counterbalanced within groups. H was the click train. All CSs were 10 s in duration. The SonAlert provided a 0.5-s signal for water delivery during shaping.

Procedure

Acclimation and shaping: On days 1–5, acclimation and shaping took place using the same procedure as that described in Experiment 1.

Preexposure: On days 6 and 7, all subjects received daily 120-min sessions, which consisted of two interspersed nonreinforced presentations of each CS each day. The order of stimulus presentations for all subjects was white noise, houselight on, low tone, flashing light, click, houselight on, flashing light, white noise, click, and low tone. The mean ITI was 12 min (range: 6–16 min). Water was not available during this phase or the remainder of the experiment until reacclimation.

Phase 1: On days 8–15, Group Inhib was given pretraining using the same procedure as Condition Inhib in Experiment 2a. Group Ctrl was given pretraining using the same procedure as Condition Ctrl in Experiment 2a. To maintain consistency with Experiment 2a, one of the two compounds in Group Inhib (in this case, EG) was composed of two stimuli of the same modality. In Group Ctrl, both compounds were composed of stimuli of different modalities (i.e., one auditory and one visual stimulus). Just as in Experiment 2a, this confound should, if anything, lead to more configuring in the experimental group, which could only weaken our manipulation.

Phase 2: On day 16, all subjects received one 60-min session during which both groups received three nonreinforced compound presentations of D and E (mean ITI = 20 min). For both groups, D and E were of different modalities.

Phase 3: On day 17, all groups received one 60-min session during which both groups received four reinforced presentations of D (mean ITI = 15 min). The CS and US coterminated.

Reacclimation and testing: On days 18 and 19, all subjects were reacclimated to the context, using the same procedure as that described in Experiment 1. On day 20, all subjects were tested for conditioned suppression to E, using the same procedure as that described in Experiment 1. Suppression ratios were similarly calculated. During testing, the test stimulus was presented for 30 s during each presentation.

Results and discussion

We observed weaker suppression in Group Inhib than in Group Ctrl, which indicates that there was less sensory preconditioning of excitation from D to E in Group Inhib. This demonstration supports our assumption that the perceptual learning procedure used in Experiment 2a was effective in establishing an inhibitory association between the two nontarget exciters, D and E. The following statistics support this conclusion.

A one-way ANOVA was conducted on leverpressing during the 120 s prior to the first CS presentation to assess possible baseline differences. The two groups did not differ, $p > .51$. A similar ANOVA was conducted on the suppression ratio data (see Fig. 5). This revealed less suppression in Group Inhib relative to Group Ctrl, $F(1, 22) = 7.50$, $MSE = .03$, $p < .05$, Cohen's $f = .52$. According to our analysis, strong suppression was observed in Group Ctrl due to sensory preconditioning of excitation from D to E mediated by the within-compound association formed in phase 2. However, in Group Inhib, this within-compound association was retarded in being formed, due to the existing inhibitory association established between D and E during phase 1. Thus, less excitation was mediated to E in Group Inhib, resulting in less suppression to E at test. We did not include a negative summation test because the two groups received the same amount of preexposure and training with the test cue E. Normally, in the test of a conditioned inhibitor, retarded excitatory responding can be explained by reduced attention being paid to the presumed conditioned inhibitor, relative to a novel cue. However, in the present experiment, the test stimulus was equally familiar in both groups. There is no principled reason for why Group Inhib should have paid less attention to the test stimulus E than Group Ctrl. Thus, if the weak conditioned suppression we observed in Group Inhib was due to reduced attention to E, the same retardation effect should also have been evident in Group Ctrl, which we did not observe. Therefore, the retardation effect we observed is unlikely to have been the result of reduced attention to the target CS. We conclude that the pretraining manipulation in Group Inhib established an inhibitory within-compound association between D and E in Group Inhib, which retarded the formation of an excitatory D–E association when they were subsequently paired. In Group Ctrl, the pretraining procedure left D and E associatively neutral with respect to each other, and through sensory preconditioning, E was left with behavioral control mediated by its strong association with D.

