Further evidence that conditioned inhibition is not the mechanism of an extinction cue's effect: A reinforced cue prevents spontaneous recovery

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Previous research has demonstrated that discrete cues presented during extinction of a conditioned response (*extinction cues*) subsequently reduce spontaneous recovery and the renewal effect. In order to assess whether an extinction cue's effect is due to conditioned inhibition, the effect of pairing an extinction cue with food on the cue's capacity to modulate spontaneous recovery was investigated in an appetitive conditioning experiment with rats. Conditioned inhibitors paired with the unconditioned stimulus lose their potential to inhibit responding. The food-paired extinction cue did not lose its potential to reduce spontaneous recovery. In fact, it reduced spontaneous recovery more than did an extinction cue that was not paired with food. The results indicate that extinction cues attenuate postextinction recovery of conditioned responding through a mechanism other than conditioned inhibition. The cue's action appears to be similar to that of serial negative occasion setters. Theories of spontaneous recovery and the relationship of extinction cues to other modulatory stimuli are discussed.

During an experimental phase in which the conditioned response (CR) elicited by a conditioned stimulus (CS) is extinguished, a brief (30-sec) visual or auditory cue presented during 75% of the intertrial intervals (ITIs) between presentations of the CS acquires the ability to subsequently reduce performance to the CS in a spontaneous recovery or renewal test (e.g., Brooks, 2000; Brooks & Bouton, 1993, 1994; Brooks, Palmatier, Garcia, & Johnson, 1999). We refer to such a cue as an *extinction cue* (EC). The existing research indicates that ECs do not appear to reduce spontaneous recovery and renewal after extinction as a result of unconditioned disruption, generalization decrement, or excitation (Brooks, 2000; Brooks & Bouton, 1993, 1994). Also, summation and retardation tests have provided no evidence that the EC was a conditioned inhibitor (Brooks & Bouton, 1993, 1994); those tests, however, depended on null results.

The overall purpose of the present experiment was to continue to explore the characteristics of ECs. On the basis of the results available at the time, Brooks and Bouton (1994) suggested that serially presented ECs may reduce spontaneous recovery and the renewal effect through a mechanism much like that of a negative occasion setter

(see Schmajuk & Holland, 1998). An EC may come to activate a CS–no-unconditioned-stimulus (US) memory that forms during extinction. Bouton's (1993) memory retrieval theory of Pavlovian conditioning can account for spontaneous recovery, renewal, and the potential an EC has to reduce those effects. Conditioning results in the formation of a CS–US association or memory; as conditioning proceeds, presentation of the CS comes to activate that memory, and the CR is elicited. Extinction does not destroy the conditioning memory but, rather, results in the encoding of a separate association involving the CS (a CS–no-US memory). As extinction proceeds, that memory increasingly interferes with retrieval of the conditioning memory. The extinguishing CS activates or retrieves the extinction memory, and a weakened CR results. Immediately following the completion of the extinction phase, presentation of the CS triggers strong retrieval of the recently formed extinction memory, and little or no CR occurs. However, the extinction memory is context specific; that is, following the extinction phase, retrieval of the extinction memory depends on the presentation of the CS along with some or all of the non-CS circumstances that were present during extinction. Changes of physical setting (provided by the experimental apparatus) and/or the passage of time are instances of changes from the circumstances of extinction and result in a failure to retrieve the extinction memory. These changes result in less interference by the extinction memory with retrieval of the conditioning memory, and the CS thus elicits a strong CR again (e.g., spontaneous recovery or renewal).

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Bouton's (1993) theory would treat an EC as a physical component (visual or auditory) of the extinction context. Upon presentation in testing, the EC could at least partially reinstate some of the circumstances of extinction. It may therefore facilitate retrieval, or activation, of the otherwise "forgotten" extinction memory. According to this account, facilitated retrieval of the extinction memory should result in the CS's eliciting a relatively weak CR, consistent with EC's potential to reduce spontaneous recovery and renewal.

