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Primacy effects induced by temporal or physical context shifts are attenuated by a preshift test trial

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Abstract

When subjects are sequentially trained with a cue (A) paired separately with two outcomes (B and C) in different phases (i.e., A–B pairings followed by A–C pairings) testing in the training context after short retention intervals often reveals recency effects (i.e., stronger influence by A–C). In contrast, testing after long retention intervals or testing in a context different from that of training sometimes reveals primacy effects (A–B). Three experiments were conducted using rats in a Pavlovian conditioned bar-press suppression preparation to ascertain whether a nonreinforced test trial in the training context soon after training can attenuate this shift to primacy. Experiment 1 demonstrated that exposure to A shortly after both phases of training, but prior to a long retention interval, can attenuate shifts from recency to primacy otherwise observed with a long retention interval. Experiment 2 showed that exposure to A in the training context can also eliminate the shift from recency to primacy otherwise produced by shifting the physical context between training and test. Experiment 3 discredited a potential account of the results of Experiments 1 and 2. The effects observed in Experiment 1 and 2 are interpreted as early testing in the training context serving to initiate rehearsal of the A–C association due to the temporal proximity of A–C training.

The passage of time alone often attenuates the expression of previously acquired information. That is, animals tend to forget over the course of time, resulting in a reduced expression of prior learning (Ebbinghaus, 1885/1913). The cognitive basis of the forgetting process is still a point of debate. Although there are researchers who regard forgetting as a result of permanent memory loss or alteration (e.g., Loftus & Loftus, 1980), more recent views implicate retrieval interference and/or priming mechanisms that presumably attenuate the expression of a specific memory (e.g., Anderson, Bjork, & Bjork, 1994, 2000; Capaldi & Neath, 1995). Moreover, there are many reports across a wide variety of tasks and species that indicate that memory performance does not necessarily decay as a function of time. Instead, the expression of certain memories may actually be augmented with the passage of time.

One well-documented effect of memory performance increasing with time is the recency-to-primacy shift. This effect is observed on many tasks that involve serial list learning (learning a number of items in a fixed order) and subsequent recall or recognition testing. A recency effect refers to the fact that subjects tested after a short retention interval tend to express memories of the most recently learned items better than the first-learned items. However, when testing occurs after a long retention interval, expression of the most recently acquired

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memories is weaker. In some cases, this decrease in recency is observed in concert with an absolute increase in primacy (i.e., enhanced expression of the memory of the first-learned items; e.g., Neath, 1993). This absolute increase in primacy and simultaneous decrease in recency has been reported in a number of tasks using a variety of subjects and tasks such as human recognition of verbal stimuli (e.g., Knoedler, Hellwig, & Neath, 1999), human recognition of nonverbal stimuli (e.g., Neath, 1993; Wright, Santiago, Sands, Kendrick, & Cook, 1985), pigeon recognition memory (e.g., Santiago & Wright, 1984), and monkey recognition memory (e.g., Wright et al., 1985).

Effects similar to the recency-to-primacy shift seen in studies of serial list learning may be observed in studies of Pavlovian conditioning, particularly those that involve phasic conditioning (in which the subject receives different treatments in temporally distinct phases of training). For example, a conditioned stimulus (CS) that has been paired with an unconditioned stimulus (US) in one phase and then repeatedly presented alone in a second phase (i.e., extinction) elicits little conditioned responding when presented immediately after the extinction treatment. However, when tested after a long retention interval, subjects often recover responding to the CS (i.e., spontaneous recovery from extinction; e.g., Pavlov, 1927, p. 58). This effect can be theoretically viewed as a shift from responding based on recent memory of nonreinforcement (i.e., CS–noUS) to responding based on the initially acquired memory of reinforcement (i.e., CS–US).