This result is consistent with previous literature showing that such a treatment produces an inhibitory association (e.g., Dwyer et al., 2001; Dwyer & Mackintosh, 2002). Moreover, this adds to the literature by being the first demonstration to directly measure inhibition produced by this procedure using only audio and visual stimuli; previous demonstrations with rats all used flavor conditioning (indirect evidence for an inhibitory-like association was demonstrated by Amundson et al., 2008, using audiovisual stimuli). In sum, this experiment showed that interspersed presentations of two compounds produced inhibition between the unique elements—in this case, D and E—as assessed through a retardation test.

Experiment 3

Experiment 2a showed that link 3.2 (see Fig. 2) is critical in attenuating the deepened extinction effect, as indexed by stronger recovery of suppression (i.e., renewal). In a related manner, Experiment 3 assessed the contribution of link 3.3 by latently inhibiting one of the added excitatory stimuli (D) to retard the expression of the association between D and the US (see Table 4). According to the ECH, preexposing a stimulus should produce a strong association between that stimulus and the context. In Condition E2, this should have the consequence of attenuating the expression of link 3.3, which should make D ineffectual, thereby allowing the second excitatory cue, E, to down-modulate conditioned suppression to X. In Condition E1, D is X's only excitatory comparator stimulus. Preexposing D should increase conditioned suppression to X because now X has no effective stimuli to down-modulate its behavioral control. Thus, Groups E1-LI and E2-LI should show opposite effects as a result of preexposing D relative to their respective control groups, which did not receive preexposure to D. As a check of our preexposure manipulation, we preexposed G in the control groups, E1-Ctrl and E2-Ctrl, and assessed retardation of behavioral control by G in those groups relative to Groups E1-LI and E2-LI, which did not receive preexposure to G.

Method

Subjects—Subjects were 24 male and 24 female experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Body weight ranges were 305 g for males (range: 233–366 g) and 211 g for females (range: 184–248 g). Subjects were randomly assigned to one of four groups ($n = 12$), counterbalanced within groups for sex. The animals were housed and maintained according to the same procedures as those used in Experiment 1.

Apparatus—The apparatuses and stimuli were the same as those described in Experiment 1.

Procedure

Acclimation and shaping and preexposure: On days 1–7, acclimation and shaping and preexposure were conducted in the same manner as that described in Experiment 1.

Phase 1: Latent inhibition: On days 8–11, in context 1, all subjects received extensive preexposure consisting of 24 daily presentations of a stimulus during a 48-min session (ITI = 2 min). Subjects in Groups E1-LI and E2-LI received presentations of D, and subjects in Groups E1-Ctrl and E2-Ctrl received presentations of G. This preexposure treatment was intended to produce latent inhibition to the respective stimulus.

Phase 2: Acquisition: On days 12 and 13, all subjects received daily 48-min acquisition training sessions in context 1. Subjects received interspersed trials consisting of one daily reinforced presentation each of X, D, E, and G. Excitatory training of G was included in order to later test for latent inhibition. The mean ITI was 12 min (range: 7–20 min). The CS and US coterminated. Fewer reinforced trials were given to increase sensitivity to the latent inhibition treatment.

Phase 3: Extinction: On days 14–19, all subjects received extinction training. Condition E1 was extinguished in the same manner as Group E1 in Experiment 1. Condition E2 was extinguished in the same manner as Group E2 in Experiment 1.

Reacclimation and testing: On days 20 and 21, all subjects were reacclimated in context 3 in the same manner as that described in Experiment 1. On day 22, all subjects were tested on

X alone in the same manner as that described in Experiment 1. On day 23, all subjects were tested for conditioned suppression to G in Context 3 to assess latent inhibition. If the LI treatment was successful, we expected to observe less conditioned suppression in Groups E1-Ctrl and E2-Ctrl, which received preexposure to G relative to Groups E1-LI and E2-LI, which did not receive preexposure to G. Testing was conducted in the same way as testing on X.

Results and discussion

Two subjects were eliminated from data analyses, one because it did not make any responses during the test session (Group E2-LI) and one due to equipment problems (Group E2-Ctrl).