At least one other published finding is compatible with this extension of Bouton's (1993) memory theory. Brooks (2000, Experiments 1–3) reported that each of the different ECs that terminate either 15 sec before, 120 sec before, or at variable intervals (40–120 sec) before the extinguishing CS reduces spontaneous recovery when subsequently presented before the CS during recovery testing. Those results were obtained when each cue terminated 15 sec before the CS during testing. This suggests that an EC's potential does not depend on either a close or a fixed temporal relationship between the EC and the CS during extinction. Nor does it depend on a similar temporal relation between those stimuli during extinction and testing. Of course, physical contextual stimuli also diminish the CR elicited by the CS once they have been experienced during extinction and then the CS is then tested in the physical context of extinction. For instance, renewal effects obtained when the CS is tested in a physical context different from that of extinction do not occur if the contexts of extinction and testing are the same (e.g., Bouton & Peck, 1990). In terms of temporal dynamics, ECs appear to be similar to contextual stimuli because, during extinction and testing, contextual stimuli are likely to be attended to at variable intervals (e.g., semirandomly) with respect to the CS. Contextual control of performance to the CS also may not depend on a close, fixed, or consistent temporal relationship between a period of processing contextual stimuli and presentation of the CS.

That finding by Brooks (2000) suggests a distinction, if only procedural, between ECs and negative occasion setters. In serial negative occasion-setting discriminations, reinforced and nonreinforced CS trials are intermixed, and a serial negative occasion setter (X) terminates closely in time, and at a fixed interval, before nonreinforced CS trials (e.g., $X \rightarrow CS-, CS+$). And the occasion setter comes to reduce the CR elicited by the CS. However, in contrast to contextual or EC control of the CR elicited by the CS, such control by an occasion setter seems to depend more critically on the temporal relation between the occasion setter and the CS. In the available literature, occasion-setting control over responding elicited by the CS is diminished or lost if the interval between those stimuli used in testing (e.g., 5 sec) differs from that used in training (e.g., 25 sec; Holland, Hamlin, & Parsons, 1997; Holland & Morell, 1996).

In addition to this procedural difference, Brooks (2000, Experiments 4 and 5) reported another finding that can distinguish ECs and serial negative occasion setters. If an EC

were to obtain the characteristics of a serial negative occasion setter as a result of its presentation during extinction, the EC should subsequently acquire discriminative control over responding readily to that CS when programmed in a serial negative occasion-setting discrimination. That effect was not evident when an EC was so trained, indicating, albeit with a null result, that ECs fail to show at least one characteristic fundamental to serial occasion setters.

Other characteristics of ECs remain unexplored. The literature on occasion setting and contextual modulation provides a rich source of information and procedures for assessing additional properties of a stimulus that modulates performance to the CS. For example, once trained, a serial negative occasion setter typically maintains its potential to reduce responding to the training CS even after the occasion setter has been reinforced (i.e., paired directly with the US; e.g., Holland, 1984; Rescorla, 1991; see Holland, 1992, for a review). This finding is commonly viewed as direct evidence that the occasion-setting stimulus reduces the CR through a mechanism other than conditioned inhibition; in contrast, conditioned inhibitors paired with the US lose their inhibitory potential (e.g., Holland, 1985). Therefore, it is commonly held that serial negative occasion setters do not enter into a direct inhibitory association with the US (Holland, 1992).

The first objective of the present experiment was to assess the potential of an EC to influence spontaneous recovery after the EC had been paired with the US (food). This provided a direct test of whether ECs reduce test performance to the CS as a result of conditioned inhibition—that is, a direct inhibitory association with the US. If a food-paired EC still reduces spontaneous recovery, that effect could not be viewed as being due to conditioned inhibition. The main objective of the experiment was to test this hypothesis.

A second objective was to test conflicting predictions of *occasion setting* and *physical extinction context* accounts of a food-paired EC's effect on spontaneous recovery. As was noted, an occasion-setting account predicts that such an EC should maintain its potential to *reduce* responding to the CS during testing after pairings with food. An extinction context account could be viewed as making the opposite prediction. If contextual stimuli present during extinction are subsequently paired with the US following extinction of responding to the CS, those contextual stimuli do not reduce responding to the CS when the CS is later tested in the presence of those contextual stimuli. Instead, that testing procedure typically produces reinstatement—an *increase* in the CR elicited by the CS (e.g., Bouton & Bolles, 1979; Bouton & Peck, 1989; Rescorla & Heth, 1975). Thus, the extinction context account predicts that a food-paired EC should lose its potential to reduce spontaneous recovery and, in fact, might increase the CR elicited by the CS during recovery testing.

