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Comparing Context Specificity of Extinction and Latent Inhibition

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Abstract

Exposure to a cue alone either before (i.e., latent inhibition treatment) or after (i.e., extinction) the cue is paired with an unconditioned stimulus (US) results in attenuated conditioned responding to the cue. Here we report two experiments in which potential parallels between the context specificity of the effects of extinction and latent inhibition treatments were directly compared in a lick suppression preparation with rats. The reversed ordering of conditioning and nonreinforcement in extinction and latent inhibition designs allowed us to examine the effect of training order on the context specificity of what is learned given phasic reinforcement and nonreinforcement of a target cue. Experiment 1 found that when CS conditioning and CS nonreinforcement were administered in the same context, both extinction and latent inhibition treatments had reduced impact on test performance relative to excitatory conditioning when testing occurred outside the treatment context. Similarly, Experiment 2 found that when conditioning was administered in one context and nonreinforcement was administered in a second context, the effects of both extinction and latent inhibition treatments were attenuated when testing occurred in a neutral context relative to the context in which the CS was nonreinforced. The observed context specificity of extinction and latent inhibition treatments have both been previously reported, but not in a single experiment under otherwise identical conditions. The results of the two experiments convergently suggest that memory of nonreinforcement becomes context dependent after a cue is both reinforced and nonreinforced independent of the order of training.

Keywords

Latent inhibition; CS preexposure; release from latent inhibition; extinction; renewal; context shifts

Contiguous pairings between a conditioned stimulus (CS) and an unconditioned stimulus (US) endow the initially neutral CS with the potential to elicit a conditioned response (CR) that is usually characterized by the US (Pavlov, 1927). In a fear conditioning preparation, an initially neutral CS (e.g., a noise) which is paired with an aversive US (e.g., a mild footshock) comes to elicit conditioned suppression of some appetively motivated baseline

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behavior as if the subject anticipated an impending footshock. Central to the present experiments, conditioned responding is usually reduced by nonreinforced presentations of the CS, either after (i.e., extinction treatment; Pavlov, 1927) or before (i.e., latent inhibition treatment, which is also known as CS-preexposure; Lubow & Moore, 1959) excitatory conditioning (i.e., CS-US pairings).

The behavioral consequences of both extinction and latent inhibition treatments have been reported to be relatively specific to the contexts in which those treatments were administered. That is, responding is ordinarily greater outside the context of nonreinforcement (e.g., Harris, Jones, Bailey, & Westbrook, 2000; Rescorla, 2008; Westbrook, Jones, Bailey, & Harris, 2000). Moreover, even when reports concerning the context specificity of extinction and latent inhibition effects appeared in the same publication, the observations typically have been made in separate experiments in which only extinction or only latent inhibition were examined, and the extinction and latent inhibition experiments have usually used distinctly different parameters. Thus, prior conflicting reports concerning the similarity of context specificity with respect to extinction and latent inhibition effects may actually reflect superficial differences in parameters used in or across experiments rather than actual differences in the context specificity of the response attenuating effects of extinction and latent inhibition treatments (e.g., Lovibond, Preston, & Mackintosh, 1984; Maes, 2002). Critically, the present research examined the context specificity of extinction and latent inhibition effects within the same experiments using operationally matched parameters such as number of trials and trial spacing. This facilitated assessment of similarities and differences in context specificity of extinction and latent inhibition effects based uniquely on the information content of what is learned in the two types of nonreinforced treatments (i.e., differing only in terms of whether nonreinforcement follows or precedes reinforced training). We postpone until later in the paper discussion of why the similarities and differences in the context specificity of extinction and latent inhibition effects are of theoretical importance.

The operational similarities of extinction and latent inhibition treatments as well as the cross-experiment reported similarities in context specificity of expression of what is learned in these two situations encouraged us to expect similarities in context specificity in the present experiments. However, the two nonreinforcement treatments occur on opposite sides of reinforced training with respect to time, which results in an extinction treatment constituting omission of a specific expected US in contrast with a latent inhibition treatment constituting nonreinforcement in the absence of expectation of any US. These two inherent differences (timing and information content of nonreinforcement) resulting from procedure suggest that there may be differences in what is learned in the two situations. Consequently, one might expect differences in the context specificity of extinction and latent inhibition effects despite their both operationally consisting of nonreinforced presentations of the target CS.

In both Experiments 1 and 2, we employed 2 × 2 mixed designs, with different cues being used in the extinction and latent inhibition conditions being the within-subjects independent variable, and test context (that of nonreinforcement or a context neutral with respect to the test cue) being a between-subjects independent variable. In both experiments, we omitted inclusion of a group that received no CS-alone presentations because we had previously demonstrated using similar parameters that the present conditioning treatment alone results in robust conditioned suppression in the form of a mean suppression latency of 2.0 log s compared to unconditioned rats with a mean suppression latency of 0.9 log s (e.g., Wheeler, Chang, & Miller, 2003, Experiment 2).

Given phasic reinforcement and nonreinforcement of a cue, there are many accounts of why a shift in context at the time of test to a context other than where nonreinforcement of the cue had occurred enhances conditioned responding. The two most widely cited accounts both were proposed by Bouton (e.g., 1993). The first posits that memory of nonreinforcement is context specific, so a shift from the context of nonreinforcement at the time of test attenuates retrieval of what was learned about nonreinforcement irrespective of the order of training (i.e., nonreinforcement before or after conditioning). Consequently, in the context shift condition deficient retrieval of memory of nonreinforcement should lead to more robust expression of excitatory conditioning (i.e., stronger behavioral control by the target cues) outside of the context of nonreinforcement (Group Different in the present experiments) than in the context of nonreinforcement (Group Same). Moreover, this enhancement of behavioral control should be equal for the extinguished and latently inhibited CSs. Bouton's second account posits that second-learned information about a cue is context specific, that is, retrieval of whichever memory about a cue was acquired second should be impaired when testing occurs outside of the context in which the second-learned relationship was acquired. Based on this mechanism, after a latent inhibition treatment, excitatory conditioning should only weakly transfer to a context in which the target cue has not previously been presented, resulting in attenuated behavioral control by the preexposed CS. In contrast, following an extinction treatment, nonreinforcement learning should only weakly transfer, resulting in relatively strong behavioral control by the extinguished CS. Note that both of these accounts attribute an occasion setting property to one of the treatment contexts, but they differ in the factor (i.e., site of nonreinforcement or site of second-learned information concerning the target cue) that determines which of the two treatment contexts will serve as the occasion setter. Although these two accounts of the context specificity of stimulus control following phasic reinforcement and nonreinforcement are by far the most widely cited, there are other accounts, some of which we consider in the General Discussion.