Test X—We replicated the attenuated deepened extinction effect, as indexed by more conditioned suppression, which was demonstrated in Experiments 1 and 2a. Moreover, we found that latently inhibiting one of the added excitatory stimuli (D) prior to any other training decreased conditioned suppression (i.e., decreased renewal) to X in Group E2-LI. Notably, the same treatment increased conditioned suppression (i.e., increased renewal) to X in Group E1-LI (see Fig. 6). These results are consistent with the predictions of the ECH. The following statistics support these conclusions.

A 2 (phase 1: Ctrl vs. LI) $\times$ 2 (phase 3: E1 vs. E2) ANOVA was conducted on leverpressing during the 120 s prior to the first CS presentation to assess baseline differences. There were no significant main effects or an interaction, smallest $p = .09$. A similar ANOVA was conducted on the suppression ratio data. This did yield a significant interaction, $F(1, 42) = 10.01$, $MSE = .14$, $p < .01$, Cohen's $f = .43$. The main effects were not significant, smallest $p = .36$. Planned contrasts were conducted between Groups E2-Ctrl and E2-LI to assess the effect of preexposing one of the two comparator stimuli that was compounded with the target during extinction. This yielded a significant difference, $F(1, 42) = 4.20$, $p < .05$, with less suppression in Group E2-LI than in Group E2-Ctrl. Seemingly, preexposure to stimulus D attenuated the counteraction between D and E, resulting in weaker behavioral control by X. That is, making D ineffectual allowed E to down-modulate behavioral control by X, which was demonstrated by less renewal. A contrast was also conducted between Groups E1-Ctrl and E1-LI. According to the ECH, preexposing D in this condition should strengthen the behavioral control by X, which is what we observed, $F(1, 42) = 5.92$, $p < .05$. Presumably, this is because D was X's only effective comparator stimulus. Latently inhibiting D attenuated the potential for D to down-modulate behavioral control by X, leaving the target cue without any effective comparator stimulus. This resulted in more renewal. Lastly, we compared responding in Groups E1-Ctrl and E2-Ctrl to ensure that the basic effect from Experiment 1 was replicated. We observed stronger behavioral control in Group E2-Ctrl relative to Group E1-Ctrl, $F(1, 42) = 8.40$, $p < .01$, replicating our results from Experiments 1 and 2a.

Test G—Following the test on X, a test on G was conducted to check the effectiveness of our latent inhibition treatment. Groups E1-Ctrl and E2-Ctrl, which received preexposure to G, should have exhibited less suppression to G after it was paired with the US (during phase 2), relative to Groups E1-LI and E2-LI, which received preexposure to D. A 2 (phase 1: Ctrl vs. LI) $\times$ 2 (phase 3: E1 vs. E2) ANOVA was conducted on leverpressing during the 120 s prior to the first test presentation of G, similar to the baseline assessment for the X test. There were no significant main effects and no interaction, smallest $p = .10$. A similar ANOVA was conducted on the G test suppression ratios. This revealed a main effect of latent inhibition, $F(1, 42) = 6.80$, $MSE = .13$, $p < .05$. There was no main effect of phase 3 and no interaction (smallest $p = .13$). Both of these null results were expected. We had predicted that the groups would be differentiated by the phase 1 treatment (i.e., whether they

received preexposure to G or D), which is what we observed. There was no reason to think that the phase 3 treatment (extinction compound) would have a differential effect across groups on a test of G, nor was there reason to think that the two main effects should interact (see Fig. 7). Thus, these results provide evidence that our CS preexposure manipulation produced latent inhibition. As was expected, there was not a difference between Groups E1-Ctrl and E2-Ctrl, $p = .27$, nor between Groups E1-LI and E2-LI, $p = .31$. We had predicted that the phase 1 treatment would differentiate between the groups based on the preexposure treatment; however, there was not a difference between Groups E1-Ctrl and E1-LI, $p = .06$, and between Groups E2-Ctrl and E2-LI, $p = .08$. Likely, this attenuated difference is due to test order effects given that this was the second test of these groups and some generalization of extinction of responding was expected. However, the main effect of latent inhibition treatment was significant.

