Recovery of conditioned suppression after backward pairings

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In four conditioned suppression experiments with rats (*Rattus norvegicus*), backward pairings of a shock unconditioned stimulus (US) and a tone conditioned stimulus (CS) eliminated an already established conditioned response (CR), but there was recovery of the CR if the shock was later withheld. In Experiment 1, there was recovery after backward pairings, regardless of whether the period after the US was normally shock free or not. In Experiment 2, the occurrence of recovery depended on the CS's being presented closely after the US in response elimination. Levels of recovery were positively correlated with the resistance of the response to elimination during backward pairings (Experiments 3 and 4). Taken together, these data support the notion that recovery after backward pairings is a form of renewal (see, e.g., Bouton, 1991) and is not due to *protection from extinction*.

The usual method for eliminating an already established conditioned response (CR) is to present the conditioned stimulus (CS) in the absence of the unconditioned stimulus (US). With this method, extinction, the probability of the CR decreases over trials, although there is some tendency for responding to *spontaneously recover* if the animal is returned to the conditioning context after a rest period (see, e.g., Pavlov, 1927; Robbins, 1990). Other methods for response elimination have received less attention. For example, the CS and US can be presented independently of one another (e.g., Ayres, Mahoney, Proulx, & Benedict, 1976; Durlach, 1986; Lindblom & Jenkins, 1981), or the CS can be presented in a backward arrangement at the termination of the US (e.g., Burdick & James, 1973; Durlach, 1986; Hemmes, Brown, Jakubow, & Cabeza de Vaca, 1997). These alternative methods for eliminating the CR also result in a type of recovery. After response elimination, there is recovery of responding if the CS is presented in extinction in the absence of the US.

A good example of the latter type of recovery is found in an experiment conducted by Burdick and James (1973). In Stage 1 of their experiment, rats were given a single pairing of a white noise CS and a shock US in each session (forward pairings). As expected, the rats quickly learned to fear the white noise CS, as measured by the suppression of drinking. Next, Burdick and James altered the temporal location of the CS so that instead of preceding the US, it followed the US. After the rats had experienced five such backward pairings, one per session, there was

little suppression to the CS. It appeared as if the CS–US association had been unlearned. However, this rapid weakening of suppression during backward pairings was not unlearning at all. When the CS was later tested without an antecedent US, suppression returned to nearly its original level. Thus, backward pairings neutralized the excitatory CS, but they did not erase the original CS–US association.

The present experiments focus on two competing accounts of the recovery of conditioned suppression after backward pairings in rats. Ayres et al. (1976) pointed out that recovery after backward pairings might be explained by the familiar summation principle of the Rescorla–Wagner model (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972). That model holds that contextual and temporal cues act in the same fashion as do nominal CSs; they can acquire either excitatory or inhibitory associative strength, which can summate with that of the CS. To explain recovery, the model assumes that contextual cues become excitatory as a result of the occurrence of the US. In conditioning, if the USs are separated by long intertrial intervals (ITIs), the temporal stimuli arising in the immediate post-US period may become inhibitory because these stimuli are nonreinforced in the presence of contextual excitation. In response elimination, the CS begins at US termination; hence, the excitatory CS would now join the inhibitory temporal cues of the post-US period. It should be readily apparent that if the excitatory associative strength of the CS were then to summate with the inhibitory associative strength of the post-US temporal cues, the CS would be inhibited and *protected from extinction* (e.g., Soltysik, Wolfe, Nicholas, Wilson, & Garcia-Sanchez, 1983). In summary, recovery might occur for much the same reason that responding occurs to A when B is absent in an A+, AB− discrimination (where "+" indicates US and "−" no US).

Ayres et al. (1976) reported the results of two conditioned suppression experiments that were consistent with

the summation account but did not demand it. In their Experiment 1, rats first received 10 forward CS–US pairings for two conditioning sessions with short and variable ITIs. Trials occurred on average every 68 sec (range, 8–216 sec). This was followed by three sessions of response elimination in which the CS followed, rather than preceded, the US. In each session, 12 backward US–CS pairings were presented on average every 65 sec (range, 55–75 sec). In Experiment 2, the rats experienced four trials per session in forward conditioning with long intervals between successive USs (range, 7–19 min). These same long ITIs were used later in the backward pairings stage. The major finding was that a short and variable ITI did not appear to support recovery (Experiment 1), whereas a consistently long ITI did (Experiment 2). Short ITIs would presumably have left the local temporal cues of the post-US period excitatory rather than inhibitory. If the post-US temporal cues were excitatory, they could not have protected the CS from extinction.

There are a number of reasons why these data, although suggestive, do not force us to accept an account based on the summation principle. First, it is possible that long ITIs support more conditioned responding than do short ITIs (e.g., Gibbon & Balsam, 1981), making the long-ITI condition more susceptible to recovery. That is, there might have been more recovery with long ITIs, regardless of whether the post-US temporal cues were inhibitory. Second, the critical evidence was based on a between-experiment comparison, which is always problematic. In particular, Experiments 1 and 2 differed in many other ways than just the length of the ITI. Finally, Ayres et al. (1976) were not entirely sure that recovery had been absent in their Experiment 1, which had used short ITIs. In that experiment, they could not directly tell whether recovery had occurred, because the backward pairings were conducted off the instrumental baseline. Instead, a lack of recovery in the backward group was inferred from a between-groups comparison. In test, the backward group was less suppressed than a group that had received CS-only presentations, suggesting that backward pairings had permanently eliminated the CR. However, it is also conceivable that backward pairings had eliminated suppression and that there was recovery of suppression in extinction, but not to the level of the CS-alone group.

Whether the summation account of recovery after backward pairings is correct or not is no trivial matter. If local contexts can protect CSs from extinction, current wisdom about how context influences performance to a CS would have to be reassessed. Bouton and his colleagues (for reviews, see Bouton, 1991, 1993, 1994) have studied the role of context in a variety of *interference paradigms*. These are situations in which the CS's association with the US changes across contexts or time. One of the best-studied examples of interference occurs in the renewal paradigm (e.g., Archer, Sjöden, Nilsson, & Carter, 1979; Bouton & Bolles, 1979; Bouton & King, 1983; Bouton & Peck, 1989; Bouton & Swartzentruber, 1989). If con-

ditioning and extinction are conducted in different contexts, a return to the conditioning context causes recovery (renewal) of the original CR. Bouton (1991, 1993) argues that context acts as a retrieval cue in the renewal paradigm. According to this account, conditioning establishes a CS–US association that is never lost. During extinction, a new association is formed. The CS is associated with *no US*. Both of these conflicting associations are retained, but they are not always accessed. In the renewal paradigm, the extinction context is thought to act as a retrieval cue for the CS–no-US association. Activation of the CS–no-US association in extinction prevents the occurrence of the CR (Bouton & Nelson, 1994). If the CS is returned to the conditioning context, the CS–no-US association is not retrieved, and responding to the CS is *renewed*. Bouton and his colleagues have found very little evidence that renewal is due to protection from extinction (Bouton & Ricker, 1994; Brooks & Bouton, 1993, 1994) or that contexts, and presumably local temporal cues, can actually become inhibitory for that matter (Bouton & Swartzentruber, 1986).

Retrieval cue theory provides an attractive explanation for recovery after backward pairings. The switch from forward to backward pairings can be viewed as an interference procedure. The animal's task is to learn a CS–no-US association (e.g., Moscovitch & LoLordo, 1968) that conflicts with an already established CS–US association. In addition, the animal can readily discriminate when the CS will be reinforced or not. The switch from forward to backward pairings would necessarily be accompanied by a salient change. During backward pairings, the CS would suddenly follow a biologically potent event, the US. Under these conditions, the US should serve as a discriminative cue: The animal should not respond to the previously reinforced CS after just having experienced the US. During backward pairings, retrieval of the CS–no-US association would interfere with the expression of the CS–US association. In test, conditioned suppression should be renewed in the absence of a recent US. In support of this prediction, Bouton, Rosengard, Achenbach, Peck, and Brooks (1993) have demonstrated that rats can use cues arising from changes in US density to predict whether a CS will be reinforced or not. Importantly, when the response-eliciting and cuing functions of the US were put in opposition to each other, the behavior of their rats came under discriminative control.

The purpose of the present experiments was to provide a test of the summation and retrieval cue accounts of recovery after backward pairings in conditioned suppression. In Experiment 1, we examined whether recovery occurs if the post-US period is excitatory, and thus cannot protect the CS from extinction. Experiment 2 tested the prediction of the retrieval cue account that recovery of conditioned suppression should occur only if the CS immediately follows the US in response elimination. In Experiments 3 and 4, we examined whether more recovery occurs if responding is slow to be eliminated, a prediction made by

the retrieval cue account that does not follow from the summation principle.