This similarity between phasic Pavlovian learning and serial list learning has not gone unnoticed by learning theorists. Bouton's (1997) retrieval interference theory allows for a recency-to-primacy shift after extinction as a consequence of three tenets concerning the expression of acquired information: (a) different memories concerning a CS compete for expression when the CS is tested; (b) these memories are differentially subject to priming by the context of testing, with first-learned memories concerning a CS being less context dependent than are the later learned memories concerning that CS; and (c) time as well as spatial location is part of the context. The reason that later learned memories are more context dependent is that the CS becomes ambiguous at the time that the later learned memories are acquired. In this framework, extinction of conditioned responding occurs because memories of CS nonreinforcement retroactively interfere with retrieval of memories of CS reinforcement. At a short retention interval, the temporal context is most similar to that of extinction treatment, which facilitates the expression of the recent memories of CS nonreinforcement, resulting in attenuated conditioned responding. However, after a long retention interval, the temporal context of testing has changed from that of the more recent phase of treatment, and responding reflects the first-acquired (i.e., unambiguous) memory of the CS. This account explains both spontaneous recovery from extinction and renewal after extinction, the former through a change in the temporal context and the latter through a change in the spatial context.

These assumptions are supported by data in addition to spontaneous recovery from extinction (e.g., Bouton & King, 1983; Bouton & Nelson, 1994; Bouton & Peck, 1992; Nelson, 2002). For example, a CS that is preexposed alone before CS–US pairings elicits retarded conditioned responding relative to a CS that is not preexposed before CS–US pairings (i.e., latent inhibition; Lubow & Moore, 1959). The response retarding effect of CS–preexposure may be augmented by the imposition of a long retention interval between CS–US training and testing of the CS (i.e., super-latent inhibition; e.g., De la Casa & Lubow, 2000, 2002; Wheeler, Stout, & Miller, 2004; but see Killcross, Kiernan, Dwyer, & Westbrook, 1998; Kraemer, Randall, & Carbary, 1991), provided that the retention interval is spent outside the experimental apparatus. In contrast to experimental extinction, in the case of latent inhibition, the memories of the nonreinforced CS are the first-learned memories, and imposition of a long retention interval following the CS–US pairings results

in enhanced expression of the CS–noUS memory, thereby producing a larger decrement in conditioned responding than that observed with a short retention interval. The super-latent inhibition effect can also be observed with a shift of the physical context rather than the temporal context (e.g., Swartzentruber & Bouton, 1992; Westbrook, Jones, Bailey, & Harris, 2000).

While the aforementioned classical conditioning research deals with nonhuman participants, a recent study conducted in our laboratory has revealed both spontaneous recovery from extinction and super-latent inhibition in humans using a predictive judgement task (Stout, Amundson, & Miller, 2005). In one experiment, Stout et al. exposed participants to an abstract visual cue that was sometimes followed by a picture, which served as an outcome. Participants were trained with paired presentations of the cue (trials in which the cue was followed by the outcome), occurring prior to (extinction), after (CS-preexposure), or intermixed with (partial reinforcement) unpaired presentations of the cue. The predictive value of the cue was then assessed by asking participants to rate the probability (0–100%) that the outcome would follow a test presentation of the cue. This assessment occurred either immediately or after a long 48-hr retention interval. Participants tested immediately after training displayed a recency effect; the assessed predictive value of the cue reflected the most recently experienced trial type. In contrast, participants tested after a long retention interval showed a primacy effect, with responding of the participants in each group reflecting the first-experienced trial type. These results are consistent with many of the aforementioned experiments with one interesting caveat. Participants did not show a recency-to-primacy shift when they were tested at both a short and a long retention interval. That is, the recency effect was preserved at a long retention interval (i.e., protected from the shift ordinarily produced by the passage of time) if the participants gave a predictive rating shortly after training.

Stout et al. (2005) suggested that the recency-to-primacy shift was prevented by the short-delay test because participants had already evaluated the predictive status of the cue. After evaluating the predictive status of the cue, subjects may cease to process the memories of the different trial types. The participants may simply remember and retrieve their last (and only) response. However, there are other less theoretically relevant interpretations. For example, it is possible that the participants were responding to a perceived experimenter demand with regard to consistency. Participants may have valued response consistency because they felt that the experimenter was testing their memory of their last response, as opposed to their memory of training. Also, it is possible that the memory for the linguistically based response (a predictive numeric rating) was easier to recall than the object-based training (involving the presentation of abstract shapes) simply because of the modality of encoding. In order to provide a clear interpretation of this phenomenon as well as to expand the generality of the phenomenon, we conducted two experiments using rats as subjects. Presumably, rats are relatively immune to any effects of experimenter demand and are not prone to linguistic encoding of visual or auditory stimuli.