We investigated the effect of pairing an EC with the food US after the extinction phase involving the CS and

the EC. We assessed the effect of this EC treatment, using a test for spontaneous recovery to the CS with the presentation of the EC just before the CS, as in prior tests of EC's effects in appetitive conditioning (Brooks, 2000; Brooks & Bouton, 1993, 1994). There were four groups, each of which received conditioning and extinction and then spontaneous recovery testing with the CS 9 days after extinction. With the present parameters, an 8-day retention interval produces strong recovery to the CS alone. During extinction, each group received an EC that terminated 40 sec before 75% of the CS trials. Then, two groups (EC+C and EC+NC; C indicates testing with the EC, NC testing with no EC) received pairings of the EC with the US (EC+) over 4 days, until the EC itself elicited reliable responding. On those 4 days, the other groups (C and NC) did not receive the EC or the US; they were simply placed in the apparatus. All the groups then remained in their home cages for 4 additional days. Then, on the test, Groups C and EC+C received the EC before each CS; Groups NC and EC+NC received only the CS (see Table 1). Groups C and NC were included to control for the effect of a nontreated EC with the present procedures.

Strong recovery of responding to the CS was anticipated in Groups NC and EC+NC. Less recovery was expected in Group C; based on earlier findings (Brooks, 2000; Brooks & Bouton, 1993), the extent of recovery reduction in Group C was expected to be moderate, but not complete. If conditioned inhibition explains the EC's previous effect on spontaneous recovery and renewal or if the extinction context reinstatement hypothesis is correct, Group EC+C should show more spontaneous recovery than does Group C. On the other hand, if an EC's potential to reduce spontaneous recovery is not due to conditioned inhibition, the food-pairing treatment should not abolish its potential to reduce recovery. In fact, in light of Holland's (1984) and Rescorla's (1985, 1991) findings that separate reinforcement of a negative occasion setter enhances its modulatory effect, we could expect even more strongly attenuated spontaneous recovery in Group EC+C than in Group C.

METHOD

Animals

Sixty-four Wistar rats (48 female, 16 male) bred at the California State University, Fresno, were used. They were approximately 150 days old and ranged in weight from 200 to 275 gm (females) and from 325 to 450 gm (males) at the start of the experiment. The rats were housed individually in standard stainless steel cages in a

room maintained on a 14:10-h light:dark cycle. The experiment was conducted on consecutive days during the light portion of the cycle. The rats were food deprived and kept at 85% of their initial body weights throughout the experiment. Prior to this experiment, the rats had participated in a taste aversion experiment in which they received saccharin and lithium chloride. The rats were assigned to groups in this experiment orthogonally to groups in the earlier experiment and balancing by sex.

Apparatus

The experiment was conducted in two counterbalanced sets of four conditioning boxes (Med Associates, Georgia, VT). Each box measured 32 × 30 × 24 cm and was housed in a sound- and light-attenuating chamber. The front and back walls and the ceiling were stainless steel; the left and right walls were clear acrylic plastic. On the front wall was a stainless steel recessed food cup positioned 2.5 cm above the floor, which was accessed through an opening 5 cm square. The floor consisted of 4-mm-diameter bars mounted parallel to the front wall and spaced 13 mm apart. A recessed food cup was centered on the front wall. In one set of boxes, the left wall had 2.5-cm horizontal white stripes spaced 3 cm apart. A dish containing 10 ml of distilled white vinegar was located on the floor of the sound-attenuation chamber near the food cup. In the second set of boxes, the left wall was unstriped. A similarly positioned dish contained approximately 5 gm of Vicks VapoRub (Richardson-Vicks Inc., Shelton, CT). The differences in striping and odors in the boxes have served to define different physical contexts in other research in our laboratory but were not used for this purpose here. Illumination was provided by three 4-W white incandescent bulbs (houselights) mounted on the ceiling of each sound-attenuation chamber, 28 cm above the box floor. A background 60-dB white masking noise was generated by a speaker located on the floor of the room approximately 5 ft from the sound-attenuation chambers.