EXPERIMENT 1

In Experiment 1, the question of whether recovery occurs when the CS is presented in a backward arrangement in the presence of excitatory temporal cues was examined. The experiment consisted of three stages: (1) conditioning, (2) response elimination, and (3) simple extinction. The experiment was a 2 × 3 factorial design, with manipulations in both conditioning (safe or unsafe) and response elimination (backward, US-only, or CS-only). In conditioning, all groups received a single pairing of a 2-min tone CS that terminated with a footshock US. This initial CS–US pairing was followed by an unsignaled footshock after either a short (2 min, unsafe condition) or a long (20 min, safe condition) delay. The purpose of this manipulation was to make the period shortly after the CS–US pairing a shock-free time for only the rats of the safe condition. Next, the rats were given one of three different response elimination treatments. Some of the rats received the tone CS in a backward relation with the US. Other rats received either CS-only or US-only presentations. This produced a total of six groups: safe/backward, unsafe/backward, safe/CS-only, unsafe/CS-only, safe/US-only, and unsafe/US-only. After 16 sessions of response elimination, the CS was tested in the absence of the US in simple extinction.

The predictions of the summation account for this experiment are straightforward. In conditioning, the local temporal cues following the US should become inhibitory for the safe/backward group and excitatory for the unsafe/backward group. In response elimination, given that reductions in associative strength are thought to occur only when the obtained US is less than expected (e.g., Wagner & Rescorla, 1972), in the safe/backward group the CS should lose associative strength only to the extent that it is not fully inhibited by post-US temporal cues. By contrast, in the unsafe/backward group, the post-US period should not be a safe time, and the CS should not be protected from extinction. Group differences in the loss of associative strength to the CS should be evident in the test. Recovery should occur in the safe/backward group when the CS is no longer inhibited by the local contextual cues of the post-US period. No recovery should be observed in the unsafe/backward group. In response elimination, the gradual loss of responding would be due to a true loss of associative strength.

On the other hand, a quite different prediction is made by the retrieval cue account (Bouton, 1991, 1993). If the rats are using a recent US as a retrieval cue for the CS–no-US association, there should be recovery, regardless of whether the post-US period is safe or unsafe.

Method

Animals

The animals were 52 male rats (*Rattus norvegicus*) of Sprague-Dawley descent (Charles River Canada, St. Constant, QC). They weighed approximately 275 g and were 100 days old on arrival. The rats were housed individually in wire mesh cages and, following a 2-week adaptation period, were placed on a food-restricted diet that maintained them at 80% of their free-feeding weights. Water was freely available in the home cages at all times. The colony room was lit for 16 h each day (0600–2000 h). Experimental sessions occurred during the light portion of the light:dark cycle.

Apparatus

The apparatus consisted of eight identical chambers (30.8 × 22.0 × 27.5 cm) that were contained within light- and sound-attenuating shells (Grason-Stadler, West Concord, MA). The stimulus panel and back wall of each chamber were made of aluminum; the side walls and ceiling were made of clear Perspex. The stimulus panel contained a recessed food tray located in a 5.0 × 5.0 cm opening in the center of the stimulus panel, 2 cm above the floor. A single 45-mg food pellet (Bio-Serv, Frenchtown, NJ) could be delivered into the food tray when the rat pressed the lever, located 3.5 cm to the immediate right of the food tray and 5 cm above the floor. A 10-kHz tone delivered from a speaker mounted on the ceiling served as the CS. The tone was presented 10 dB (A) above the background noise level, approximately 72 dB (A), depending on the chamber. An ENV–410/412 shock generator and scrambler (MED Associates, East Fairfield, VT) could deliver a shock US (1 sec, 1.0 mA) to the floor of the chamber. The floor was composed of 18 stainless steel rods, which were 5 mm in diameter, spaced 11 mm on center. The illumination of a 28-V houselight signaled the start of the session. The houselight was centered on the back wall, 3 cm from the ceiling.

Experimental events were controlled by an IBM-compatible PC (Mind Inc., Winnipeg, MB), using the MED-PC software package (MED Associates, East Fairfield, VT). The events occurring in each chamber were programmed independently, which allowed different conditions within an experiment or different experiments to be run simultaneously. As much as possible, the groups were matched for the physical chamber in which the individual rats were trained.

Procedure

Before the experiment began, the rats were allowed to sample the food pellets that would later be used as reinforcers. A small number of pellets (10–15) were placed in a dish in each rat's home cage. The next 4 days were designed to establish the leverpress baseline. All the rats were first trained to approach the food cup and consume the pellets. Pellets were delivered in the absence of a leverpress response on a variable time (VT) 30-sec schedule. If the rat pressed the lever, a food pellet was immediately delivered, and the next interval began. The session ended after either 50 responses or 30 min, whichever came first. During the second session, leverpressing was continuously reinforced until each rat had earned 50 pellets. Rats that failed to emit 50 responses were shaped to press the lever, using the method of successive approximations. In Session 3, all rats earned food pellets on a VI 30-sec schedule. They were trained on the terminal VI 60-sec schedule in Session 4. Sessions 3 and 4 lasted 60 min or until each rat had earned 70 pellets, whichever came first. For the remainder of the experiment and in all subsequent experiments, the conditioning trials were presented while the rats earned food pellets on the VI 60-sec schedule. These sessions all lasted 60 min.

Conditioning. In Stage 1, all rats received two shock USs in each session; the first US was always signaled, and the second US was always unsignaled. On signaled trials, the 2-min tone CS was immediately followed by a shock US. The CS began no earlier than 12 min and no later than 30 min into the session. Groups of rats were trained with different intervals between the two USs; the US–US interval was either 2 min (unsafe condition) or 20 min (safe condition). Every 3rd day, the rats were allowed to earn food reinforcement on the VI 60-sec schedule in the absence of any tones or shocks. These VI-only sessions were given to protect the instrumental baseline against any depressive effect of shock. Stage 1

lasted six cycles (a cycle is defined as two conditioning sessions followed by a single VI session). Thus, the conditioning stage lasted 18 days in total (six cycles of 3 days).

Response elimination. In Stage 2, the rats were given one of three possible response elimination treatments to complete the 2 × 3 factorial design. Rats of the unsafe/backward (n = 8) and safe/backward (n = 9) groups received an unsignaled US that terminated with the onset of the 2-min tone CS. This US–CS pairing occurred 24–32 min into the session. There were no other CSs or USs for the remainder of the session. The rats of the unsafe/CS-only (n = 9) and safe/CS-only (n = 8) groups received only the CS, whereas those of the unsafe/US-only (n = 9) and safe/US-only (n = 9) groups received only the US. Thus, the CS-only groups were not equated for exposure to the US and received a standard extinction treatment. As in the prior stage, every third session was a VI-only session with no scheduled events. The response elimination stage lasted six cycles.

Simple extinction. To test for recovery of conditioned suppression, the CS was then presented in the absence of a recent US. Stage 3 sessions were identical to those received by the CS-only groups in Stage 2. A single unreinforced CS was presented in each of 12 consecutive sessions. Because the rats were no longer receiving shocks, the VI-only sessions were omitted. Taken together, the CS-only and US-only control groups provide boundary points to evaluate the magnitude of any recovery effect. The US-only groups indicate the maximum amount of conditioned suppression that one could expect in the test (i.e., complete recovery). Repeated US presentations after acquisition have no impact on the strength of an existing CS–US association (e.g., Ayres & Benedict, 1973); however, they may produce some habituation (e.g., Randich & Haggard, 1983). If habituation *deflates* the US, substantial although perhaps not complete suppression would be expected in the US-only group. The CS groups indicate the level of suppression that would normally be left after 12 extinction trials.

Suppression. Conditioned fear was evaluated by calculating a suppression ratio, using the formula A/(A+B), where A refers to the number of responses made during the trial period and B refers to the number of responses made in a stimulus-free period of equal duration (called the pretrial period). During conditioning and simple extinction, the pretrial period was the 2-min interval just prior to the presentation of the CS, and the trial period was the period in which the 2-min CS occurred. In response elimination, the pretrial period was the 2-min period before the unsignaled US in the backward and US-only groups. The CS-only groups did not receive the US, and the corresponding time interval was used (i.e., the period that began 121 sec before CS onset and ended 1 sec prior to the CS). In the backward and US-only groups, the 2-min period after the US was the trial period. In the CS-only groups, the corresponding period after the 1-sec empty interval in which the US might otherwise have occurred was the trial period. Therefore, the CS was present in the trial period for the CS-only groups and the backward groups, but not for the US-only groups. Suppression ratios were analyzed using analysis of variance (ANOVA) with a two-tailed rejection criterion of p < .05. The between-subjects factors were conditioning (safe or unsafe) and elimination (CS-only, US-only, or backward), and the within-subjects factor was session. Procedures for calculating degrees of freedom for between-groups contrasts in a mixed ANOVA are provided by Satterthwaite (1946).

Results and Discussion

All the rats quickly learned to fear the tone CS during forward conditioning (see the top panel of Figure 1). Suppression to the CS increased over sessions and was asymptotic by Session 4. There was slightly faster acquisition of suppression in the unsafe groups than in the safe

groups. This produced a main effect for conditioning [$F(1,46)$ = 4.86, MS_e = 0.072]. There were no other differences, except for a main effect of session [$F(11,506)$ = 60.90, MS_e = 0.0087], which reflects the acquisition of conditioned suppression.