EXPERIMENT 1

In order to investigate the effect of early testing on later performance in rats, we employed a design used by Wheeler et al. (2004) in which target CS training was embedded within a sensory preconditioning procedure. They had observed recency-to-primacy shifts as evidenced by an augmented CS-preexposure effect and spontaneous recovery from extinction over long retention intervals. The subjects tested after a short retention interval showed a recency effect; only a small CS-preexposure effect was observed, but a large extinction effect was apparent. This recency effect shifted to a primacy effect after a long

retention interval; the deleterious effect of CS-preexposure was more robust than that of extinction after a long retention interval.

One peculiarity of the design used by Wheeler et al. (2004) is the use of sensory preconditioning. Sensory preconditioning was used in the present studies primarily to replicate Wheeler et al.'s recency-to-primacy shifts. A recency-to-primacy shift after extinction treatment (i.e., spontaneous recovery) is fairly ubiquitous throughout the literature, but a similar shift after latent inhibition treatment (i.e., super-latent inhibition) is observed less often. Both Killcross et al. (1998) and Kraemer et al. (1991) have reported a recovery from latent inhibition after a long retention interval, which is the opposite of a spontaneous super-latent inhibition effect. These observations both used a first-order conditioned fear preparation. Wheeler et al. speculated that the use of first-order conditioning might hinder the ability to observe super-latent inhibition because the more recent memories (of reinforcement) are more salient than the initial memories of nonreinforcement. This design decision was motivated by Bouton's (1993) supposition that memories of reinforcement are less context dependent than memories of nonreinforcement. By using sensory preconditioning, Wheeler et al. avoided the use of reinforcement during training. Although the reasoning behind this design was largely speculative, it is clear that the super-latent inhibition effect is parameter dependent. Therefore, in order to study a reliable recency-to-primacy shift in latent inhibition, sensory preconditioning was used here.

Experiment 1 of the present series was designed to determine whether the recency-to-primacy shift observed by Wheeler et al. (2004) would be affected by presenting the test stimulus after training, but prior to a long retention interval. The results of Stout et al. (2005) with humans suggest that this manipulation can attenuate a recency-to-primacy shift. Table 1 summarizes the design of Experiment 1. Subjects in the preexposure (PE) condition received exposure to X alone in Phase 1 followed by X → S pairings in Phase 2. Subjects in the extinction condition received similar training, with the order of treatments reversed. Control subjects were divided into two subgroups that received X → S pairings in either Phase 1 (extinction-control) or Phase 2 (PE-control), with no exposures to X alone, so there was no ambiguity concerning the predictive value of X. Phase 3 consisted of S → US pairings for all subjects. A total of 3 days after Phase 3, subjects in the 2Test condition were tested on the X stimulus. Based on Stout et al.'s results, we expected that this brief exposure would prevent a recency-to-primacy shift in responding that ordinarily occurs when a long retention interval is interposed between the last phase of treatment and testing. A total of 27 days after Phase 3, all subjects were tested on the X stimulus. If the recency-to-primacy shift that we expected in the 1Test condition is eliminated in subjects in the 2Test condition, we can conclude that the effect observed by Stout et al. can be replicated with nonhumans, which would make it difficult to explain in terms of experimenter demands or linguistic encoding.

Method

Subjects—The subjects were 36 male and 36 female, experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Bodyweight ranges were 244–361 g for males and 182–265 g for females. Subjects were randomly assigned to one of six groups ($n_s = 12$), counterbalanced within groups for sex. The animals were individually housed in standard hanging stainless-steel wire-mesh cages in a vivarium maintained on a 16/8-hr light/dark cycle. Experimental manipulations occurred near the middle portion of the light phase. The animals were allowed free access to Purina Lab Chow, whereas water availability was limited to 20 min per day following a progressive deprivation schedule initiated 1 week prior to the start of the study. From the time of weaning until the start of the

study and during the long retention interval, all animals were handled for 30 s, three times per week.