The identity of the CS and EC was counterbalanced. One stimulus was the 30-sec presentation of a 3000-Hz tone (80 dB re $\mu\text{N}/\text{M}^2$ [A]) provided by a signal generator wired to identical speakers centered behind the back wall of each chamber and 22 cm above the floor. The other stimulus was the 30-sec termination of the houselights, which produced complete darkness. The US consisted of two 45-mg Noyes food pellets (Noyes, Traditional Formula; P. J. Noyes, Lancaster, NH) delivered 0.2 sec apart. CS-elicited food magazine entry responses were detected by photocells mounted within the food cups.

Procedure

The experiment was conducted in two replications that used the opposite physical stimuli as the EC and CS (i.e., the tone and the darkness stimuli). Groups were equally represented in each replication. The procedures took place on consecutive days. Each rat received all sessions in the same conditioning box throughout the experiment. Parameters and procedural details of the pretraining, conditioning, extinction, and testing phases were similar to those used in previous appetitive conditioning experiments involving extinction cues (Brooks, 2000; Brooks & Bouton, 1993).

Pretraining. On Day 1, all the rats received 20 min of exposure to the chambers. The food cups were baited with four pellets at the start of this session. On Day 2, each rat received a 20-min session

Table 1
Design of the Experiment

Group	Conditioning	Extinction	Retention Interval	Test
EC+NC	CS+	EC → CS−, CS−	EC+	CS−
EC+C	CS+	EC → CS−, CS−	EC+	EC → CS−
NC	CS+	EC → CS−, CS−	−	CS−
C	CS+	EC → CS−, CS−	−	EC → CS−

Note—The CS and EC were represented by a tone or a light-off stimulus, counterbalanced; +, food US; −, no US; → indicates the serial relation of the EC and CS; − indicates mere exposure to the apparatus.

in which it was trained to eat food pellets upon their delivery to the food cup. At the start of this session, food cups were baited with two pellets. Twelve USs were delivered in each session.

Conditioning and extinction. All four groups received seven daily 60-min conditioning sessions (Days 3–8) in which the CS was paired with the US. In each session, there were 12 CS–food pairings, with food delivery coinciding with CS termination. The first CS presentation occurred 4.5 min into the session. Subsequent ITIs ranged from 210 to 320 sec with a mean of 270 sec. One of the rats in each of Groups C, NC, and EC+C failed to condition (elevation scores never averaged above 1.0 in any conditioning session); their data were eliminated from the experiment (the remaining *ns* in those groups = 15; Group EC+NC, *n* = 16).

After conditioning, all of the groups received two 60-min cued extinction sessions (Days 9 and 10). These sessions were similar to those used in prior research on extinction cues (Brooks, 2000; Brooks & Bouton, 1993). Each session was identical for all the rats and began with four EC trials presented at 2-min intervals from the start of the session. Then, CS extinction trials began. There were 12 nonreinforced presentations (CS–) in each session. The first CS– occurred at Minute 12; subsequent CS– trials occurred every 240 sec. Three of every four CS presentations were preceded by the EC; on those trials, the EC terminated 40 sec before the onset of the CS. Pre-CS data were collected in the 30-sec period immediately before the CS. Analogous baseline response data were also collected in the 30-sec period immediately before the EC.

Extinction cue treatment and retention interval. To permit spontaneous recovery from extinction, 8 days (Days 11–18) intervened between the last day of CS extinction and the spontaneous recovery test. On each of the 4 days after extinction (Days 11–14), each group received a 60-min session. In each session, Groups EC+C and EC+NC received pairings of the EC and the US, using the same parameters as in the initial conditioning phase involving the CS. Groups C and NC received no events during these sessions; however, data were collected during the same times during the sessions as for the EC+ groups. During the next 4 days, all of the rats remained in their home cages in the colony room. They were weighed daily and maintained at 85% of their free-feeding weights.