Experiment 1: Nonreinforcement and conditioning in the same context; test in treatment context or a context that is neutral with respect to the target cue

In Experiment 1, we examined the sensitivity to test context of extinction and latent inhibition effects by administering nonreinforced exposure and conditioning of the target CSs in the same context, and then testing in the same context (Group Same) or a different context (Group Different). Conditioning without nonreinforced trials is known to transfer rather well to contexts different from that of conditioning (e.g., Bouton & King, 1983; Nelson, 2002). Our question was whether the effects of an extinction treatment and a latent inhibition treatment (i.e., nonreinforced CS exposure) would transfer equally to a context different from that of treatment (i.e., where both conditioning and nonreinforced exposures to the CS had occurred) given identical operational treatments within the same experiment except for the temporal order of nonreinforcement of the target cues with respect to their reinforcement.

In Experiment 1 (see Table 1), using the conventional nomenclature of context shift effects in which the first of three letters specifies the context of Phase 1 treatment, the second letter specifies the context of Phase 2 treatment, and the third letter specifies the test context, we compared an AAB context shift condition (Different) with an AAA control condition (Same) for both extinction and latent inhibition conditions. All rats received preexposure to CS Y in Context B prior to independent pairings of CS Y with a footshock US in Context B and CS X with the same US in Context A, followed by extinction of CS X in Context A. At test, half of the rats were tested for conditioned suppression to X and Y in the contexts in which each of these cues were nonreinforced [as well as reinforced] (Group Same: Y in Context B and X in Context A). The other half of the rats were tested for suppression to X and Y in contexts different from those used for treatment of the cue being tested (Group Different: Y in Context A and X in Context B). This procedure allowed us to directly compare conditioned suppression after an extinction treatment in an AAB renewal design (i.e., AAB vs. AAA) with suppression in the analogous design for latent inhibition (i.e., BBA vs. BBB in the notation of Table 1). Context specificity of expression of knowledge concerning nonreinforcement should have been equal for extinction and latent inhibition treatments. However, if what was learned second was context specific, testing outside the context in which the target cue was nonreinforced should have generated a greater recovery in the extinction condition than the latent inhibition condition. Such an effect would take the form of an interaction between cue (X vs. Y) and test context (Same vs. Different).

Methods

Subjects—The subjects were 24 male (224–315 g) and 24 female (173–218 g), young adult, experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Subjects were randomly assigned to one of two groups (Groups Same and Different, *n*s = 24), 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 one 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—Twenty-four experimental chambers of two different types were used to create two distinct contexts. Chamber V (12 instances) was a 27-cm long box in a truncated-V shape (29.5-cm height, 21.5-cm wide at top, and 5.5-cm wide at bottom). The floor was comprised of two 27-cm long, 2-cm wide stainless plates, with a 1.5-cm gap between the two plates. A constant-current footshock, produced by a high voltage AC circuit in series with a 1.0-MΩ resistor could be delivered through the metal walls and floor of the chamber. The ceiling was clear Plexiglas, the front and back walls were black Plexiglas, and the sidewalls were stainless steel. Each instance of Chamber V was housed in a separate sound- and light-attenuating environmental isolation chest. The chamber was illuminated by a 7-W (nominal at 120 VAC, but driven at 50 VAC) light bulb, which was mounted on the inside wall of the environmental enclosure, approximately 30-cm from the center of the experimental chamber. The light entered the chamber primarily by reflection from the ceiling of the environmental chest. Each Chamber V could be equipped with a water-filled lick tube that extended 1-cm into a cylindrical niche, which was 4.5 cm in diameter, left-right centered, with its bottom 1.75-cm above the floor of the apparatus and 5.0 cm deep. There was a photobeam detector 1-cm in front of the lick tube that was broken whenever a subject licked the tube.

Chamber R (12 instances) was rectangular, measuring 24.0 × 9.0 × 12.5 cm (l × w × h). The walls and ceiling of Chamber R were clear Plexiglas, and the floor was composed of stainless steel rods measuring 0.5-cm diameter, spaced 1.3-cm apart (center to center) with the rods connected by NE-2 bulbs which allowed the delivery of a constant-current footshock. Each instance of Chamber R was housed in a separate light- and sound-attenuating environmental isolation chamber. Each chamber was dimly illuminated by a 2-W (nominal at 120 VAC, but driven at 50 VAC) incandescent house light mounted on an inside wall of the environmental chest located approximately 30-cm from the animal enclosure. Each Chamber R could be equipped with a water-filled lick tube identical to that in Chamber V.

Two 45-Ω speakers on the inside walls of each isolation chest could deliver a click train (6 Hz, 6 dB above background) and a complex tone (450 and 550 Hz simultaneously, 6 dB above background). Ventilation fans in each isolation chest provided a constant 76-dB background noise. All auditory cues were measured on the C-scale. The light intensities inside chambers V and R were approximately equal due to the difference in opaqueness of the walls.

A 30-s click train and a 30-s complex tone served as CS X (target cue to be extinguished) and CS Y (target cue to be preexposed), counterbalanced within groups, and a 0.7-mA, 0.5-s footshock served as the US. The physical identities of Contexts A and B were counterbalanced between Chambers R and V within groups. Importantly, the design used in this experiment (as well as the subsequent one) assured that the test contexts were matched with respect to total exposure as well as reinforced and nonreinforced events that occurred in them except for which specific CS (extinguished or preexposed cue) had been nonreinforced in it.

Procedure

Acclimation: On Day 1, all subjects were acclimated to Contexts A and B for 30 min each with the order of sessions counterbalanced within groups. The time between sessions was approximately 200 min. In these sessions, subjects had free access to water-filled lick tubes and no nominal stimuli were programmed to occur.