Apparatus—The apparatus consisted of 12 operant chambers each measuring 30.5 cm × 27.5 cm × 27.3 cm (l × w × h). All chambers had clear Plexiglas ceilings and side walls, and metal front and back walls. On one metal wall of each chamber, there was an operant lever and adjacent to it a niche (4.5 × 4.0 × 4.5 cm) centred 3.3 cm above the floor through the top of which a solenoid-driven valve could deliver 0.04 ml of water into a cup at the bottom of the niche. Chamber floors were grids, 4 mm in diameter, spaced 1.7 cm apart centre-to-centre, connected with NE-2 neon bulbs, which allowed a 0.5-mA constant-current footshock US to be delivered by means of a high-voltage AC circuit in series with a 1.0-MΩ resistor. All chambers were housed in sound- and light-attenuating environmental chests. Two 45-Ω speakers mounted on two different interior walls of each environmental chest could deliver a 6/s click train and a white noise, both at 8 dB (C-scale) above the ambient background sound of 78 dB that was produced primarily by a ventilation fan. An overhead flashing (0.25 s on/0.25 s off) light stimulus was provided by a 60-W (nominal at 120 VAC) incandescent bulb driven at 112 VAC. Each chamber was illuminated by a dim (#1820; Chicago Miniature) houselight. In Experiment 1, the X stimulus was the click train, and the S stimulus was the flashing light. Chamber assignments between the six groups were counterbalanced.

Procedure

Acclimation and shaping: On Days 1–5, all subjects were trained to bar-press for water (0.04 ml) during daily 60-min sessions. To facilitate magazine training and bar-pressing, the onset of the water delivery was accompanied by the onset of a 0.5-s white noise. On Days 1 and 2, a fixed-time 2-min schedule of noncontingent water delivery occurred concurrently with a continuous reinforcement schedule. On Day 3, noncontingent water was discontinued, and subjects were trained on the continuous reinforcement schedule alone. Subjects that did not finish this session with more than 50 responses were hand-shaped through successive approximation. On Days 4 and 5, a variable-interval 20-s (VI-20) schedule was imposed. This schedule of reinforcement prevailed throughout the remainder of the experiment including reshaping and testing.

Phase 1: On Days 6 and 7, Phase 1 training occurred in daily 60-min sessions. For the subjects in the two PE groups, each day included six X-alone presentations separated by 9 ± 4.5 -min intertrial intervals (ITIs). For the rats in the two extinction groups and half of the subjects in each control group (the extinction–control subgroup), each day included six X → S pairings separated by 9 ± 4.5 -min ITIs (see Table 1). The onset of the 5-s stimulus S occurred at the end of the 60-s stimulus X. The other half of the control subjects (the PE–control subgroup) were placed in the operant chambers and presented with no nominal stimuli.

Phase 2: Phase 2 also consisted of 2 days of daily 60-min sessions. For the PE groups and the control subjects that had previously received no X–S pairings (the PE–control subgroup), the session included six X → S pairings separated again by 9 ± 4.5 -min ITIs. The extinction groups received six exposures to X-alone with the same ITIs. The control subjects that had previously received X → S pairings (the extinction–control subgroup) were placed in the operant chambers and presented with no nominal stimuli.

Phase 3 First-order conditioning of the surrogate stimulus: On Day 10, all rats experienced four S → US pairings in a 60-min session. These pairings were separated by 15

± 7.5 -min ITIs. The onset of the 0.5-s footshock US occurred 4.5 s into the 5-s presentation of S and coterminated with the CS.

Short retention interval reshaping and Day 13: On Days 11 and 12, in order to restabilize bar-pressing the animals from all groups experienced daily 60-min sessions that allowed uninterrupted bar-pressing. The animals that registered fewer than 50 responses on Day 11 were given an extra 30-min session on that day. On Day 13, subjects in the 2Test condition were tested for suppression to X in a 30-min test session. During the session, there was one presentation of X alone, 60 s in duration. The onset of the stimulus occurred 4.5 min following placement in the operant chamber. The subjects in the 1Test condition were placed into the chambers for a 30-min session, during which no nominal stimuli were presented. For the 2Test subjects, the numbers of bar-presses emitted during the 120-s immediately prior to the onset of the test trial CS and during the presence of the test trial CS were both recorded. The suppression ratio for each subject consisted of the total number of bar-presses (BP) made during the presentation of the 60-s CS divided by the sum of that number plus half the total number of bar-presses made during the 120-s interval that immediately preceded the CS—that is, $BP_{CS}/(BP_{CS} + 0.5BP_{pre-CS})$. We used a 2-min baseline measure as opposed to a 1-min measure based on the assumption that a larger sample of time would better assess baseline rates of responding.