Test. On the 9th day after extinction treatment (Day 19), all the groups were tested for responding to the CS. Testing took place during a single 60-min session. For Groups EC+C and C, the session began with four presentations of the EC at 2-min intervals from the start of the session. Eight test trials with the CS then began; on each trial, the EC was presented and terminated 15 sec before the CS. The first CS occurred at Minute 12. CS ITIs were variable, with a mean of 310 sec and a range of 260–400 sec. Groups EC+NC and NC received the same treatment with the CS but did not receive the EC. Pre-CS data were collected 75–45 sec before each CS—that is, in the period immediately prior to the EC (for Groups EC+C and C) or to the corresponding empty period (for Groups EC+NC and NC).

Data collection and analysis. An elevation score was calculated on each trial by subtracting the number of pre-CS responses from the number of CS responses. Elevation scores and pre-CS data were analyzed using analyses of variance (ANOVAs). Planned comparisons using linear contrasts were conducted with the standard methods discussed by Howell (1987, pp. 330–337, 431–441). All statistical tests used a rejection criterion of $p < .05$.

RESULTS

There were no effects or interactions that were due to the replication factor (i.e., the identity of the CS and EC; $F_s < 1$); therefore, this factor was not included in the analyses reported.

Conditioning and Extinction

The groups reached similar levels of conditioning. Mean elevation scores on the last four-trial block of conditioning for Groups C, NC, EC+C, and EC+NC were 6.7, 6.4, 6.3, and 6.7, respectively. An EC treatment (the EC paired with the US after extinction vs. no treatment with the EC) $\times$ test cue condition (testing with vs. without the EC) ANOVA revealed no effect of EC treatment or test cue condition and no interaction ($F_s < 1$). Pre-CS rates on this block for Groups C, NC, EC+C, and EC+NC averaged 3.3, 3.6, 4.1, and 4.0, respectively. There were no pre-CS differences between groups ($F_s < 1$).

Extinction of responding to the CS proceeded similarly in all groups. Mean elevation scores on the first trial of extinction for Groups C, NC, EC+C, and EC+NC were 6.9, 7.1, 7.8, and 7.3, respectively. Responding decreased over the two extinction sessions. An EC treatment $\times$ test cue condition $\times$ extinction trial type (the CS cued by the EC vs. the CS uncued) $\times$ session ANOVA on mean elevation scores to the CS during those sessions (separated by trial type) revealed an effect of session [$F(1,57) = 8.92$], indicating less responding in the second extinction session. There were no other effects or interactions [$F_s(1,57) < 2.01$, $p_s > .16$]. The left portion of Figure 1 shows the final extinction trial. Pre-CS rates during CS extinction for Groups C, NC, EC+C, and EC+NC averaged 2.1, 2.4, 1.9, and 2.0, respectively. There were no pre-CS differences between groups ($F_s < 1$).

Extinction Cue Treatment

Reliable responding developed to the EC in Groups EC+C and EC+NC during the phase in which it was paired with food. Mean elevation scores to the EC during the last session of this phase for those groups were 6.3 and 7.0, respectively. Mean elevation scores during that session in corresponding empty periods for Groups C and NC were 0.0 and 0.1, respectively. An EC treatment $\times$ test cue condition $\times$ session ANOVA on session mean elevation scores to the EC or in the corresponding empty periods revealed an effect of session [$F(3,171) = 22.52$], indicating an increase in responding over sessions. There was an effect of EC treatment [$F(1,57) = 12.17$] and an EC treatment $\times$ session interaction [$F(3,171) = 27.66$], indicating that there was more responding in the groups that received EC–US pairings than in those that did not. There were no other effects or interactions ($F_s < 1$). Baseline response rates in this phase for Groups C, NC, EC+C, and EC+NC averaged 1.1, 1.2, 2.9, and 2.6, respectively ($F < 1$).