As a manipulation check, we measured suppression in the 2-min interval immediately following the CS–US pairing in conditioning (see the bottom panel of Figure 1). In the first few sessions, leverpressing was disrupted in the 2-min period following the CS–US pairing in all groups. In the safe groups this initial suppression gradually diminished over sessions. Suppression did not diminish in the unsafe groups in which the CS–US pairing was closely followed by a second US. These differences produced main effects for conditioning [$F(1,46)$ = 35.61, MS_e = 0.10] and session [$F(11,506)$ = 18.12, MS_e = 0.014] and a conditioning × session interaction [$F(11,506)$ = 4.65, MS_e = 0.014].

The data of the response elimination stage are presented in Figure 2. The CS-only groups (top panel) have been separated from the US-only and backward groups (bottom panel) because they are not comparable. In the CS-only groups, the trial period followed a stimulus-free interval, whereas in the backward and US-only groups, the trial period followed a shock US. As can be seen in the top panel, suppression declined at roughly similar rates in the safe/CS-only and unsafe/CS-only groups. There was a main effect for sessions [$F(11,165)$ = 13.38, MS_e = 0.016] but no interaction between conditioning and sessions. These null findings are important because they indicate that a more resilient CS–US association had not developed in the unsafe groups that in the safe groups. Such a difference would have been problematic, because it could have influenced the magnitude of later recovery. Thus, final asymptotic levels of conditioning were indistinguishable as measured by resistance to extinction.

Data from the remaining US-only and backward groups were analyzed together (bottom panel of Figure 2). There were main effects for conditioning [$F(1,31)$ = 17.09, MS_e = 0.042], elimination [$F(1,31)$ = 28.41, MS_e = 0.042], and session [$F(11,341)$ = 9.82, MS_e = 0.0099], as well as interactions of conditioning × elimination [$F(1,31)$ = 4.07, MS_e = 0.042, p < .06], conditioning × session [$F(11,341)$ = 1.98, MS_e = 0.0099], elimination × session [$F(11,341)$ = 2.72, MS_e = 0.0099], and conditioning × elimination × session [$F(11,341)$ = 1.87, MS_e = 0.0099]. The triple interaction is of particular interest, because it was caused by unequal rates of extinction in the unsafe/backward and safe/backward groups.

Turning first to the data of the US-only groups, there were clear differences in the level of suppression as a function of conditioning (safe vs. unsafe). In the safe/US-only group, there was no evidence of suppression at all, as might be expected if the temporal cues during the post-US period had become inhibitory. In the absence of formal tests for conditioned inhibition (see, e.g., Rescorla, 1969), it would be risky to conclude that inhibition had actually been acquired. At a minimum, we can conclude that the
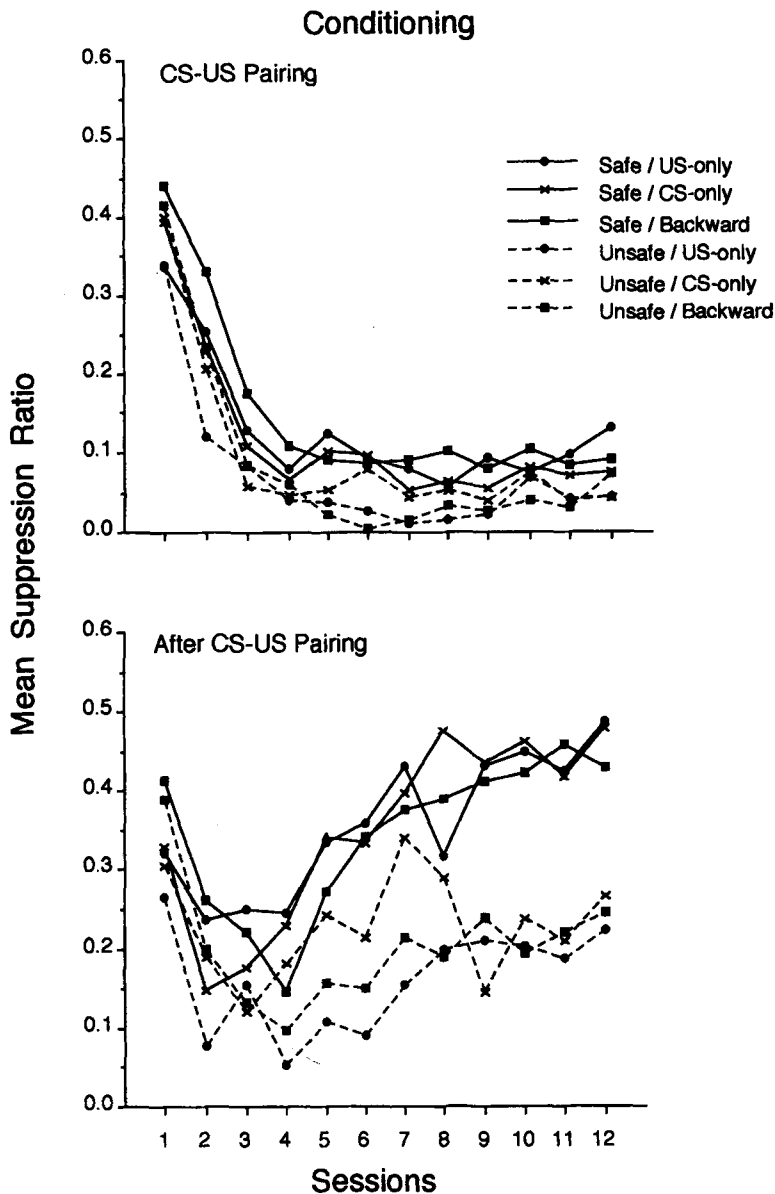
Figure 1. Mean suppression ratios in the conditioning stage of Experiment 1 are shown as a function of conditioning (safe vs. unsafe), elimination (US-only, CS-only, and backward), and session. The data shown in the top panel (CS–US pairing) are from the trial period (pooled MS_e = 0.014), whereas those in the bottom panel (after CS–US pairing) are from the stimulus-free period right after the CS–US pairing (pooled MS_e = 0.021).

post-US temporal cues were less excitatory for the safe/US only group than for the unsafe/US-only group. This conclusion follows because, in the unsafe/US-only group, there was a moderate amount of suppression in Session 1, which extinguished by Session 3. Apparently, the rats of this group did learn that the CS–US pairing was followed shortly thereafter by a second US. If this same situation holds for the rats of the unsafe/backward group (which it should, because the groups were treated identically until this point), the summation principle would

then predict that there should be no recovery in the unsafe/backward group.

As for the data of the backward groups, the bottom panel of Figure 2 indicates that responding was eliminated more slowly in the unsafe/backward group than in the safe/backward group. There were pairwise differences between the unsafe/backward group and its control, the unsafe/US-only group, in each of Sessions 1 through 8 [smallest reliable difference, $F(1,246)$ = 4.13 on Session 1, MS_e = 0.0126]. Thus, suppression in the unsafe/backward
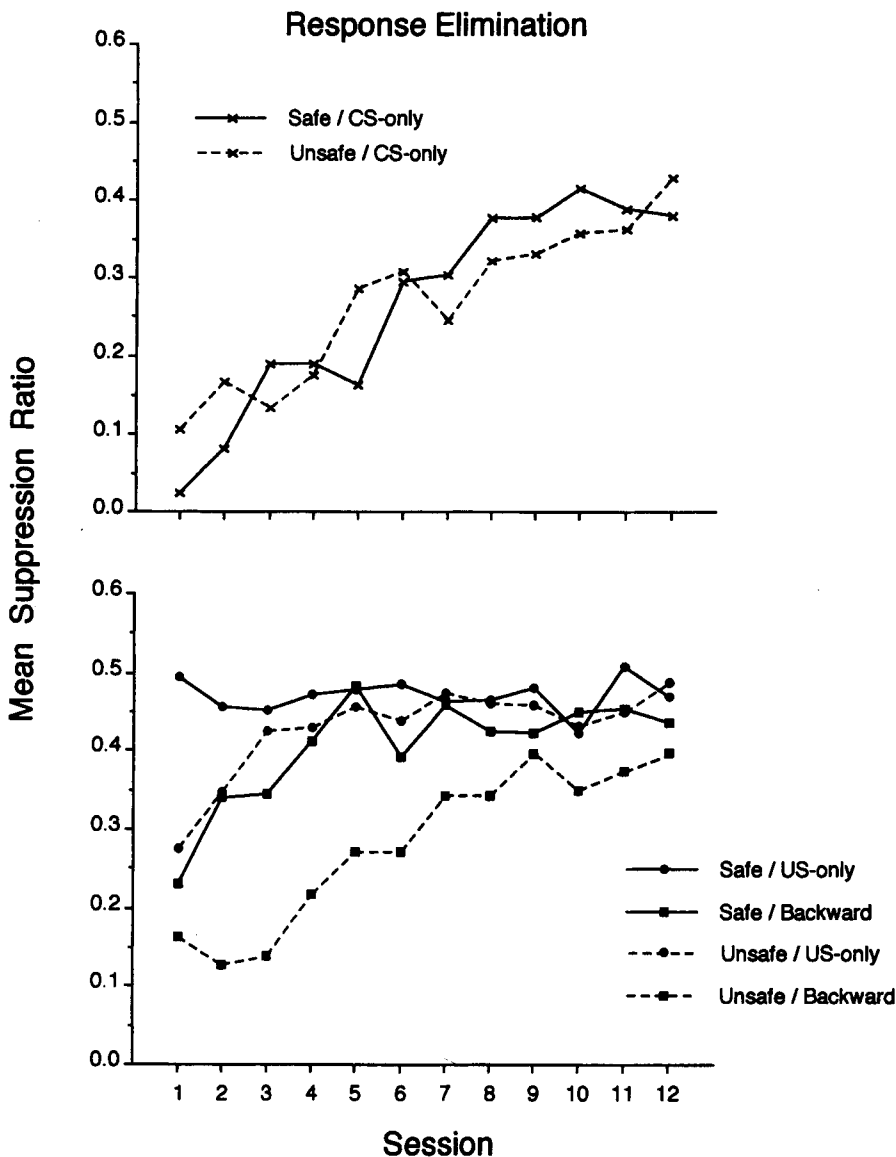
Figure 2. Mean suppression ratios in the response elimination stage of Experiment 1 are shown in the period after the US (or the empty 1-sec gap in the CS-only groups) as a function of conditioning (safe vs. unsafe) and session. Data from the CS-only groups are presented in the top panel (pooled $MS_e = 0.029$), whereas data from the US-only and backward groups are presented in the bottom panel (pooled $MS_e = 0.013$). The CS was actually present only in the CS-only and backward groups.