CS Preexposure: On Days 2 and 3, all subjects received a daily 60-min session in Context B with no lick tube present. Subjects in both groups received 16 daily nonreinforced presentations of Y with a mean intertrial interval (ITI) of 3.75 min, from CS onset to CS onset.

CS Conditioning: On Days 4 and 5, all subjects received two daily 60-min sessions, one consisting of two presentations of CS X co-terminating with the US in Context A with 30-min ITIs (from CS onset to CS onset), and the other consisting of two presentations of Y coterminating with the US in Context B with the same ITI. The order of these sessions was counterbalanced within groups

CS Extinction: On Days 6 and 7, all subjects received a daily 60-min session in Context A with no lick tube present. Subjects in both groups received 16 daily nonreinforced presentations of X with a mean ITI of 3.75 min, from CS onset to CS onset.

Reacclimation: On Days 8–11, all subjects were reacclimated to Contexts A and B during daily 120-min sessions, with the order of sessions counterbalanced within groups. The time between sessions was approximately 240 min and no nominal stimulus was programmed to occur during this phase. On Days 10 and 11, but not on Days 8 and 9, all subjects had free access to water-filled lick tubes. Sessions in this phase had two aims: a) to provide similar baseline drinking behavior in both contexts across both groups, and b) to increase sensitivity to context shift effects in extinction and latent inhibition designs when reinforced and nonreinforced trials occurred in the same context. Prolonged exposure to the test context (i.e., context extinction) has been shown to enhance responding following extinction (e.g., Laborda, Witnauer, & Miller, 2011) and latent inhibition (e.g., Escobar, Arcediano, & Miller, 2002) paradigms in which reinforced and nonreinforced trials have been presented in the same context, like in the present design. Without the additional context extinction, recovery from the effects of extinction and latent inhibition treatments is relatively hard to detect when both acquisition and nonreinforcement are given in the same context. The extensive amount of reacclimation was necessitated by the fact that during conditioning, footshocks had been administered in Contexts A and B.

Testing: All subjects were tested once daily on two consecutive days (Days 12–13). During test sessions, subjects had free access to the water-filled tubes. All subjects were tested for conditioned lick suppression to X and Y on separate days, with the order of testing counterbalanced within groups. Subjects in Group Same were tested in the contexts in which each CS was trained (i.e., X in Context A and Y in Context B), whereas subjects in Group Different were tested in contexts different than those in which each CS was trained (i.e., X in Context B and Y in Context A). On both tests, upon placement in the test chamber, time spent drinking by each subject was recorded. Immediately after completion of an initial 5 cumulative seconds of licking in the absence of any nominal stimulus, subjects were presented with the target cue. Thus, all subjects were drinking at the time of CS onset. Time to complete an additional 5 cumulative seconds of licking in the presence of the target cue was recorded and interpreted as reflecting subjects' conditioned fear of the CS. The test session was 11 min in duration with a ceiling score of 10 min on the time to complete 5 cumulative seconds of drinking in the presence of the target cue. All test scores were converted to $\log_{10}$ to better approximate the within-group normal distributions assumed by parametric statistical tests. Following the convention of our laboratory, all animals that took more than 60 s to complete their first 5 cumulative seconds of licking (i.e., prior to CS onset) during the test session were scheduled to be eliminated from the study because such long latencies were considered indicative of unusually great fear of the test context. In practice, one animal from Group Same was eliminated from the subsequent statistical analysis.

Results

The results of Experiment 1 are depicted in Figure 1. When subjects were tested outside the context of treatment for the target cues (Group Different), they exhibited strong conditioned suppression to cues that received an extinction treatment (X) or a preexposure treatment (Y), compared with the behavior of subjects when testing occurred in the context of treatment for the test cue (Group Same). More specifically, testing an extinguished cue in a neutral (with respect to that cue) but familiar context produced more conditioned suppression than testing the same cue in the context in which the conditioning and extinction treatments had taken place. Likewise, testing a preexposed cue in a neutral (with respect to that cue) but familiar context produced more conditioned suppression than testing the same cue in the context in which preexposure and conditioning had occurred. Additionally, conditioned suppression to X and Y was equivalent in Group Same and was also equivalent in Group Different. The following statistical analysis supported these conclusions.

A 2 (Context of testing: Same vs. Different) × 2 (Cue: X vs. Y) × 2 (Order of tests: X first vs. Y first) ANOVA applied to the log pre-CS latencies on the test days detected no significant main effect or interaction (smallest $p = .17$), indicating that the experimental groups did not appreciably differ in their baseline drinking. PreCS means were 1.16 log s (Group Same X), 1.20 log s (Group Same Y), 1.23 log s (Group Different X), and 1.24 log s (Group Different Y). The same analysis on latencies to complete 5 cumulative seconds of drinking in the presence of the CS detected a main effect of Context of testing, $F(1, 86) = 28.81$, $p < .01$, $MSE = 0.19$, partial $\eta^2 = 0.25$ (95% CIs = .11, .39). This indicates that, overall, when subjects were tested in a context different from that of nonreinforcement treatment, they displayed strong conditioned suppression compared to subjects tested in the context of treatment. All other main effects and interactions were nonsignificant, smallest $p = .12$.

Planned comparisons were performed to evaluate differences between responding to X and Y within each group. A nonsignificant difference in responding to X and Y in Group Same, $F(1, 86) = 0.48$, $p = .49$, and a nonsignificant difference in responding to the same cues in Group Different, $F(1, 86) = 2.37$, $p = .13$, indicate that suppression to X and Y did not appreciably differ in either group. The similarity of means between responding to X and Y in Group Same and between responding to X and Y in Group Different were confirmed by Bayesian analyses (Rouder, Speckman, Sun, & Morey, 2009), with odds of 21.36 in favor of the null hypothesis for the comparison in Group Same and with odds of 5.21 in favor of the null hypothesis for the comparison in Group Different.