Test

Figure 1 shows mean elevation scores to the CS during the final trial of extinction (Ext, left) and the first two trials of spontaneous recovery testing (right). The figure suggests that the groups demonstrated similar terminal extinction performance and that the NC groups showed strong spontaneous recovery on the first test

Figure 1. Group mean elevation scores to the CS during the final trial of extinction (Ext, left) and the first two trials of spontaneous recovery testing (right) for Groups EC+C, EC+NC, C, and NC.

trial. It also suggests that, on that trial, Group C showed less spontaneous recovery than did Group NC and that Group EC+C showed less recovery than did Group C. An EC treatment $\times$ test cue condition $\times$ trial (last extinction vs. first test) ANOVA on mean elevation scores revealed an effect of trial [$F(1,57) = 50.77$], indicating greater responding on the test than at the end of extinction. There was also an effect of test cue condition [$F(1,57) = 18.36$], indicating less responding in the groups tested with the extinction cue. The trial $\times$ test cue condition interaction was significant [$F(1,57) = 5.06$]. The EC treatment $\times$ test cue condition $\times$ trial interaction was not significant [$F(1,57) = 3.74, p = .058$]. There were no other effects or interactions [$F_s(1,57) < 1$].

Planned comparisons revealed no differences between the groups at the end of extinction ($F_s < 1$). Comparisons of responding at the end of extinction with that on the test revealed spontaneous recovery in Groups NC and EC+NC [$F_s(1,57) > 19.88$] and in Group C [$F(1,57) = 12.50$], but no spontaneous recovery in Group EC+C [$F(1,57) < 1.58, p > .21$]. On the test, there was less responding in Group C than in Group NC [$F(1,57) = 4.97$], and less responding in Group EC+C than in Group EC+NC [$F(1,57) = 18.98$]. Finally, there was less responding in Group EC+C than in Group C [$F(1,57) = 4.05$]. Pre-CS scores on the last trial of extinction and the first test trial averaged 0.5 and 1.9 for Group C, 0.5 and 3.1 for Group NC, 2.0 and 2.3 for Group EC+C, and

1.0 and 3.0 for Group EC+NC; these scores did not differ between groups during either trial ($F_s < 1$). Pre-CS rates on the second test trial for Groups C, NC, EC+C, and EC+NC averaged 1.1, 1.0, 1.3, and 2.3, respectively ($F < 1$). Analyses of pre-CS responding on Test Trials 1 and 2 revealed no overall change in responding and no group differences ($F_s < 1$). Thus, the elevation score test results cannot be accounted for by differences in baseline responding.

Extinction Cue Performance During Testing

We assessed responding during the cues on the test. For Group EC+C, the EC itself elicited responding during its initial presentations in the test session. Mean elevation scores during the EC on its presentation before the first CS of the test for Groups EC+C and C were 4.9 and 0.4, respectively, and during the corresponding empty (no cue) period for Groups EC+NC and NC were 1.6 and 0.5, respectively. An EC treatment $\times$ test cue condition ANOVA on those means revealed an effect of EC treatment and an EC treatment $\times$ test cue condition interaction [$F_s(1,57) > 9.71$]. There was no effect of test cue condition ($F < 1$). Comparisons revealed greater responding in Group EC+C than in any of the other groups [$F_s(1,57) > 10.11$] and no differences among the other three groups ($F_s < 1$), indicating that, at the time of testing, the food-paired EC continued to be excitatory, whereas similar to prior research on extinction cues that have not been reinforced, the other cue was not excitatory (Brooks, 2000; Brooks & Bouton, 1993, 1994).

We also assessed responding just after the cue. Some conditioning methods and procedures can produce an excitatory stimulus, the termination of which is inhibitory (e.g., Hinson & Siegel, 1980). The food-paired EC's effect on responding to the CS might be explained as inhibiting responding after the cue terminates. Following each of the initial four cues (or empty periods) of the test sessions, we measured responding during the 30-sec period that began 15 sec after the cue period terminated (the period during which the CS was presented once test trials with the CS began). We compared responding during that period for the food-paired cue group (Group EC+C) with responding during that period for the other groups; for Group C, that period occurred after presentation of the cue that was not food-paired, whereas for Groups EC+NC and NC, that period followed a corresponding period in which the cue was not presented. Mean responding during those four periods for Groups EC+C and C averaged 2.5 and 2.0, respectively, and during the corresponding empty period for Groups EC+NC and NC averaged 3.0 and 1.0, respectively. An EC treatment $\times$ test cue condition ANOVA revealed an effect of EC treatment [$F(1,57) = 4.89$], indicating more responding after the cues than after a corresponding period in which the EC was absent. Importantly, there was no effect of test cue condition and no interaction ($F_s < 1$), indicating that responding after each cue was not suppressed, as com-

pared with responding in a corresponding period that was not preceded by any cue.