General discussion

In four experiments, we investigated the effect of cue interactions during compound extinction on responding in a renewal situation. In Experiment 1, we showed that extinguishing the target cue in compound with one additional excitator and one neutral stimulus yielded weak renewal, as indexed by weak conditioned suppression, which is indicative of deepened extinction, relative to extinguishing the target in compound with two associatively neutral stimuli (which is arguably comparable to elemental extinction), which showed strong conditioned suppression. However, extinguishing the target in compound with two additional excitors yielded strong conditioned suppression relative to extinction with one additional excitator and one neutral stimulus (i.e., attenuated deepened extinction). Most associative learning models do not predict this effect. To our knowledge, only the ECH can account for this pattern of data. According to this model, X retained (relatively) strong behavioral control in Group E0 because both of its comparator stimuli were associatively neutral (i.e., they lacked associations to the US; link 3 within the comparator framework). Therefore, they were unable to activate a strong representation of the US. Suppression to X was reduced in Group E1 because its behavioral control was down-modulated by D through the link 2 and link 3 associations. D was relatively unaffected by F, which did not have an association with the US. Thus, deepened extinction was the product of a strong first-order comparator process. Lastly, suppression in Group E2 was moderately strong because both of its companion stimuli were conditioned excitors. Therefore, they both had an association with the US (link 3.1/3.3), and they shared a within-compound association with each other (link 3.2), causing them to counteract each other in their potential to down-modulate behavioral control by X.

We further investigated this attenuated deepened extinction effect within a comparator framework by assessing the contribution of links 3.2 and 3.3. Experiment 2a showed that weakening the association, which was assessed in Experiment 2b, between the two added excitors (link 3.2) reduced the behavioral control by the target cue (i.e., restored the initial deepened extinction effect). Similarly, Experiment 3 showed that weakening the association through CS preexposure between one of the two added excitors and the US (link 3.3) decreased the target's behavioral control if it was extinguished in compound with two added excitors. If the target was extinguished in compound with only the preexposed added excitator and a neutral stimulus (i.e., Condition E1), its behavioral control was greater relative to a nonpreexposed control group. According to the ECH, these results occurred because weakening the counteraction effect allowed each of the comparator stimuli to more effectively down-modulate conditioned suppression to X. However, in Group E1-Ctrl, making X's only excitatory comparator stimulus ineffective reduced deepened extinction of X.

There are a number of reports of deepened extinction following compound extinction with another conditioned excitor, relative to elemental extinction or other various control conditions. Wagner (1969) demonstrated that extinction of the target stimulus in compound with a highly excitatory stimulus resulted in more extinction than when it occurred with a weakly excitatory stimulus. Similarly, Rescorla (2006) showed deepened extinction, as indexed by less spontaneous recovery, relative to elemental extinction, and Rescorla (2000) and Urcelay et al. (2009, Experiment 3, using an ABC renewal design) both showed deepened extinction relative to a control condition in which the target was extinguished in compound with an associatively neutral stimulus. Additionally, two articles have looked at the effect of extinguishing three excitors in compound. Thomas and Ayres (2004) trained rats on three different stimuli with a footshock US in an ABA renewal design. Then the rats were extinguished on all three excitors either elementally (Group E) or in compound (Group C). Group C received one third of the number of trials as Group E to equate the total number of presentations of each stimulus. A third control group did not receive any extinction (Group FC). Thomas and Ayres observed less ABA renewal (i.e., less suppression) to the elements and the compound after compound extinction, relative to elemental extinction.