If one assumes that excitatory conditioning and nonreinforced exposures to a target cue in the present situation each produced its own memory independent of the order of training, and that as Bouton (1993) suggested there are two and only two (potentially additive) factors that contribute to the context specificity of a memory (i.e., the memory is a second-learned contingency concerning the cue[1], and the memory is one of nonreinforcement), the present observations provide a means of dissociating the influence of these two factors. With these assumptions, context specificity of a latent inhibition effect reflects *only* the context specificity of memory of nonreinforcement, and context specificity of an extinction effect reflects the sum of the context specificity of memory of nonreinforcement *and* the context specificity of nonreinforcement being the second thing learned. Applying this reasoning to the results of Experiment 1, the observed context specificity of the latent inhibition effect with CS Y (the preexposed cue) evidences significant context specificity of the latent inhibition effect arising from Y being nonreinforced. Moreover, the absence of greater context specificity of extinction effects with CS X (the extinguished cue) suggests that nonreinforcement of X acquired no additional context specificity due to its being the second-learned relationship concerning X over the context specificity of the memory of X-alone trials resulting from X having been nonreinforced. Alternatively stated, Experiment 1 provided evidence of memory of nonreinforcement being context specific, but no evidence of the second-learned memory of nonreinforcement being any more context specific than when the corresponding memory was not second learned.

The above reasoning ignores the possibility that the *excitatory* conditioning of CS Y was to some degree context specific because it was the second thing learned about Y. However, to the extent that this process reduced suppression to CS Y in Condition Different, it could only have masked an even greater context specificity of nonreinforcement of CS Y than was observed. Context specificity of the effect of excitatory conditioning of CS Y would have favored less conditioned suppression to CS Y in Context Different than Context Same, potentially contributing to less of a context shift effect with CS Y than CS X, which was in fact not observed. Alternatively stated, any context specificity of memory of excitatory training of CS Y would have contributed to a difference in context specificity between CS X and CS Y in the opposite direction to that needed to explain why suppression to CS X was not greater than that to CS Y. Of course, the "*if*" opening the preceding paragraph is critical; there were a number of assumptions made there on which the subsequent reasoning depends. We delay until the General Discussion an alternative account of the results of Experiment 1 that is based on Wagner's (1981) SOP model.

Experiment 2: Nonreinforcement and conditioning in different contexts; test in nonreinforcement context or a context that is neutral with respect to the target cue

Experiment 1 suggested that given phasic reinforcement and nonreinforcement of a CS in the same context, expression of memory of CS nonreinforcement is specific to the treatment context independent of whether reinforcement or nonreinforcement was experienced first. A potential complication in interpreting the results of Experiment 1 is that by testing inside of

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[1] Here we refer to the view that second-learned information about a cue is context dependent. Nelson (2009) has demonstrated that this position for two-phase training situations is a special case of a more general position in which anything learned about a cue that is inconsistent with prior learning about that cue (i.e., second, third, etc. learned information) is context specific.

the context of nonreinforcement treatment (Group Same), we were also testing inside the context in which excitatory conditioning of the CS had occurred. Thus, the context specificity of expression of learning about noneinforcement was confounded by the potential context specificity of expression of excitatory learning. This raises the question of whether the context specificity of expression of memories because they were acquired second that was not observed in Experiment 1 might be observed with a design in which nonreinforced exposure to the target CS occurred in a context different from that of conditioning, and testing occurred in the nonreinforcement context or a context that was neutral with respect to the target cue. Experiment 2 was designed to answer this question.

In Experiment 2 (see Table 2), all rats received preexposure to CS Y in Context C prior to independent pairings of CS X and CS Y with a footshock US in Context A, followed by extinction of CS X in Context B. At test, half of the rats were tested for conditioned suppression to X and Y in the contexts in which each of these cues were nonreinforced (Group Same: X in Context B and Y in Context C), and the other half of the rats were tested for suppression to X and Y in contexts different from those used for nonreinforced treatment of the cue being tested (Group Different: X in Context C and Y in Context B). As a result of being tested outside the context of nonreinforcement for that particular CS, Group Different was expected to exhibit a release from latent inhibition (CS Y) and recovery from extinction (CS X). This procedure allowed us to directly compare conditioned suppression to CS X after an extinction treatment in what is conventionally referred to as an ABC renewal design (i.e., ABB vs. ABC) with suppression in the analogous design for latent inhibition (i.e., CAB vs. CAC in the notation of Table 2). Again, context specificity of expression of knowledge concerning nonreinforcement per se should have been equal for extinction and latent inhibition treatments. However, if what was learned second about the target CS was also context specific, testing in a ‘neutral’ context (i.e., neutral with respect to the cue being tested) relative to the context of nonreinforcement should have generated greater recovery in the extinction condition than the latent inhibition condition. This is because in the extinction condition increased stimulus control in the neutral context should reflect release from context specificity of nonreinforcement due to nonreinforcement being context specific plus release from any context specificity of the nonreinforcement treatment due to nonreinforcement being second learned. In contrast, in the latent inhibition condition increased stimulus control in the neutral context should reflect release from context specificity of nonreinforcement due to nonreinforcement being context specific *minus* any context specificity of the excitatory conditioning due to excitatory conditioning being second learned. Thus, context specificity of what was learned second would take the form of an interaction between cue (X vs. Y) and test context (Same vs. Different).

Methods

Subjects—The subjects were 24 male (183–325 g) and 24 female (161–219 g), experimentally naive, Sprague Dawley descended rats obtained from our own breeding colony. Subjects were randomly assigned to one of two groups (Same and Different, *n*s = 24), counterbalanced within groups for sex. Housing and maintenance of all subjects was identical to Experiment 1.

Apparatus—As in Experiment 1, a 30-s click train and a 30-s complex tone served as CS X and CS Y (counterbalanced within groups), and a 0.7-mA, 0.5-s footshock served as the US. Six instances of Chamber R (which now contained Plexiglas floor on top of the steel rod floor) and 6 instances of Chamber V were used as Contexts B and C, counterbalanced within groups. A third chamber, Chamber Modified-R, (12 instances) was used as Context A for all subjects. This chamber was the same as Chamber R with five modifications: (1) a different instance of Chamber R, (2) the Plexiglas floor covering was removed to reveal the stainless steel rods beneath, (3) the house light was off, (4) a daily drop of methyl salicylate was placed onto a small block of wood located inside the isolation chest, and (5) no lick tube was present in this context.