group reached control levels only near the end of response elimination. It appeared as if there had been true extinction. On the other hand, if the time after the US previously had been shock free (safe/backward group), the excitatory CS was more quickly neutralized. There was more suppression in the safe/backward group than in the safe/US-only group in Sessions 1–3 only [smallest difference, $F(1,246) = 4.13$ on Session 3, $MS_e = 0.0126$]. Although this rapid loss of conditioned suppression can be explained in other ways, it is clearly consistent with the idea that the post-US temporal cues were inhibiting the excitatory

CS, at least to some extent if not fully. On the last day of response elimination, there were no statistically detectable levels of suppression remaining in the backward groups.

The purpose of Experiment 1 was to discover whether recovery would occur after backward pairings in both the safe and the unsafe groups. Figure 3 shows the amount of suppression evoked by the CS during its last presentation prior to simple extinction (L) and during simple extinction itself. In the US-only group, the CS was last present in conditioning, whereas for the remaining groups, the CS was last present in response elimination. The important
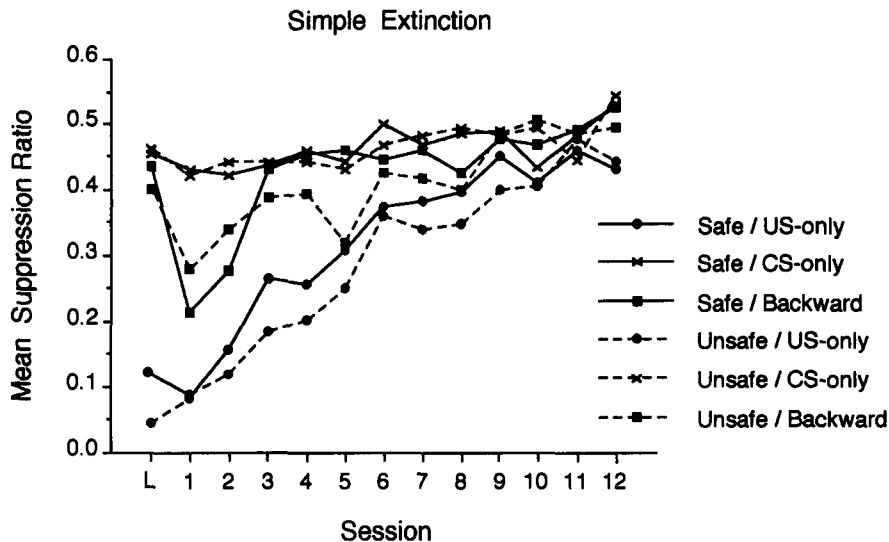
Figure 3. Suppression evoked by the CS is plotted for the simple extinction stage of Experiment 1 (pooled $MS_e = 0.011$). Data are shown from the last (L) session in which the CS was presented prior to the test (i.e., the last session of conditioning for the US-only groups and the last session of response elimination for the CS-only and backward groups) and for the 12 sessions of simple extinction.

data are from the two backward groups. In Session 1, suppression in the two backward groups was roughly similar and fell between the CS-only and US-only control levels. Suppression then declined as testing continued. Thus, the major finding of Experiment 1 was that recovery occurred in both backward groups, as the retrieval cue account predicted.

We looked for statistical evidence of recovery in two ways. First, the data of the entire simple extinction stage were analyzed with a 2 × 3 × 12 ANOVA. There were main effects for elimination [$F(2,46) = 26.52$, $MS_e = 0.046$] and session [$F(11,506) = 38.91$, $MS_e = 0.0072$] and an elimination × session interaction [$F(11,506) = 6.48$, $MS_e = 0.0072$]. Tests for pairwise differences, using the pooled error ($MS_e = 0.011$) indicated more suppression in the unsafe/backward group than in its extinguished control, the unsafe/CS-only group, in Sessions 1 and 5 [i.e., recovery, smallest $F(1,272) = 5.79$]. There was also more suppression in the safe/backward group than in its extinguished control, the safe/CS-only group, in Sessions 1 and 2 [smallest $F(1,272) = 7.11$]. In a second analysis, we compared suppression during the last presentation of the CS before simple extinction (the last day of response elimination in all groups except for the US-only group) and that during the first 6 days of simple extinction. Only the first six sessions of simple extinction were examined, because group differences were largest at this time. This analysis revealed main effects for elimination [$F(2,46) = 57.99$, $MS_e = 0.033$] and session [$F(6,246) = 20.35$, $MS_e = 0.0086$] and an elimination × session interaction [$F(12,276) = 6.65$, $MS_e = 0.0086$]. The elimination × session interaction was due to increased suppression in the two backward groups com-

bined when the CS was initially presented without a prior US [$F(1,276) = 26.90$, $MS_e = 0.0086$]. In both analyses, there were no main effects of conditioning (safe vs. unsafe), nor did conditioning interact with any other factor. In summary, there was no statistical evidence that recovery after backward pairings was more pronounced in one group than in the other.

In Experiment 1, recovery of suppression after backward pairings occurred regardless of whether the after-US period was normally shock free or not. Both of the unsafe/backward and safe/backward groups could use the recent occurrence of the US as a retrieval cue for the CS–no-US association, and thus, the similar levels of recovery found in these two groups is consistent with the predictions of the retrieval cue account (Bouton, 1991, 1993). That theory could appeal to a number of different mechanisms to explain group differences in response elimination. For example, the presence of contextual excitation in the unsafe/backward group could have slowed extinction of conditioned suppression, because contextual excitation was an important feature of the context of acquisition.

The findings of Experiment 1 cast doubt on the protection-from-extinction account of the recovery of suppression after backward pairings (Ayres et al., 1976). That account does not permit *any* recovery in the unsafe/backward group, because excitatory temporal cues cannot protect a CS from extinction. According to the summation principle, the excitatory associative strengths of the CS and the post-US temporal cues should have summated, and their individual associative strengths should then have been decremented in proportion to their relative salience. A CS that carries more excitatory strength by virtue of

its higher salience might be expected to contribute more associative strength to the compound, but it should also lose more associative strength because it is the more salient component.

Of course, it is always possible that recovery occurred for different reasons in the two backward groups. That is, inhibitory temporal cues may have protected the CS from extinction in the safe/backward group but not in the unsafe/backward group. One problem for this proposal is that a prediction that recovery should occur in the safe/backward group, although consistent with the spirit of the Rescorla–Wagner model, cannot in fact be derived from it. According to the Rescorla–Wagner model, post-US temporal cues become inhibitory because they are unreinforced in the presence of contextual excitation. At asymptote, the model predicts that inhibition arising from the temporal cues should come to offset excitation from the surrounding context. Thus, in formal terms, the Rescorla–Wagner model does not actually predict that backward pairings can protect a CS from extinction, although it is said to (e.g., Ayres et al., 1976). If the inhibitory post-US temporal cues arise from the rat's being in an excitatory context, the combined associative strength of the contextual and temporal cues will be zero at best. In keeping with a more informational theory (Janssen, Farley, & Hearst, 1995), it might be assumed that a long wait until the next US allows a local context to become inhibitory. The predictions of such an account are tested in Experiments 2–4.