Long retention interval reshaping and Day 36: On Days 34 and 35, all rats were given daily 60-min reshaping sessions. On Day 36, all rats were tested for suppression to X. The testing procedure was identical to that used after the short retention interval, with the exception that all subjects were exposed to the target stimulus X.

Results and discussion

The subjects that were tested on Day 13 (the first test for the 2Test condition) displayed a recency effect; that is, subjects in the PE condition ($M = .30$, $SE = .05$) suppressed more than subjects in the extinction condition ($M = .53$, $SE = .03$). Subjects in the control condition suppressed the most ($M = .00$, $SE = .00$). When these subjects were tested after a long retention interval, there was a trend toward extinction (or forgetting) in all groups, but it is clear that the recency effect remained consistent between the two tests (Figure 1 shows the means obtained on Day 36). Conversely, the subjects that were not tested at the short retention interval (the 1Test condition) behaved in a way that was congruent with the first phase of training; that is, responding after the long retention interval reflected a primacy effect. Specifically, subjects in the extinction condition suppressed more than did the PE subjects, and the control subjects (both the PE and the extinction control subgroups) showed the greatest suppression.

An α -level of .05 was adopted for all statistical analyses. Prior to analysing the Day 13 scores, any differences in conditioned suppression between the control subgroups were assessed using a t test to compare the PE control and extinction control subgroups. This analysis revealed no significant effects, $p > .30$. Therefore, the control subgroups were pooled for all further analyses. The pre-CS scores (the baseline rate of lever pressing measured in the 2 min before the CS presentation on test day) were then analysed to determine whether there were any differences in baseline contextual fear among the groups. The results of a one-way analysis of variance (ANOVA) on the pre-CS scores showed that there was no significant effect of group on Day 13, $p > .75$, indicating that any group differences in fear expressed to the CS were not likely to be influenced by fear of the context summing with fear of the CS.

Due to the nature of the experimental design, direct comparisons between the Day 13 scores and Day 36 scores were inappropriate because the subjects received less context exposure in

the two reshaping sessions before Day 13 than in the four reshaping sessions before Day 36. The different amounts of context exposure did seem to produce a difference in the rate of baseline lever pressing between the Day 13 and Day 36 tests, $F(1, 66) = 6.53$. Therefore, the scores from the two different test days were analysed separately. In order to determine the subjects' conditioned fear to CS X, the Day 13 data were analysed using another one-way between-subjects ANOVA, this time with the suppression ratio as the dependent variable. This test found an effect of treatment, $F(2, 33) = 62.98$. A planned comparison revealed a latent inhibition effect, as the control-2Test group suppressed more than the PE-2Test group, $F(1, 33) = 41.14$. Furthermore, the extinction-2Test group showed the least suppression to the stimulus, suppressing less than the PE-2Test group, $F(1, 33) = 22.73$. Therefore, on the short retention interval test, both the PE and extinction conditions exhibited less suppression than the control condition. But moderate suppression was apparent in the PE condition (reflecting the most recent presentations of the target stimulus, which were paired with S), and no suppression was apparent in the extinction condition (reflecting the most recent presentations of the target stimulus, which were not paired with S).

Before analysing the Day 36 suppression ratios, differences between the subgroups of each of the two control groups were assessed using a 2 (treatment: PE-control vs. extinction-control) $\times$ 2 (test: 1Test vs. 2Test) ANOVA. This analysis revealed no significant effects. Therefore, the control subgroups were pooled forming the two control groups for all further analyses. Also before analysing the Day 36 suppression ratios, the pre-CS lever pressing rates were assessed using a 3 (treatment: control vs. PE vs. extinction) $\times$ 2 (test: 1Test vs. 2Test) ANOVA, which found no significant effects. To test responding to the CS, another 3 (treatment: control vs. PE vs. extinction) $\times$ 2 (test: 1Test vs. 2Test) ANOVA was conducted using the Day 36 suppression ratios in response to X as the dependent variable. The results of this analysis revealed an effect of treatment, $F(2, 66) = 60.28$, and an interaction between treatment and test, $F(1, 66) = 14.57$. The effect of test was not significant, $p > .05$. Planned comparisons showed that the subjects in group control-2Test suppressed more than those in group PE-2Test, $F(1, 66) = 22.77$. Moreover, the extinction-2Test group showed the least suppression to the stimulus, suppressing less than the PE-2Test group, $F(1, 66) = 12.09$. This pattern of results is similar to that observed when the subjects were tested shortly after training (Day 13), with responding in the extinction and PE conditions reflecting the most recent (Phase 2) training.