Procedure

Acclimation: On Day 1, all subjects were acclimated to Contexts B and C for 30-min each with the order of sessions counterbalanced within groups. Procedural details were exactly as in Experiment 1.

CS Preexposure: On Days 2 and 3, all subjects received a daily 60-min session in Context C with no lick tube present. Subjects in both groups received 48 daily nonreinforced presentations of Y with a mean ITI of 1.25 min, from CS onset to CS onset. The number of nonreinforced presentations was increased from 16 per day in Experiment 1 to 48 with the intent of avoiding a ceiling effect for conditioned suppression, which was relatively likely within a design in which the latent inhibition treatment is administered in a context different from that of excitatory conditioning. That is, latent inhibition effects are smaller when the latent inhibition treatment is administered outside the conditioning context (Bouton & Bolles, 1979; Channell & Hall, 1981; Hall & Minor, 1984). The present increase in the number of nonreinforced exposures to the target CSs was intended to compensate for this.

CS Conditioning: On Days 4 and 5, all subjects received two daily 60-min sessions, one consisting of two presentations of X co-terminating with the US in Context A with 30-min ITIs (from CS onset to CS onset), and the other consisting of two presentations of Y co-terminating with the US in Context A with the same ITI. Procedural details were identical to those in Experiment 1.

CS Extinction: On Days 6 and 7, all subjects received a daily 60-min session in Context B with no lick tube present. Subjects in both groups received 48 daily nonreinforced presentations of X with a mean ITI of 1.25 min, from CS onset to CS onset.

Reacclimation: On Days 8 and 9, all subjects were reacclimated to Contexts B and C for 30-min each with the order of sessions counterbalanced within groups. The time between sessions was approximately 200 min. In these sessions, subjects had free access to water-filled lick tubes and no nominal stimulus was programmed to occur. The purpose of these sessions was to reestablish stable drinking behavior (which might have been differentially disrupted by prior training), thereby producing similar baseline behavior across the two groups in both Contexts B and C upon which conditioned lick suppression could be assessed.

Testing: All subjects were tested once daily on two consecutive days (Days 10 and 11). During test sessions, subjects had free access to water-filled tubes. All subjects were tested for conditioned lick suppression to X and Y on separate days, with the order of testing counterbalanced within groups. Subjects in Group Same were tested in the contexts in which each CS had been nonreinforced (i.e., X in Context B and Y in Context C), whereas subjects in Group Different were tested in contexts different than those in which each CS had been nonreinforced (i.e., X in Context C and Y in Context B). Except for the contexts of testing, all procedures, data recording, and transformations were done as in Experiment 1. No subjects were excluded from the present experiment based on the elimination criterion.

Results

The results of Experiment 2 are depicted in Figure 2. When subjects were tested outside the context of nonreinforced treatment for the target cue (i.e., Group Different), they exhibited strong conditioned suppression to the cues that were extinguished (X) and preexposed (Y), compared with suppression by subjects tested in the contexts in which they had received nonreinforced treatment with that target cue (i.e., Group Same). More specifically, testing an extinguished cue in a neutral but familiar context produced more conditioned suppression than testing the same cue in the context in which the extinction treatment had taken place (i.e., ABC renewal). Likewise, testing a preexposed cue in a neutral but familiar context produced more conditioned suppression than testing the same cue in the context in which preexposure occurred (i.e., release from latent inhibition). Additionally, conditioned suppression to X and Y was similar in Group Same and was also similar in Group Different. The following statistical analysis supported these conclusions.

A 2 (Context of testing: Same vs. Different) × 2 (Cue: X vs. Y) × 2 (Order of tests: X first vs. Y first) ANOVA applied to the log pre-CS latencies (i.e., time to complete the first 5 cumulative seconds of drinking in the absence of the CS) on the test days detected no significant main effect or interaction (smallest $p = .10$), indicating that the experimental conditions did not appreciably differ in baseline drinking. PreCS means were 1.23 log s (Group Same X), 1.19 log s (Group Same Y), 1.22 log s (Group Different X), and 1.17 log s (Group Different Y). A parallel analysis of latencies to complete 5 cumulative seconds of drinking in the presence of the CS detected a main effect of Context of testing, $F(1, 88) = 17.26$, $p < .01$, $MSE = 0.12$, partial $\eta^2 = 0.16$ (95% CIs = .05, .30), indicating that overall, when subjects were tested in a context different from that in which nonreinforced treatment had occurred, they displayed greater conditioned suppression. That is, Group Different exhibited more conditioned suppression than Group Same. All other main effects and interactions were nonsignificant (smallest $p = .13$).

Planned comparisons were performed to evaluate differences between responding to X and Y within each test context group (i.e., Same and Different). A nonsignificant difference in responding to X and Y in Group Same, $F(1, 88) = 0.19$, $p = .66$, and a nonsignificant difference in responding to the same cues in Group Different, $F(1, 88) = 0.79$, $p = .38$, suggest that responding to the two cues was approximately equivalent in each group. The near equality of means between responding to X and Y in Group Same and between responding to X and Y in Group Different were confirmed by Bayesian analyses (Rouder et al., 2009), with odds of 32.29 in favor of the null hypothesis for the comparison in Group Same and with odds of 16.34 in favor of the null hypothesis for the comparison in Group Different.

Notably, in Experiment 2 the critical comparison was between the context specificity of the effects of extinction (i.e., ABC vs. ABB) and the context specificity of the effects of latent inhibition treatment (i.e., CAB vs. CAC). Thus, the control condition for extinction was tested in the same context as Phase 2 [nonreinforcement] treatment (i.e., ABB), whereas the control condition for latent inhibition tested in the same context as Phase 1 [also nonreinforcement] treatment (i.e., CAC). Thus, one might expect the extinction treatment, by virtue of superior recency with respect to test, to have a greater impact on test performance than the latent inhibition treatment. However, in practice, three days passed between the end of Phase 2 treatment and test, during which Reacclimation occurred with multiple exposures to both context B and C. This presumably minimized any effect of differential recency of nonreinforcement relative to test between the extinction and latent inhibition conditions.