The data of Experiment 1 are also troublesome for an interference account based on the conditioning of temporal cues. In brief, when the CS was trained in a backward arrangement, the rats no longer had an exteroceptive cue by which to predict the US. They could predict the US only on the basis of the amount of time that had elapsed since their placement in the experimental chamber. Although the US time was not fixed, the US did occur within a reasonably narrow window of time after placement. Excitatory temporal cues might then have undermined the expression of the CS–US association. Interference might occur because CSs are assumed to generate responding only to the extent that they predict the US better than does the local context (e.g., Gibbon & Balsam, 1981). In simple extinction, interfering temporal cues should lose their ability to control responding, because the US is withheld. This should allow for recovery of the original CS–US association. If this were true, however, we should not have seen any recovery in Session 1 of simple extinction. In Session 1, the temporal cues signaling the US should have been well conditioned, because they had been reinforced in the previous session.

It is worth mentioning that the interference account just described also has difficulty explaining other types of recovery. For example, Dickinson and Charnock (1985) found that instrumental responding was markedly attenuated when they introduced free reinforcers to rats that were pressing a lever for saccharin reinforcement. Responding was partially restored if the rats were given a period of unreinforced exposure to the apparatus in the absence of the lever. In their experiment, the free reinforcers appeared to depress responding through their effect on context conditioning. However, the context inference account has trouble explaining the results of related experiments involving the presentation of uncorrelated USs. In pigeon autoshaping, recovery occurs only if the CS is actually present at the time at which the free reinforcers are available (Durlach, 1986; Lindblom & Jenkins, 1981). This last observation is consistent with the suggestion that a developing inhibitory association between the CS and the US (a CS–no-US association) is essential for later recovery.

EXPERIMENT 2

The purpose of Experiment 2 was to test a central assumption of the retrieval cue account—that recovery occurs because the CS closely follows the US in response elimination. Groups of rats were first trained with a single CS–US pairing in each session. Next, the CS was presented in a backward arrangement at different US–CS intervals (0, 2, 6, or 12 min). If it were found that recovery did not depend on the CS occurring immediately upon US termination, this would raise serious questions about whether the recent occurrence of the US was acting as a retrieval cue for the CS–no-US association.

Method

The animals were 47 naive male Sprague-Dawley rats of the same description as those used in Experiment 1. Preliminary training was identical to that in Experiment 1. In brief, the rats first learned to press the lever for food pellets and then were gradually shifted to the terminal VI 60-sec schedule. All subjects were treated identically in forward conditioning. A single CS–US pairing occurred on the instrumental baseline in each 60-min session. The onset of the CS began no earlier than 12 min into the session and no later than 30 min. The rats received a total of four cycles of forward conditioning. Again, a cycle consisted of two conditioning sessions, followed by one VI session. At this point, the rats were assigned to one of six groups. Four groups received a single backward US–CS pairing in each session. They differed on the interval between the termination of the US and the onset of the CS. This interstimulus interval (ISI), measured in minutes, is identified in the group's label (i.e., B_0, B_2, B_6, and B_{12}). For example, in the B_6 group, there was a 6-min interval between shock offset and tone onset, whereas in the B_0 group, the tone occurred immediately upon shock termination. The shock US occurred pseudorandomly 14–32 min after the rat was placed in the chamber. All the backward groups were composed of 8 rats, except for the B_6 group, which had 7 rats. The remaining rats were assigned to the control groups. The CS-only group ($n = 8$) received the CS but not the US. Two of the 8 subjects in this group received the CS at the same time as did the B_0 group. The remaining rats received the CS at the same time as the B_2, the B_6, or the B_{12} group (one pair of rats for each interval). The US-only group ($n = 8$) received a footshock US at the same time after placement in the chamber as did the other groups, but they never experienced the CS. After 16 sessions of response elimination, all rats were tested in
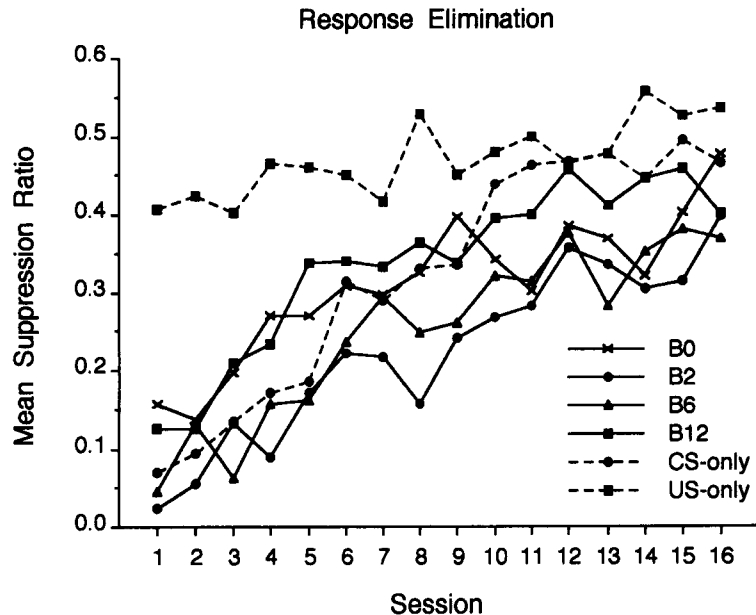
Figure 4. The figure shows suppression in the response elimination stage of Experiment 2 (pooled $MS_e = 0.016$). Suppression evoked by the tone CS is shown in the backward groups (B_0, B_2, B_6, and B_{12} at the designed interval after the US) and in the CS-only groups (at times matched to the backward groups). The data of the US-only group is from the stimulus-free 2-min period right after the US, the time corresponding to CS presentation in the B_0 group.

simple extinction in the same manner as in Experiment 1. This test for response recovery was conducted over 12 sessions.

Results and Discussion

Suppression was acquired rapidly in all the groups. There were no group differences. Figure 4 shows responding in response elimination. Five of the six groups received a CS during this stage (CS-only, B_0, B_2, B_6, and B_{12}). To calculate suppression in these groups, we used the number of responses in the pretrial period (the 2-min period before the US, or where the US would have occurred in the CS-only group) and the number of responses during the 2-min CS itself. In the US-only group, suppression is shown for the empty 2-min interval beginning immediately after the US. This is the CS time in the B_0 group. As can be seen in Figure 4, there was modest suppression in the US-only group in Sessions 1–3 and none thereafter. This shows that leverpressing was stable within sessions—the rats pressed the lever at even rates throughout the session, including the interval that immediately followed the US. Thus, we can compare suppression among the remaining groups that received the CS at different intervals. As Figure 4 shows, suppression gradually decreased to the unreinforced CS across sessions. Extinction of suppression, along with the absence of suppression in the US-only group, produced main effects for elimination [$F(5,41) = 11.02, MS_e = 0.11$] and session [$F(15,615) = 38.72, MS_e = 0.0098$] and an elimination $\times$ session interaction [$F(75,615) = 1.70, MS_e = 0.0098$].

There was a tendency for more suppression in the B_2 and B_6 groups than in the remaining groups in some sessions (see Session 8 especially). By the final session of response elimination, suppression to the CS had diminished markedly, although there was more variation in the group means than one would like [$F(5,119) = 3.21, MS_e = 0.016$].

In simple extinction, there was a quite remarkable effect of backward ISI on the degree of recovery of conditioned suppression (see Figure 5). Only in the B_0 group was there a significant increase in conditioned suppression in Session 1. Using a 6×7 ANOVA, the data from simple extinction were analyzed with elimination as the between-subjects factor and session as the within-subjects factor. The session factor included suppression to the CS on its last appearance before the test (i.e., the last day of response elimination in all groups except for the US-only group). This analysis revealed main effects for elimination [$F(5,41) = 9.38, MS_e = 0.034$] and session [$F(6,246) = 8.46, MS_e = 0.0077$] and an elimination $\times$ session interaction [$F(30,246) = 2.87, MS_e = 0.0077$]. Suppression increased by nearly 0.2 in the B_0 group [$F(1,246) = 17.62, MS_e = 0.0077$], which is similar in magnitude to the level of recovery seen in the two backward groups in Experiment 1. In the remaining backward groups, as well as in the CS-only group, there was virtually no change in suppression between the last session of response elimination and the first session of simple extinction [largest $F(1,246) = 0.72, MS_e = 0.0077$]. Additional statistical evidence of preferential recovery was
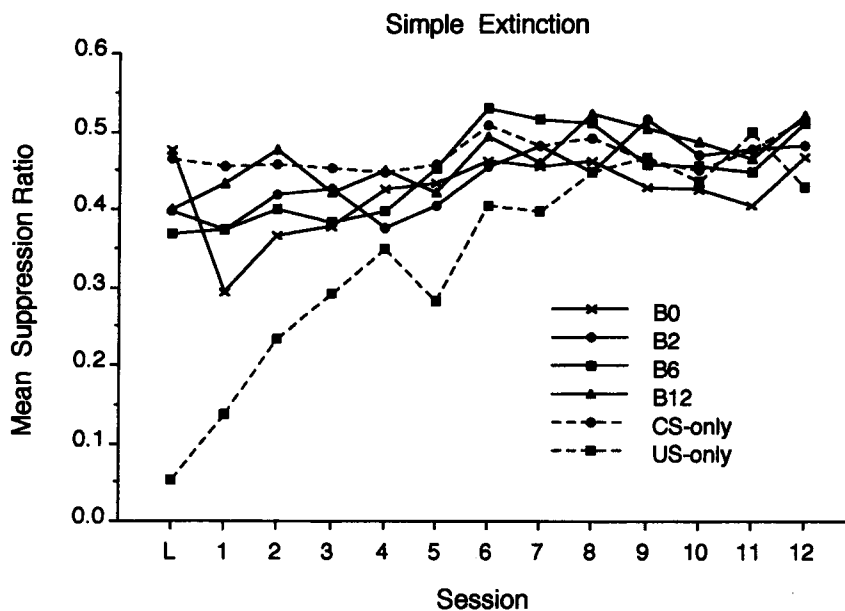
Simple Extinction