We also compared performance after the cue period with baseline responding. For each group, responding during the 30-sec period after each of the four initial cues (or empty periods, the period analyzed immediately above) was compared with responding in a 30-sec baseline period ending immediately before the onset of each of the cues (for Groups EC+C and C; or before the corresponding empty periods for Groups EC+NC and NC). Mean responding during the four initial baseline periods of the test for Groups EC+C and C averaged 2.2 and 2.0, respectively, and for Groups EC+NC and NC averaged 2.7 and 1.6, respectively. A period (baseline vs. postcue/empty period) $\times$ EC treatment $\times$ test cue condition ANOVA revealed no effects or interactions ($F_s < 1$). Neither the food-paired cue nor the non-food-paired cue inhibited responding after it terminated.

DISCUSSION

The EC that was not paired with food after extinction reduced spontaneous recovery, as similarly treated ECs have before (e.g., Brooks, 2000; Brooks & Bouton, 1993). Exposures to the conditioning chambers during the retention interval did not appear to influence that effect of the EC. More interesting, pairing of the EC with the food US clearly did not prevent the EC from reducing the CR to the CS during testing. In Group EC+C, the EC clearly maintained its potential to reduce recovery to the target CS, even though the EC itself elicited responding. This strongly suggests that an EC does not reduce postextinction recovery of the CR (e.g., spontaneous recovery and renewal; Brooks & Bouton, 1993, 1994) through conditioned inhibition. It lends support for the view that ECs do not reduce these CR recovery effects through a direct inhibitory association with the US.

Also of interest is that the food-paired EC reduced spontaneous recovery more than did the untreated EC; in fact, the food-paired EC eliminated spontaneous recovery. One might consider that the enhanced effect of the food-paired EC was the result of a generalized extinction effect. Just prior to testing the target CS, the previously food-paired EC was presented and nonreinforced a total of five times. Those presentations might be viewed as general reminders of extinction. Other research findings argue against this possibility, however. For example, Richards and Sargent (1983) demonstrated that extinction is CS specific. They found that after conditioning two CSs, extinguishing one did not result in extinguished responding to the other. In addition, a finding from a series of unpublished experiments on the conditions required for an EC to prevent the CR (Brooks, Neves, & Palmatier, 2001) bears directly on a generalized extinction hypothesis as it might be applied to the present test for spontaneous recovery after extinction. In the key condition in one experiment, rats received conditioning, extinction, and spontaneous recovery testing with the target CS (the

tone). During testing, another stimulus (X) was presented five times prior to the first CS trial, just as the EC was in the present experiment; X had been food paired on the previous 4 days but had not been presented during the extinction phase involving the CS. X did not eliminate or even reduce spontaneous recovery to the tone, indicating no role for a generalized extinction effect.

The enhanced CR reduction effect of the food-paired EC shown here is analogous to the effect observed with reinforced serial negative occasion setters (e.g., Holland, 1984; Rescorla, 1991). Thus, in this respect, ECs appear to closely resemble those stimuli. The present results are not inconsistent with the suggestion that cues correlated with extinction activate a CS–no-US extinction memory that is otherwise forgotten with the passage of time and/or with a physical context change after extinction (Bouton, 1993; see also Brooks, 2000; Brooks & Bouton, 1993; Brooks et al., 1999). But the food-paired EC's effect suggests that, much like serial negative occasion setters, an EC can take on two separate functions: to itself signal the US and, when the CS follows the EC, to signal nonreinforcement of the CS (see Holland, 1992).