These findings, in conjunction with the absence of any interaction between responding to X and Y, indicate a parallel between extinction and latent inhibition effects: both are subject to reduced impact of nonreinforced trials when testing occurs outside the context of nonreinforcement. Thus, at least with the present parameters, the magnitude of the ABC renewal effect for extinction appears to be similar to the analogous release from latent inhibition effect. This suggests that in this situation, at least with the current parameters, nonreinforcement being learned second (i.e., extinction) relative to its being learned first (latent inhibition treatment) does not appreciably influence the context specificity of learning about nonreinforcement. Thus, Experiment 2 conceptually replicated the central finding of Experiment 1, now in a situation in which conditioning and nonreinforcement occurred in different contexts.

General Discussion

Implications for Bouton's two hypotheses

As previously noted, our designs allowed us to directly compare in a single experiment conditioned suppression elicited by an extinguished cue and by a preexposed cue in the context in which each cue had been nonreinforced and outside that context. This feature permitted us to assess Bouton's (1993) two hypotheses concerning what information becomes context specific after a cue has become ambiguous by being sequentially reinforced and nonreinforced. One hypothesis is that what becomes context dependent after a cue is both reinforced and nonreinforced is the memory of nonreinforcement. In this framework, excitatory learning is thought to be less susceptible to contextual changes than is the inhibitory-like learning that may occur during nonreinforced trials. Bouton's second hypothesis, not necessarily exclusive with respect to the suggestion that information concerning nonreinforcement is context specific, is that second-learned information becomes context specific. Evidence indirectly supporting this account comes from studies in which the target cue received both excitatory conditioning and Pavlovian conditioned inhibition training (as opposed to excitatory conditioning and nonreinforced presentations of the CS as in the current research). For example, Nelson (2002) found that independent of the order of training, if a cue is sequentially trained as a conditioned excitor and as a conditioned inhibitor, information acquired second was context dependent. Sissons and Miller (2009) found that the same was true when the temporal contexts were manipulated instead of the physical context of training; that is, information learned first showed ‘spontaneous’ recovery independent of its being excitatory or inhibitory. The present experiments examined whether this second hypothesis (i.e., second-learned information concerning a cue is context dependent), that seemingly applies when the two phases of treatment consist of excitatory conditioning and Pavlovian inhibitory conditioning, also applies when the two phases of treatment consist of excitatory conditioning and simple nonreinforced presentations of the target CS as are administered in extinction and latent inhibition treatments.

These two potential mechanisms should have summative effects on responding to an extinguished CS (because in an extinction paradigm the second-learned information about the CS concerns nonreinforcement). But they should have opposing effects on responding to a preexposed CS (because in a latent inhibition paradigm the second-learned information about the CS concerns excitatory conditioning). Hence, a difference between the context specificities of extinction and latent inhibition treatments is potentially a measure of the extent to which second-learned information is context specific at least in this situation (i.e., phasic excitatory conditioning and nonreinforcement) with the present matched parameters. The observed absence of any appreciable difference between CS X and CS Y in terms of context specificity of conditioned suppression suggests that the process that makes second-learned information context specific was inoperative here. In contrast, the observed equivalent context specificity of extinction and latent inhibition treatments testifies that the process that makes information concerning nonreinforcement context specific was operative in the present situation. Critically, these conclusions depended on our use of operationally matched procedures and parameters for extinction and latent inhibition treatments.

Experiments 1 and 2 each conceptually replicate numerous prior reports of reduced attenuation of stimulus control by extinction and latent inhibition treatments when testing occurs outside of the context of nonreinforcement. This was seen regardless of whether excitatory conditioning occurred in the same context as nonreinforcement (Experiment 1) or in a different context (Experiment 2). These experiments not only conceptually replicated prior research; the present results were obtained with extinction and latent inhibition treatments being administered within the same experiment and with matched operational parameters. Clearly and unsurprisingly, the behavioral consequences of nonreinforced exposure to the target CSs transferred relatively weakly to a context different than that in which nonreinforced exposure to the CSs had occurred. Of greater interest, the absence of an appreciable interaction between cues (i.e., X vs. Y) and test context (i.e., Same vs. Different) in each experiment suggests that, in the present situation, transfer of second-learned nonreinforcement (i.e., extinction) was no different than transfer of first-learned nonreinforcement (i.e., latent inhibition treatment). Moreover, although one might expect knowledge of excitatory conditioning in the latent inhibition condition to be more context specific (than in the extinction condition) because excitatory conditioning was second learned, no suggestion of such an effect was observed. Thus, at least with the present design (i.e., nonreinforcement and excitatory aversive conditioning) and parameters, information concerning nonreinforcement of a CS did not to any large degree depend on whether nonreinforcement was the first or second thing learned about the CS. The present absence of any appreciable interaction suggests that neither second-learned nonreinforcement nor second-learned conditioning is context specific relative to their being first learned in latent inhibition and extinction situations. Alternatively stated, our results suggest that nonreinforcement alone determines which context will play the modulatory (i.e., occasion setting) role in situations like this.

Of course it is possible that a difference between the extinguished cue (X) and preexposed cue (Y) in what was learned during the nonreinforced treatment (due to whether or not conditioning preceded nonreinforcement) compensated for any greater context specificity of knowledge of nonreinforcement concerning the extinguished cue than the preexposed cue. But such a two-process account would leave unspecified the nature of this difference in learning concerning nonreinforcement and it is far less parsimonious than the view that the nature of what was second learned (i.e., nonreinforcement vs. conditioning) is irrelevant to the context specificity of knowledge concerning noneinforcement. Hence, although this two-process account cannot be categorically rejected, it appears to be relatively implausible. When two phenomena have the same properties, the most parsimonious (although not certain) conclusion is that they arise from common underlying processes. In the present case we seemingly see extinction and latent inhibition treatments as two examples of two-phase associative interference involving excitatory conditioning in one phase and simple nonreinforced presentations of the target cue in the other phase.