Figure 5. Suppression is shown for the simple extinction stage of Experiment 2 (pooled MS_e = 0.011). Data are shown from the last (L) session in which the CS had been presented prior to the test (i.e., the last session of conditioning for the US-only groups and the last session of response elimination in the CS-only and backward groups) and for the 12 test sessions of simple extinction.

shown by further examination of the simple effect of elimination in Session 1. In Session 1, we found more suppression in the B_0 group than in the other backward groups combined [$F(1,113)$ = 5.31, MS_e = 0.011], although the B_0 group did not differ individually from either the B_2 or the B_6 groups [smallest $F(1,113)$ = 2.28, MS_e = 0.011]. Lastly, some comment should be made about the non-significant tendency in the US-only group toward a loss of suppression between the last day of acquisition and the first day of simple extinction [$F(1,246)$ = 3.57, MS_e = 0.0077, p < .1]. Given the 16 sessions of exposure to the US in response elimination, some attenuation of suppression in the US-only group is not surprising. The rats in this group, along with the rats in the backward groups, may have become slightly more habituated to the US.

In summary, the results of Experiment 2 provide direct support for the notion that a recent US acts as a retrieval cue for the memory of extinction. Only in the B_0 group should the activation of the CS–no-US association have occurred in the presence of a recent US. In test, the CS–no-US association should not have been fully retrieved, because the US was absent, and responding should then have recovered. In the remaining groups, the recent occurrence of the US would not be expected to be a retrieval cue for the CS–no-US association. Thus, there would be no reason to expect recovery of responding. On the other hand, the results of Experiment 2 are inconsistent with the informational version of the protection-from-extinction account. In conditioning, the CS–US pairing was the only trial of the entire session. If rats do learn about the waiting time to the next US, the entire period after the US would

surely have become strongly inhibitory. In response elimination, the excitatory CS should have been inhibited by the post-US context. In test, the CS should have been protected from extinction, regardless of the backward ISI. Note that it is possible that local temporal cues were progressively less inhibitory as a function of the time since the occurrence of the US, as might be predicted by the Rescorla–Wagner model (Rescorla & Wagner, 1972). Of course, along with the problem of actually deriving such a prediction, that account does not explain the recovery after backward pairings in the unsafe/backward group in Experiment 1.

EXPERIMENT 3

When retrieval cues are implicated, it is usual to consider an alternative interpretation based on configural conditioning (e.g., Bouton & Swartzentruber, 1989). For example, the tone CS and the local context in which it is embedded might be perceived as being a unique stimulus complex, which may then acquire excitation or inhibition in its own right (Pearce, 1987). If so, during backward pairings, the combination of the tone and the post-shock context would constitute a new event; therefore, the shift from forward to backward pairings should produce a generalization decrement. Because of this decrement, the tone should evoke less responding in the backward arrangement than it did previously in the forward arrangement. Moreover, the magnitude of this decrement should predict the later occurrence of recovery, because the decrement is a measure of the extent to which the stim-
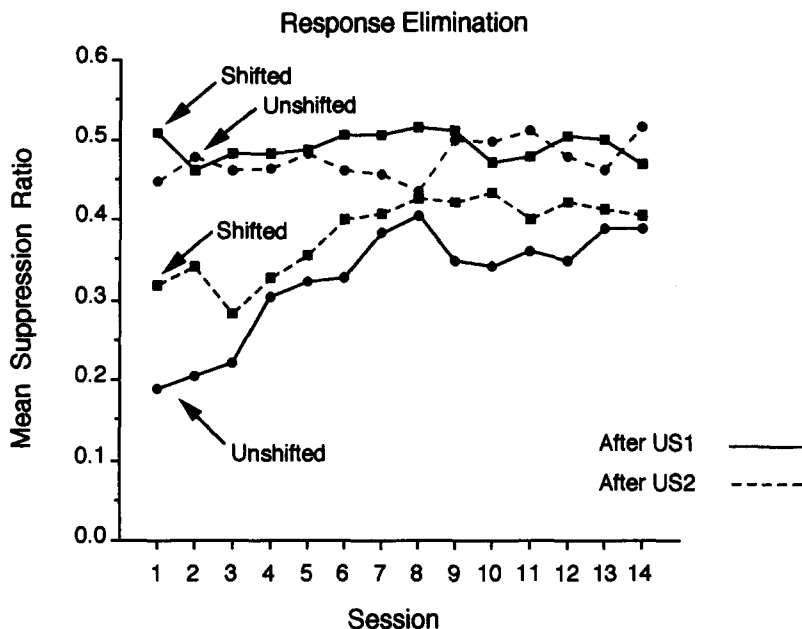
Figure 6. Suppression is shown for 2-min periods right after the first US (after US$_1$) and right after the second US (after US$_2$) in the response elimination stage of Experiment 3 (pooled MS_e = 0.0071). In Experiment 3, the CS was moved from its previous location as a signal for the first US to the period after either the first US (unshifted group) or the second US (shifted group).

ulus complex during backward pairings differs from the one that was conditioned and ultimately tested. The larger the decrement, the less inhibition that should be acquired in response elimination, and the less inhibition that should be available to generalize to the stimulus complex of conditioning.

The purpose of Experiment 3 was to provide a test of the configural conditioning account. In Experiment 3, a single CS–US pairing was followed 20 min later by an unsignaled shock. In the response elimination stage, the CS occurred in a backward relation with either the first US (the unshifted group) or the second US (the shifted group). If configural learning allows portions of the original stimulus complex to avoid losing associative strength, the magnitude of this effect should be larger in the shifted groups than in the unshifted groups. Not only would the CS suddenly appear after shock in the shifted group, it would also occur late in the session. Thus, fewer of the elements of the original stimulus complex would be present during backward pairings, and there should be less extinction and more subsequent recovery. In summary, if there is a larger stimulus generalization decrement in the shifted group than in the unshifted group, we should find better recovery.

Method

The animals were 16 experimentally naive Sprague-Dawley rats. They first received the preliminary leverpress training that was described in Experiment 1. Next, all the rats received the same conditioning treatment as the safe/backward group in Experiment 1.

After six cycles of conditioning, the rats received backward pairings to eliminate responding to the CS. The CS was presented immediately upon the termination of either the first US (i.e., US–CS, then US; the unshifted group, $n = 8$) or the second US (i.e., US, then US–CS; the shifted group, $n = 8$). The USs were presented 20 min apart. After 14 sessions of response elimination, the rats were tested for recovery to the CS. These recovery sessions were identical to the original conditioning sessions, except that the CS was now unreinforced (i.e., the first US of the session was omitted, and the second US was not omitted). The rats were tested in simple extinction for 5 sessions.