The present findings qualify the apparent similarity suggested earlier (Brooks, 2000; Brooks & Bouton, 1993) between ECs and background contextual stimuli provided by the experimental apparatus (e.g., Bouton, 1991, 1993). Here a stimulus (the EC) paired with the US clearly reduced the CR to the CS that was extinguished in the presence of that stimulus. However, if contextual stimuli are paired with the US following extinction of responding to the CS, those contextual stimuli do not reduce responding to the CS when the CS is subsequently tested in the presence of those contextual stimuli. That circumstance typically produces reinstatement (i.e., an increase in the CR elicited by the CS; e.g., Bouton & Bolles, 1979; Bouton & Peck, 1989; Rescorla & Heth, 1975). So the EC paired with the US here seems less like a contextual stimulus in this respect. (However, in some other respects such ECs may resemble contextual stimuli—through their temporal relation to the CS, for example; see Brooks, 2000.) This difference between ECs and contexts provided by the apparatus suggests that apparatus cues that define an extinction context may lose the potential to retrieve an extinction memory following pairings of the US with the context. Thus, reinstatement may occur in part because the extinction context loses the potential to retrieve an extinction memory. The apparatus context in reinstatement experiments may not be able to take on the dual functions that the US-paired EC does.

Some theories appear incompatible with the results of this experiment. Configural theory provides a potential alternative to an occasion setting view (e.g., Bouton, 1994; Brooks & Bouton, 1994; Holland, 1992; Nelson & Bouton, 1997; see Schmajuk & Holland, 1998) in accounting for CR reduction effects with ECs. In extinction, the EC might enter into a unique configuration with the CS (e.g., Pearce, 1987, 1994), so that responding is suppressed when both the EC and the CS are present. But according to this

account, reinforcement of the EC should have little effect on suppression by the EC–CS configuration. Thus, this account does not predict the difference found between Groups EC+C and C. Also, in general, it seems unlikely that rats would abstract a configural compound when the EC and the CS are presented serially (Holland, 1985), particularly when 40 sec elapse between them, as in this experiment (the time between ECs and the target CS in extinction can be over 3 min; e.g., Brooks, 2000, Experiment 3). However, configural views could be evaluated directly by testing the effect of an EC presented during extinction of one CS on responding to a different CS extinguished with a different cue (i.e., transfer; cf. Holland, 1989).

Devenport's temporal weighting rule (TWR; e.g., Devenport & Devenport, 1994; Devenport, Hill, Wilson, & Ogden, 1997) is challenged by our findings. According to TWR, when time passes both after bouts involving the US (i.e., conditioning; roughly akin to successful foraging) and after bouts involving no US (i.e., extinction), more recent experience (extinction) is discounted more readily. However, when little time passes after nonreinforcement, recent outcomes are weighed more heavily (i.e., extinction performance is expected soon after extinction). TWR thus correctly predicts spontaneous recovery over time after extinction. However, if EC–US pairings are viewed from the perspective of the test as recent experience with a good patch, TWR predicts enhanced recovery in Group EC+C, whereas we found no recovery.

The present findings, along with the available published data on extinction cues, suggest that those cues reduce CR recovery effects after extinction by a mechanism other than conditioned inhibition. They may activate or retrieve a CS–no-US extinction memory that forms during extinction. The reason reinforcement enhances an EC's spontaneous recovery-reducing effect remains to be determined. However, we offer some initial suggestions. The similar levels of spontaneous recovery in the NC groups indicate that reinforcement of the EC was unlikely to have strengthened encoding, or improved subsequent retrievability, of the extinction memory. If it had, less spontaneous recovery would be expected in Group EC+NC than in Group NC. Rather than influencing the CS–no US extinction memory itself, the EC reinforcement procedure, or some aspect of it, may have enhanced the potential of the EC to activate the extinction memory during testing. One way the reinforced EC may have gained an enhanced potential to activate this memory is that pairings with food could have promoted attention to the EC. Rescorla (1991) reported that a reinforced feature was more effective because it was more salient. Increased salience or attention (see also Williams, 1982, 1984) may promote processing of a stimulus, permitting it to more effectively modulate performance to the target CS. This readily applies to the reinforced EC and highlights the similarity between ECs and serial negative features. Empirical clarification of the specific mechanism of the reinforced EC's CR-preventing effect awaits further research.

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Erratum

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On p. 281, below the authors' note, the following statement was omitted:

—Vincent M. LoLordo served as the action editor for this article.