Thomas and Ayres's (2004) results are compatible with those of the present series. In our Experiment 1, we also demonstrated less suppression to the element after compound extinction with three excitors, relative to compound extinction of one excitor and two neutral stimuli (which is equivalent to their Group E). As was explained before, in the framework of the ECH, this is likely due to an incomplete counteraction effect. Moreover, Experiments 2a and 3 in the present article suggest that extinction with three excitors in compound produces a deepened extinction effect when the counteraction effect is reduced. (Deepened extinction could not positively be determined because these experiments lacked an E0 control group. However, the level of suppression following the critical manipulation was similar to the level of suppression in the deepened extinction group [Group E1], which used the same parameters and procedures as those in Experiment 1, in which deepened extinction was confirmed.) Thus, in both articles, better extinction, as indexed by less renewal, was observed following compound extinction of three excitors, relative to elemental extinction. The critical point we are making in the present article is that the deepened extinction effect of compound extinction is reduced when compound extinction occurs with three excitors, relative to two. Thomas and Ayres did not include a two-stimulus compound extinction group and, thus, were unable to demonstrate attenuation of the deepened extinction effect.

Witnauer and Miller (2012) showed attenuated deepened extinction, as demonstrated in an ABC renewal design, with a nontarget discrete conditioned excitor and an excitatory context. In their first experiment, they showed deepened extinction, as indicated by less ABC renewal, following extinction of the target CS in compound with an added discrete conditioned excitor, relative to a group that received elemental extinction (it should be noted that they did not equate the number of cues that were extinguished in compound across groups, as was done in the present experiments). In their second experiment, they used a 2×2 design in which half of the groups received elemental extinction of the target CS and the other half received extinction of the target CS in compound with an added discrete excitor. Orthogonal to this, half of the groups were extinguished in a neutral context, and half received unsignaled presentations of the US in the extinction context interspersed with the extinction trials, thereby making the extinction context excitatory. In the neutral context group, they replicated the deepened extinction effect, but in the group that received compound extinction and unsignaled US presentations, they observed stronger suppression, relative to the group that received compound extinction but no US presentations or US presentations but elemental extinction. Thus, they observed attenuated deepened extinction when the target CS was extinguished with two excitatory stimuli. These authors went on to

show that their results were not likely the outcome of second-order conditioning but, rather, were the result of a counteraction effect between the discrete nontarget excitator and the excitatory context, which is consistent with our analysis of the data.

These two studies are similar in that both showed less renewal, which is indicative of deepened extinction, as a result of extinguishing the target CS in compound with an additional discrete excitator. They also both showed more renewal, which is indicative of attenuated deepened extinction, when extinction of the target CS occurred in compound with two additional excitors. In Witnauer and Miller (2012), the added excitors consisted of a discrete cue and a diffuse context that was made excitatory through unsignaled US presentations. This is similar to most other demonstrations of counteraction effects (see Wheeler & Miller, 2008, for a review) in which one of the interacting comparator stimuli is the context. In the present series of experiments, the counteraction effect occurred between two discrete cues, which has been demonstrated only one other time (Witnauer et al., 2008, showed a counteraction effect between two discrete blocking cues). These experiments are also important because they demonstrate a counteraction effect during extinction treatment. Most other counteraction effects have occurred during reinforced training.

It should be mentioned that there are a number of studies that have investigated compound extinction and found results that are seemingly opposite to those shown here. Rather than observing deepened extinction (or reduced recovery from extinction), several studies have found protection from extinction, which refers to the maintenance of behavioral control by the target as a result of extinguishing the target in compound with another stimulus. Most protection studies extinguished the target cue in compound with a conditioned inhibitor, which makes theoretical sense of why the target cue should be protected (e.g., Lovibond, Davis, & O'Flaherty, 2000; McConnell & Miller, 2010; Rescorla, 2003; Soltysik, Wolfe, Nicholas, Wilson, & Garcia-Sanchez, 1983; Thomas & Ayres, 2004). Protection from extinction provided by a conditioned inhibitor is explicable in terms of both total error reduction and the ECH (see McConnell & Miller, 2010). However, there are also a small number of reports of the protection effect provided by extinguishing the target cue in compound with a single conditioned excitator (e.g., Lovibond et al., 2000; Pearce & Wilson, 1991; Pineño, 2007a). Likely this is a result of generalization decrement going from elemental acquisition to compound extinction and from compound extinction to elemental testing. Such an explanation is favored by Lovibond et al. and is supported by data from Urcelay et al. (2009, Experiments 1 and 2), in which they failed to observe reduced ABC renewal as a result of considerable generalization decrement. Most of the studies looking at compound extinction (including the deepened extinction studies) did not equate generalization decrement going from acquisition to extinction and from extinction to testing across all of their groups. This was controlled in the present experiment by training all groups on elemental stimuli during acquisition and extinguishing all groups on a three-stimulus compound. Thus, any effect of generalization decrement should have been equated across groups, ruling out a configural processing explanation.