Results and Discussion

Terminal levels of conditioned suppression to the tone CS on the last day of conditioning were .016 ($SE = .008$) and .032 ($SE = .21$) in the shifted and unshifted groups, respectively. There were no group differences. The top panel of Figure 6 shows the data of the response elimination stage in the 2-min period right after either the first US (solid lines) or the second US (dashed lines). As was expected, the CS evoked less suppression in the shifted group than in the unshifted group. This can been seen in the figure by comparing the differences between the two solid lines and between the two dashed lines. In this case, the difference between the dashed lines is the smaller of the two differences. Suppression ratios were analyzed using an ANOVA, with elimination as the between-subjects factor (unshifted or shifted) and period (after the first or the second US) and session (14 sessions) as the within-subjects factors. This analysis revealed a main effect of session [$F(13,182) = 6.98$, $MS_e = 0.0045$] and
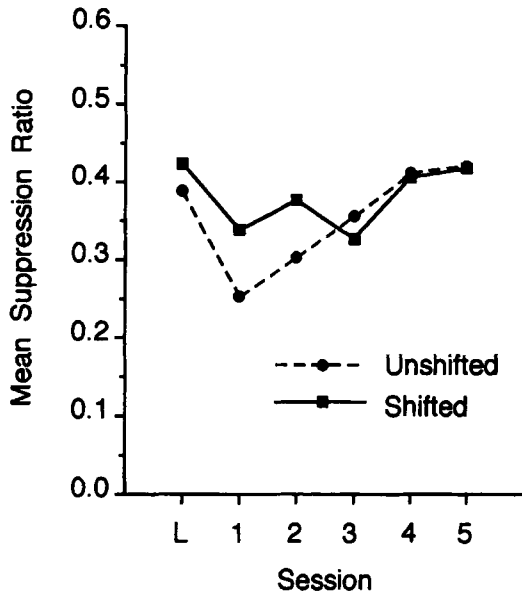
Figure 7. Suppression to the CS is shown for the simple extinction stage of Experiment 3 (pooled $MS_e = 0.0098$). Data are shown for the last (L) session of response elimination and for the five test sessions in which the CS was unreinforced (simple extinction).

interactions of elimination × period [$F(1,14) = 60.08$, $MS_e = 0.031$], and elimination × period × session [$F(13,182) = 5.45$, $MS_e = 0.0039$]. The triple interaction was due to consistently less suppression to the CS in the shifted group than in the unshifted group. Differences in suppression between the shifted and unshifted groups were especially marked in Sessions 1 and 2 [$Fs(1,116) = 9.57$ and 10.50, respectively, $MS_e = 0.0071$]. The involvement of period in the triple interaction reflects the fact that the CS was presented at different times.

The data of the simple extinction stage shown in Figure 7 provide new information about the conditions that produce recovery after backward pairings. The configural conditioning account predicts more recovery in the shifted group than in the unshifted group. Contrary to this prediction, recovery in the unshifted group was stronger than that in the shifted group, although not significantly so. A mixed ANOVA on the data shown in Figure 7 revealed a main effect of session [$F(5,84) = 5.70$, $MS_e = 0.0069$] but no elimination × session interaction. Recovery was shown by an increase in suppression on the first trial (session) of simple extinction [$F(1,84) = 13.79$, $MS_e = 0.0069$].

The failure to find better recovery in the shifted group than in the unshifted groups, despite the larger generalization decrement, can be taken as evidence against a configural conditioning account. In fact, there was a non-significant tendency toward poorer recovery in the shifted group than in the unshifted group. In the present experiment, however, the effect of shift was confounded with the effect of another variable. In the unshifted group, the CS was presented after the first US, whereas in the shifted

group, the CS was presented after the second US. Thus, the small generalization decrement and nonsignificantly greater recovery in the unshifted group might have been due to an effect of US (first vs. second) rather than of elimination (unshifted vs. shifted).

EXPERIMENT 4

In Experiment 4, the rats initially received an unsignaled US that was followed 20 min later by a CS–US pairing (the reverse of the trial order used in Experiment 3). Next, the CS was presented in a backward arrangement with either the first (shifted group) or the second (unshifted group) US. The CS was then tested for recovery. If a main effect of US, first or second, were responsible for the differences observed in Experiment 3, more recovery, if anything, would be expected in the group that received the CS in a backward relation with the first US (shifted group). On the other hand, if the differences in Experiment 3 were, in fact, caused by an effect of elimination (unshifted or shifted), there should again be stronger recovery in the unshifted group than in the shifted group.

Method

The animals were 20 naive male Sprague-Dawley rats of the same description as those in the previous experiments. The experiment was conducted in two replications with sample sizes of 15 (Replication 1) and 5 (Replication 2). Unless noted otherwise, the procedures used were identical to those in Experiment 3. In conditioning, all the rats received forward conditioning in which a 2-min tone CS signaled the second of two widely spaced shock USs. The first US was always unsignaled, and it was followed 20 min later by the second US. Again, the conditioning stage lasted six cycles, as in Experiment 3. Groups of rats then received backward pairings with either the first US (shifted group, $n = 10$) or the second US (unshifted group, $n = 10$). Onset of the CS occurred immediately upon US termination. Both USs, spaced 20 min apart, were unsignaled in this stage. After nine sessions of response elimination, the rats were tested in simple extinction for five sessions. These sessions were identical to the original conditioning sessions, except for the deletion of the second US in the session.

Results and Discussion

Conditioning was rapid, and there were no group differences. Terminal levels of suppression were $.039$ ($SE = .018$) and $.027$ ($SE = .12$) in the shifted and unshifted groups, respectively. In response elimination (see Figure 8), the CS evoked less suppression in the shifted group than in the unshifted group, just as it had in Experiment 3. As can be seen in Figure 8, there is a smaller difference between the solid lines than between the dashed lines. This pattern of responding produced effects for elimination [$F(1,18) = 4.96$, $MS_e = 0.046$], session [$F(8,144) = 7.28$, $MS_e = 0.0059$], elimination × period [$F(1,18) = 77.85$, $MS_e = 0.036$], and elimination × period × session [$F(8,144) = 3.21$, $MS_e = 0.0068$]. As in Experiment 3, the triple interaction was attributable to faster extinction in the group that had experienced the greater change in context. There were differences between the shifted and the unshifted groups on Sessions 1–3 [smallest $F(1,149) =$
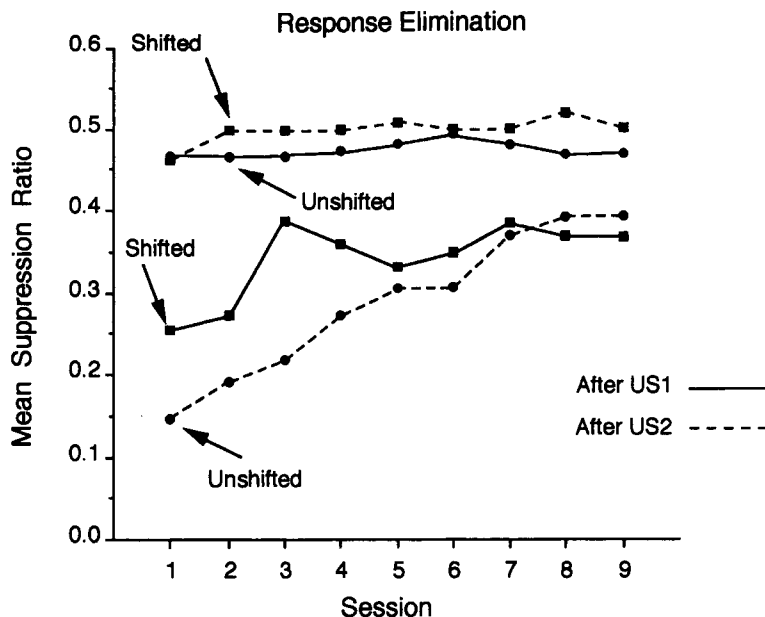
Figure 8. Suppression is shown for the periods right after the first US (after US₁) and right after the second US (after US₂) in the response elimination stage of Experiment 4 (pooled $MS_e = 0.0074$). The CS was moved from its previous location as a signal for the second US to the period after either the first US (shifted) or the second US (unshifted).

5.34, $MS_e = 0.0741$]. The excitatory CS evoked less suppression when it followed the first shock (shifted) than when it followed the second shock (unshifted). Thus, the differences in the magnitude of the decrement in suppression in Experiment 4 were caused by the shift and not by the US, first or second.

The main finding of the present experiment was that recovery occurred only in the unshifted group (see Figure 9). An ANOVA revealed a main effect for session [$F(5,90) = 4.60$, $MS_e = 0.0072$] and a session × elimination interaction [$F(5,90) = 2.42$, $MS_e = 0.0072$]. The interaction was caused by a preferential increase in suppression in Session 1 in the unshifted group [$F(1,90) = 12.74$, $MS_e = 0.0072$]. No increase in suppression was found in the shifted group ($F < 1$), which is somewhat surprising. Although more recovery might be expected in the unshifted group than in the shifted group, there was no evidence at all for recovery in the shifted group. Of course, recovery was never complete in any of the present experiments, which suggests that other powerful retrieval cues for the CS–no-US association were present in the test. For example, the CS was unreinforced in the recent sessions just prior to the test for response recovery. In any case, the results are opposite in direction to the prediction of the configural account that better recovery should occur in the shifted group than in the unshifted group.

Taken together, Experiments 3 and 4 found that recovery, if anything, was stronger in the unshifted groups than in the shifted groups. These data are accommodated by retrieval cue theory. That account holds that the magnitude of response recovery should depend on three factors:

(1) the strength and accessibility of the original CS–US association, (2) the strength of the CS–no-US association, and (3) the extent to which the CS–no-US association is activated during testing. All other factors remaining equal, the retrieval cue account would seem to demand that resistance to response elimination and subsequent recovery should be positively correlated. There are at least two ways in which this might occur. First, the CS–US association was more recently accessed in the unshifted group than in the shifted group, and more recently accessed associations may simply be more prone to recovery (the accessibility hypothesis). Second, the more resistant the response to elimination, the stronger the CS–no-US association would need to become in order to bring the level of responding to zero, and the greater the subsequent recovery if the CS–no-US association is not retrieved in test (the strength hypothesis). In summary, more recently accessed associations or those with higher strength might naturally be more susceptible to more recovery.