Implications beyond Bouton’s accounts

Although we observed that the effects of extinction and latent inhibition treatments are relatively specific to the context of nonreinforcement, and we use these findings to suggest that the effects of extinction and latent inhibition treatments may be a product of a single interference mechanism, we acknowledge the remaining possibility that the context-specificity of nonreinforcement evidenced here in extinction and latent inhibition effects might well have arisen from different mechanisms. During an extinction treatment, organisms experience a violation of an established US expectation, which may encourage the context to acquire modulatory properties (e.g., Bouton, 1993) or direct inhibitory properties (e.g., Polack, Laborda, & Miller, 2012) that support less stimulus control of behavior in the context of extinction treatment than in a neutral context. In the case of a latent inhibition treatment, there is no violation of US expectations during CS-alone presentations as the CS has not yet been reinforced. Thus, some form of conditioned inhibition is possibly at play in producing experimental extinction that could not contribute to latent inhibition effects. Thus, despite our observing a parallel in the nature of context specificity between extinction and latent inhibition effects in the present experiments, these effects still may not share a common underlying mechanism. The present observations add to the already existing evidence supportive of a common interference mechanism, but surely additional research on this issue is needed.

Inconsistency with prior research

In summary, Experiments 1 and 2 provided convergent results suggesting that the memory of nonreinforcement per se becomes equally context dependent after a cue is both reinforced and nonreinforced regardless of whether nonreinforcement precedes or follows excitatory conditioning. We make no assertion about the context specificity of conditioned excitation, as the present experiments were not designed to examine that issue. We only contrasted the context specificity of memory of nonreinforcement treatment before excitatory conditioning with the context specificity of memory of nonreinforcement treatment after excitatory conditioning. This conclusion is contrary to some prior reports, most notably Lovibond et al. (1984, Exp. 2) who also examined the context specificity of extinction and latent inhibition effects within a single experiment. However, Lovibond et al. did not use the same parameters for their extinction and latent inhibition treatments. As previously noted, our conclusion that extinction and latent inhibition effects are equally sensitive to whether testing occurs inside or outside the context used for nonreinforcement contrasts with the observed context specificity of what gets learned second when phasic excitatory conditioning and Pavlovian inhibitory conditioning are administered in Phases 1 and 2. This difference highlights the distinction between nonreinforcement in conditioned inhibition training (in which a specific US is expected at the time of nonreinforcement) and nonreinforcement during CS-preexposure treatment (in which there is no expectation of a US at the time of nonreinforcement).

Contrasting the context specificity of extinction learning with that of conditioned inhibition training

In the present experiments, the context specificity of extinction effects seems to be driven by the same or at least an analogous mechanism to that which produces context specificity of latent inhibition treatment (i.e., knowledge of nonreinforcement is context specific). This is somewhat surprising, as in recent years extinction learning (but not learning during latent inhibition treatment) has often been viewed as a form of inhibition learning because noneinforcement during extinction treatment occurs when there is an expectation of the specific US that was presented during excitatory conditioning (e.g., Bouton, 1993). However, one must note the clear operational difference between Pavlovian conditioned inhibition training in which the expectation of the US arises from a conditioned excitor that is compounded with the inhibitory CS, and extinction treatment in which the prevailing view is that the expectation of the US arises from the cue itself that is being extinguished. Whether and why this operational difference alters the mechanism responsible for context specificity of information concerning nonreinforcement is a question that future research will have to address. Moreover, the present research was not designed to examine why memories of nonreinforcement per se (as opposed to conditioned inhibition training) are more context specific than memories of excitatory conditioning. That too is a question that calls for future examination.

In contrast to a memory of target cue nonreinforcement established during cue-alone presentations being similarly context dependent whether they are formed before or after excitatory conditioning, memories of target cue nonreinforcement that are established during Pavlovian conditioned inhibition training have been reported to be far more context dependent when the inhibitory training is second learned (i.e., follows as opposed to precedes excitatory conditioning; Nelson, 2002; Sissons & Miller, 2009). Hence, the present conclusions concerning cue nonreinforcement within latent inhibition and extinction procedures should not be overgeneralized to cue nonreinforcement experienced within Pavlovian conditioned inhibition training.

Other accounts of the present data

Thus far, our analysis of the context specificity of stimulus control following phasic reinforcement and nonreinforcement has focused on Bouton's (1993) two accounts because they are the ones that are most widely cited. Notably, in both of Bouton's accounts the test context serves as an occasion setter for CS-US association being tested. However, there are other very different mechanisms that might contribute to the observed context specificity of nonreinforced exposures to a CS. For example, Wagner's (1981) SOP model suggests that many nonreinforced presentations of a CS in a given context establish a strong context-CS association. At test in the context of nonreinforcement, prior to CS onset the test context presumably activates a representation of the CS into Wagner's A2 state, which leaves the representation of CS unavailable to be activated into Wagner's A1 memory state when the CS is actually presented. According to SOP, this would reduce the potential of the CS at test to activate a representation of the US and hence to elicit a conditioned response. When applied to AAB renewal (e.g., Exp. 1) and ABC renewal (e.g., Exp 2), this account is parameter independent. Thus, SOP can fully explain our observations in both of the present experiments by positing a role for a CS-context association instead of a contextually occasion set memory of CS nonreinforcement as proposed by Bouton (1993). However, SOP fails to account for the previously cited data demonstrating that when the two phases of training consist of excitatory and inhibitory conditioning of the same cue, it is the information acquired second that is context specific.

Conclusions

In summary, the present research does not prove that the context specificity of nonreinforcement experience is due to occasion setting by the context of nonreinforcement because there are alternative accounts of our data such as is provided by Wagner's (1981) SOP model. But it does refute the view that this context specificity is due to occasion setting of retrieval of the memory of CS-alone trials by the context in which the CS-alone trials occurred that arises because the CS-alone trials were the second-learned information concerning the CS.