One might argue that the pattern of results observed in the present experiments was the result of differential protection from extinction provided by conditioned excitors. That is, on the basis of the demonstrations of protection from extinction provided by a conditioned excitator, it is possible that the stronger conditioned suppression in Experiment 1 in Group E2 was due to increased protection from extinction provided by two excitors, relative to the one in Group E1. If this were correct, one would expect the least amount of protection in Group E0, in which the target was not extinguished with any additional excitors. Thus, a protection-from-extinction account predicts a monotonic relationship between the number of additional excitors present during extinction and responding at test, such that increasing the number of excitors compounded during extinction should result in increasing levels of

conditioned suppression, presumably reflecting the increased amount of protection afforded during extinction. Lastly, as was mentioned before, the pattern of results is also not readily explicable in terms of differential second-order conditioning. Such an account predicts that increasing the number of excitors compounded during extinction should result in increasing levels of suppression to the target. These predictions are contrary to our results.

Our conclusion is that the present experiments point to additional learning mechanisms beyond simple total error reduction. Following extinction of the target in compound with zero, one, or two additional excitors, we observed strong behavioral control (presumably encouraged by ABC renewal), moderately weak behavioral control (i.e., deepened extinction), and moderately strong behavioral control (i.e., attenuated deepened extinction), respectively. These results are not consistent with predictions made by associative learning models centrally based on total error reduction, nor are the results explicable in terms of configural processing or generalization decrement, differential protection from extinction, or differential second-order conditioning. This suggests that more than simple total error reduction determines responding after extinction and, likely, after other forms of training as well.

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Fig. 1.

Mean suppression ratio of leverpressing in the presence of X in Experiment 1. 0.5 indicates no conditioned suppression; 0.0 indicates maximum conditioned suppression. Brackets indicate standard errors of the means. See Table 1 for the experimental design

Fig. 2. The extended comparator hypothesis and the original comparator hypothesis (inset). Ovals depict stimulus representations; rectangles depict physical events; diamonds represent the comparator process; arrows represent associations

Group E0

Figure 3a

Group E1

Figure 3b

Group E2

Figure 3c

Fig. 3. Depiction of the comparator process in Group E0 (a), Group E1 (b), and Group E2 (c) of Experiment 1

Fig. 4. Mean suppression ratio of leverpressing in the presence of X in Experiment 2a. Brackets indicate standard errors of the means. See Table 2 for the experimental design

Fig. 5. Mean suppression ratio of leverpressing in the presence of E in Experiment 2b. Brackets indicate standard errors of the means. See Table 3 for the experimental design

Fig. 6. Mean suppression ratio of leverpressing in the presence of X in Experiment 3. Brackets indicate standard errors of the means. See Table 4 for the experimental design

Fig. 7. Mean suppression ratio of leverpressing in the presence of G in Experiment 3. Brackets indicate standard errors of the means. See Table 4 for the experimental design

Table 1

Design of Experiment 1

Group	Preexposure ²	Phase 1 ¹ Acquisition	Phase 2 ² Extinction	Test ³
E0	4 D-/4 E-/4 F-/4 G-	4 D+/4 E+/4 X+	36 XFG-/6 X-/6 D-/6 E-/6 F-/6 G-	X
E1			36 XDF-/6 X-/6 D-/6 E-/6 F-/6 G-	X
E2			36 XDE-/6 X-/6 D-/6 E-/6 F-/6 G-	X

Note. Target CS X was a click train; CSs D, E, F, and G were a flashing light, houselight on, a low frequency complex tone, and a white noise, counterbalanced within groups with the rule that the two nontarget stimuli had to be one visual and one auditory cue.