The question of why the CS–US association should have been more easily accessed, or stronger, in the unshifted group than in the shifted group is a matter for speculation. It is clear from the data that performance to the CS depended on whether it appeared in the vicinity of the first or the second US of the session. In response elimination, the CS evoked more suppression if it was presented near the time of the US used in conditioning, regardless of whether it had been originally paired with the first US (Experiment 3) or the second US (Experiment 4). If so, the CS–US association may simply have been less
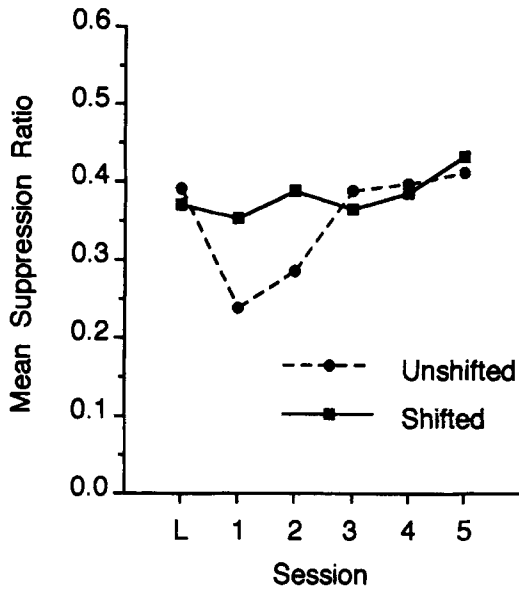
Figure 9. Suppression to the CS is shown for the simple extinction stage of Experiment 4 (pooled $MS_e = 0.014$). Data are shown for the last (L) session of response elimination and for the five test sessions in which the CS was unreinforced (simple extinction).

recently accessed in the shifted group than in the unshifted group because excitatory conditioning is to some extent context specific (Hall & Honey, 1989; Honey & Good, 1993). As for strength, given that the rats discriminated the first and second USs, it would not be surprising if the CS–US association also carried a measure of temporal specificity. In Experiment 4, for example, the CS was paired with the second US in the acquisition stage, and the CS and the first US were unpaired. Thus, the CS may have become preferentially associated with the second US. In response elimination, the unshifted group would then have continued to experience the CS in contiguity with the second US, albeit in a backward relation. This could have strengthened the association between the CS and the second US, perhaps by allowing the early portions of the CS to become associated with the second US (excitatory backward conditioning: Hearst, 1989; Heth & Rescorla, 1973).

Whatever the mechanism for the greater resistance, Experiments 3 and 4 are clearly inconsistent with other accounts of recovery after backward pairings. One already mentioned is the configural conditioning account. Another interpretation that explains the data poorly is the opponent process theory (e.g., Solomon & Corbit, 1974). At shock termination, the initial unconditioned reaction to shock (the A state) may have given way to a secondary reaction, relief (the B state). This secondary reaction to the US, dissipating soon after shock termination, would have been present when the CS occurred in a backward relation with the US. Unconditioned relief at shock termination might then have reduced the ability of the CS to evoke fear and prevented it from being extinguished. Of course,

thinking about the recovery effect in this way requires the assumption, perhaps unjustified, that an unreinforced CS does not lose associative strength if the fear CR it normally evokes is directly inhibited. In any case, such an account is inconsistent with the data of Experiments 3 and 4. The shifted groups responded less vigorously to the CS in response elimination, suggesting that fear was better protected by the B state. However, there was either statistically similar (Experiment 3) or less (Experiment 4) recovery in the shifted groups than in the unshifted groups.

Again, there is no place for the summation principle of the Rescorla–Wagner model (Rescorla & Wagner, 1972) in an explanation of the data. This account makes the same faulty prediction as the configural conditioning and opponent-process accounts: Resistance to extinction should be associated with poor recovery. In response elimination, the degree of attenuation of responding should be a measure of the strength of the conditioned inhibition acquired by post-US temporal cues. The stronger the inhibition, the better the protection from extinction.

GENERAL DISCUSSION

In Experiments 1–4 backward US–CS pairings eliminated responding to an excitatory CS, but responding later recovered in simple extinction if the US was withheld. In none of the experiments was evidence found that recovery of conditioned suppression after backward pairings was due to protection from extinction, an application of the summation principle of the Rescorla–Wagner model (Rescorla & Wagner, 1972). That account proposes that post-US temporal cues become inhibitory in conditioning. In response elimination, these inhibitory post-US temporal cues are thought to summate with, and thereby protect, the excitatory CS from losing associative strength. On the other hand, all of the results were easily handled by retrieval cue theory (Bouton, 1993), which assumes that recovery after backward pairings is a type of renewal. During the backward pairings, the rats appeared to be using the recent occurrence of the US as a cue for nonreinforcement of the CS, allowing the response to recover if the US was later withheld.

Contrary to the predictions of the summation account, in Experiment 1, it was found that recovery after backward pairings occurs if the post-US temporal cues are excitatory. According to the summation account, an excitatory local context cannot protect a CS from extinction, and thus, no recovery should have been seen under these conditions. Instead, these data encourage the view that the rats were using the recent occurrence of the US as a discriminative cue. The rats might have learned that in the presence of a recent US, the CS would not be reinforced. Experiment 2 confirmed a central prediction of the US cuing hypothesis. Responding to the CS recovered in simple extinction when the CS followed a recent US in response elimination, but not when the CS followed the US at longer delays. The data of Experiment 2 were inconsistent with an informational version of the protection-

from-extinction account, which suggests that a long wait to the next US results in conditioned inhibition and, thus, that protection from extinction should have occurred across a large range of US–CS intervals. If anything, in Experiments 3 and 4, better recovery was found if the response was difficult to eliminate. According to retrieval cue theory, slow elimination of conditioned suppression would be a sign that the CS–US association was stronger or more readily accessed. In test, if the CS–no-US association were not well retrieved, the original response would be especially likely to be evoked. A stronger or more recently accessed CS–US association should support better recovery. Just the opposite pattern of predictions is made by the protection-from-extinction account. During backward pairings, the excitatory CS should lose strength only to the extent that it is not fully inhibited by post-US temporal cues. The more slowly the response is eliminated, the greater the loss of associative strength, and the smaller the opportunity for recovery.

In addition to protection from extinction, the present experiments rule out a variety of other accounts of recovery after backward pairings. These include the context interference and opponent process accounts and, perhaps most importantly, the configural conditioning account. Bouton (1991, 1993) has argued for some time that interference effects in Pavlovian conditioning are probably not due to configural conditioning. Unfortunately, his arguments have always been based on null results. He finds little role for unique cues in his laboratory, because excitatory CSs transfer readily across contexts. With his procedures, there is no obvious loss in responding when a CS is moved from Context A to Context B (e.g., Bouton & King, 1983). In addition, he has used total darkness as a CS (Bouton & Swartzentruber, 1989), which he argues cannot be experienced differently in different contexts—a debatable point. In the present experiments, the US itself was the discriminative cue influencing performance to the CS. In Experiments 3 and 4, there was an effect of context switch on performance to the excitatory CS. In response elimination, the CS evoked less suppression in the shifted groups than in the unshifted groups. However, a large stimulus generalization decrement in response elimination did not predict better recovery as the configural account holds. In Experiment 4, there was actually better recovery in the unshifted group than in the shifted group. Getting the result backwards is more than a null result and eliminates the configural conditioning account.

It is interesting to compare recovery effects in conditioned suppression with those in pigeon autoshaping. In autoshaping, backward, random, and unpaired presentations of the CS and US eliminate responding, and responding then recovers in simple extinction when the US is withheld (Durlach, 1986; Lindblom & Jenkins, 1981). In her review of this literature, Durlach (1989) could find no compelling reason to dismiss a cuing account of recovery. As would be predicted by retrieval cue theory, recovery in pigeon autoshaping also appears to depend on

a previously reinforced CS's acquiring an inhibitory association in the response elimination stage (i.e., CS–US, followed by CS–no-US). Recently, Hemmes et al. (1997) reported that recovery of autoshaped keypecking after backward pairings is influenced by the probability of the US following the CS in conditioning, a result that is also accommodated by retrieval cue theory.

In closing, it is worthwhile summarizing why these data are important. First, great emphasis has been placed on the contrast between the predictions of the protection-from-extinction account and those of the retrieval cue account. However, an important point of agreement has not been emphasized. Both accounts suggest that recovery is due to an intact CS–US association. Thus, the present data make contact with current literature suggesting that old learning is not lost (Bouton, 1991, 1994). Second, and more important, the data indicate that performance in a number of interference paradigms can be parsimoniously explained by a retrieval cue analysis. Backward pairings do not support a special type of recovery that is explained by the summation principle of the Rescorla–Wagner model (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972). Recovery after backward pairings is another example of renewal.

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