Additionally, independent of the specific mechanism by with behavior consistent with nonreinforcement of a CS becomes specific to the context in which nonreinforcement of the CS was experienced, an important new conclusion can be drawn from the present data. That is, much, if not all, of the response deficits produced by extinction and latent inhibition treatments are due to performance deficits rather than an absence of knowledge concerning excitatory conditioning (i.e., a lack of learning in the case of a latent inhibition treatment or an irrevocable erasure of memory of conditioning in the case of extinction). This is a widely recognized aspect of extinction (e.g., Bouton, 1993; total error reduction models of learning such as that of Rescorla & Wagner [1972] nothwithstanding), but it is less recognized for the response deficit produced by a latent inhibition treatment. Latent inhibition effects are still often regarded as a consequence of an attention deficit that irrevocably disrupts subsequent excitatory acquisition (e.g., Lubow, 1989). Considerable evidence now indicates that nonreinforced presentations of a CS after CS-US pairings do not erase previously acquired excitatory associations in the case of extinction nor prevent excitatory acquisition in the case of latent inhibition. Instead, during nonreinforced trials a new association (i.e., CS-noUS) is formed that competes for behavioral control with the original CS-US association (e.g., Bouton, 1993). Whether the CS-US or the CS-noUS association is behaviorally expressed at test depends on both the strength of each association and the facilitatory cues for each association that are present at test (Laborda & Miller, 2012; Miller & Laborda, 2011). Of course the test context, which we have examined here, is a potentially facilitatory cue present at test (Bouton, 1993).

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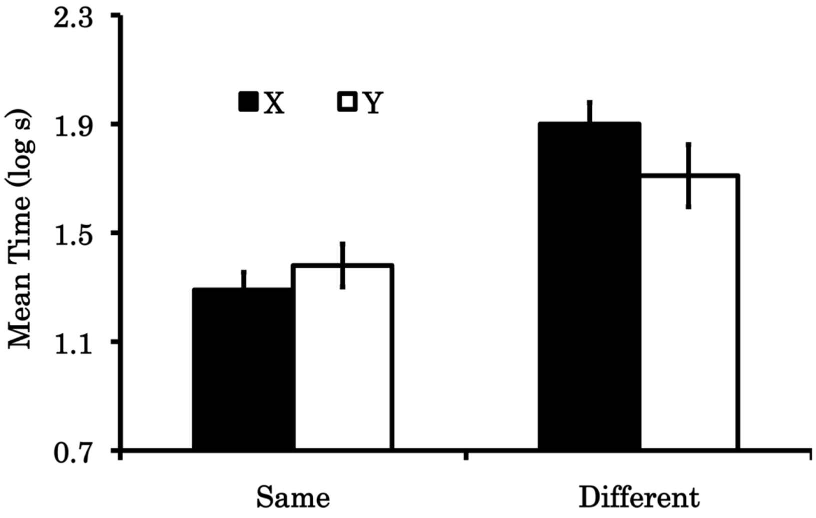

Figure 1.

Results of Experiment 1. Mean $\log_{10}$ time to complete 5 cumulative seconds of licking in the presence of the target CSs X and Y. X = target cue that received extinction treatment; Y = target cue that received CS-preexposure treatment; Same = group that was tested for responding to X and Y in the contexts in which each cue was trained (i.e., X in Context A and Y in Context B); Different = group that was tested for responding to X and Y outside the contexts in which each cue was trained (i.e., X in Context B and Y in Context A). Brackets represent the standard error of the means. Higher scores indicate more conditioned fear. 0.7 log s was the lowest possible score. See text and Table 1 for further details.

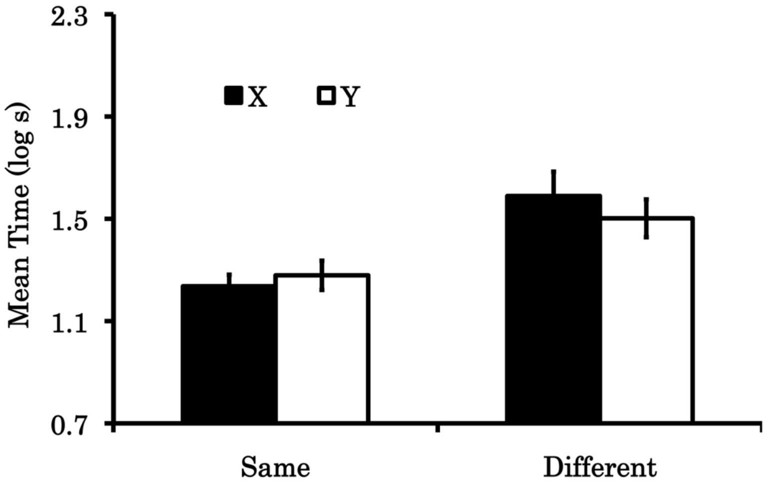

Figure 2.

Results of Experiment 2. Mean $\log_{10}$ time to complete 5 cumulative seconds of licking in the presence of the target CSs X and Y. X = target cue that received extinction treatment; Y = target cue that received CS-preexposure treatment; Same = group that was tested for responding to X and Y in the contexts in which each cue was nonreinforced (i.e., X in Context B and Y in Context C); Different = group that was tested for responding to X and Y outside the contexts in which each cue was nonreinforced (i.e., X in Context C and Y in Context B). Brackets represent the standard error of the means. Higher scores indicate more conditioned fear. 0.7 log s was the lowest possible score. See text and Table 2 for further details.

Table 1

Design Summary of Experiment 1

Groups	CS Preexposure	Conditioning	CS Extinction	Context Extinction	Test
Same	32 Y− (B)	4 X+ (A) 4 Y+ (B)	32 X− (A)	480 min (A) 480 min (B)	X (A) Y (B)
Different					X (B) Y (A)

Note: Same and Different refer to whether testing occurred in the context used for both nonreinforcement treatment and excitatory conditioning (Same) or in a different context. X and Y were a click train and a tone, counterbalanced. “+” denotes reinforcement with a mild footshock. “− ” denotes no reinforcement. Letters in parentheses indicate contexts. Context A and B were counterbalanced. Numbers preceding letters indicate total number of trials in that phase.

Table 2

Design Summary of Experiment 2

Groups	CS Preexposure	Conditioning	CS Extinction	Test
Same	96 Y− (C)	4 X+ (A) 4 Y+ (A)	96 X− (B)	X (B) Y (C)
Different				X (C) Y (B)

Note: Same and Different refer to whether testing occurred in the context of nonreinforcement treatment (Same) or in a different context, both of which were dissimilar to the context of conditioning. X and Y were a click train and a tone, counterbalanced. “+” denotes reinforcement with a mild footshock. “−” denotes no reinforcement. Letters in parentheses indicate contexts. Context B and C were counterbalanced. Numbers preceding letters indicate total number of trials in that phase.