“+” denotes reinforcement with a footshock.

“-” denotes no reinforcement.

Superscripts indicate contexts.

Numbers preceding letters indicate total number of trials in that phase.

Design of Experiment 2a

Table 2

Group	Preexposure ²	Phase 1 ² Inhib train	Phase 2 ¹ Acquisition	Phase 3 ² Extinction	Test ³	ECH
E1-Ctrl	4 D-/4 E-/4 F-/4 G-	32 DG-/32 EF-	4 D+/4 E+/4 X+	36 XDF-/6 X-/6 D-/6 E-/6 F-/6 G-	X	cr
E1-Inhib		32 DG-/32 EG-		36 XDF-/6 X-/6 D-/6 E-/6 F-/6 G-	X	cr
E2-Ctrl		32 DG-/32 EF-		36 XDE-/6 X-/6 D-/6 E-/6 F-/6 G-	X	Cr
E2-Inhib		32 DG-/32 EG-		36 XDE-/6 X-/6 D-/6 E-/6 F-/6 G-	X	cr

Note. Target CS X was a click train; CSs D, E, F, and G were a flashing light, houselight on, a low-frequency complex tone, and a white noise, counterbalanced within groups with the rule that the two nontarget stimuli during extinction training had to be one visual and one auditory cue.

“+” denotes reinforcement with a footshock.

“-” denotes no reinforcement.

Superscripts indicate contexts.

Numbers preceding letters indicate total number of trials in that phase.

Inhib indicates Inhibitory training.

ECH indicates the predicted levels of suppression by the extended comparator hypothesis.

Cr indicates moderate conditioned suppression;

cr indicates weak conditioned suppression.

Table 3

Design of Experiment 2b

Group	Preexposure	Phase 1	Phase 2	Phase 3	Test
Inhib	4 D-/4 E-/4 F-/4 G-/4 H-	32 DG-/32 EG-	3 DE-	4 D+	E→ cr
Ctrl		32 DG/32 EF-			E→ CR

Note. CS H was a click train; CSs D, E, F, and G were a flashing light, houselight on, a low-frequency complex tone, and a white noise, counterbalanced within groups with the rule that compounds always consisted of one auditory and one visual stimulus, with the exception of EG in Group Inhib, which was composed of two auditory stimuli.

“+” denotes reinforcement with a footshock.

“-” denotes no reinforcement.

Numbers preceding letters indicate total number of trials in that phase.

Design of Experiment 3

Table 4

Group	Preexp ²	Phase 1 ¹ LI train	Phase 2 ¹ Acquisition	Phase 3 ² Extinction	Test X ³	ECH	Test G ³	ECH
E1-Ctrl	4 D-/4 E-/4 F-/4 G-	96 G-	2 D+/2 E+/2 X+/2 G+	36 XDF-/6 X-/6 D-/6 E-/6 F-/6 G-	X	cr	G	cr
E1-LI		96 D-		36 XDF-/6 X-/6 D-/6 E-/6 F-/6 G-	X	Cr	G	CR
E2-Ctrl		96 G-		36 XDE-/6 X-/6 D-/6 E-/6 F-/6 G-	X	Cr	G	cr
E2-LI		96 D-		36 XDE-/6 X-/6 D-/6 E-/6 F-/6 G-	X	cr	G	CR

Note. Target CS X was a click train; CSs D, E, F, and G were a flashing light, houselight on, a low-frequency complex tone, and a white noise, counterbalanced within groups with the rule that the two nontarget stimuli during extinction training had to be one visual and one auditory cue.

“+” denotes reinforcement with a footshock.

“-” denotes no reinforcement.

Superscripts indicate contexts.

Numbers preceding letters indicate total number of trials in that phase.

LI indicates latent inhibition training.

ECH indicates the predicted levels of suppression by the extended comparator hypothesis.

CR indicates strong conditioned suppression;

Cr indicates moderate conditioned suppression;

cr indicates weak conditioned suppression.