Finally, planned comparisons were performed to determine the pattern of responding for subjects in the 1Test condition. In contrast to the subjects that received posttraining exposure to the stimulus prior to the long retention interval, the subjects in group extinction-1Test suppressed more than group PE-1Test, $F(1, 66) = 17.17$. This pattern of responding is more congruent with the first phase of training, suggesting a shift to primacy in the conditioned responding. There was still a clear deficit in responding to the target stimulus in the extinction condition, as the extinction-1Test group exhibited less suppression to the stimulus than did the control-1Test group, $F(1, 66) = 23.55$. These results are consistent with the hypothesis that exposure to the target stimulus soon after training and before the long retention interval attenuates the recency-to-primacy shift observed when there is no such exposure. To demonstrate this point further, extinction-1Test and PE-1Test groups were compared with their 2Test counterparts. These analyses revealed more suppression in group PE-1Test than in group PE-2Test, $F(1, 66) = 23.55$, and less suppression in group extinction-1Test than in group extinction-2Test, $F(1, 66) = 13.03$.

Although the results of Experiment 1 indicate that the initial test preserved the recency effect over a long retention interval, there are alternative interpretations. Possibly, the presentation of the CS at a short retention interval simply extended the recency effect; thus,

we might have observed a recency-to-primacy shift with a longer retention test. Moreover, it is possible that testing at the short retention interval acted as another X-alone learning trial. This possibility is especially problematic when interpreting the results of the extinction condition, in which the group extinction–2Test technically received more unpaired exposure to X than did group extinction–1Test. Perhaps the extra extinction trial served to preclude spontaneous recovery. However, such an explanation would be difficult to apply to the PE condition. The nonreinforced exposure to the CS on Day 13 caused the PE–2Test group to suppress more than the PE–1Test group on Day 36. The idea that nonreinforcement can yield an increase in responding has been noted previously (e.g., an extinction spike, Dudley & Papini, 1997), but it is counterintuitive. Because of the difficulty in interpreting the effect of repeated unpaired testing on changes in responding to an extinguished CS, Experiment 2 focused exclusively upon the recency-to-primacy shift observed in the PE condition.

EXPERIMENT 2

Experiment 2 was designed to examine the effect of repeated testing upon changes in responding that occur due to a change in the physical context. As mentioned in the Introduction, Bouton's (1997) interference theory posits that effects such as spontaneous recovery from extinction and development of super-latent inhibition occur because time serves as a context that primes retrieval of different memories of a CS. At a short retention interval, the recent temporal context primes retrieval of recently acquired memories. When that recent temporal context is removed (i.e., when a long retention interval is interposed), the first-learned memories are expressed more strongly than the more recent memories because the later learned memory is not strongly primed, thereby releasing the first-learned memory from interference. Theoretically, a physical context shift should produce recency-to-primacy shifts that are similar to those produced by a temporal context shift.

Unlike Experiment 1, only the physical context was manipulated in Experiment 2, and all subjects were tested on both stimuli after a relatively short retention interval. In Experiment 1, the training and short retention interval testing presumably took place in similar temporal contexts, whereas the long retention interval testing took place in a temporally distinct context. In order to simulate this temporal context shift in Experiment 1, the physical context had to be altered after training and prior to testing. Hence, in Experiment 2 both phases of training occurred in a consistent context followed by testing in a distinctly different context (e.g., an AAB context shift design). If the augmented CS-preexposure effect observed in Experiment 1 resulted from a shift in the temporal context between training and testing, we would expect a similar effect to occur with a shift in the physical context between training and testing.

One potential problem with using an AAB renewal design is that a shift in physical context between training and testing may cause a recovery of responding as opposed to an augmentation of the CS-preexposure effect. This result has been observed in a number of studies of latent inhibition in which the context of preexposure differed from the context of training (e.g., Hall & Channell, 1983; Lovibond, Preston, & Mackintosh, 1984; McLaren, Bennett, Plaisted, Aitken, & Mackintosh, 1994). However, shifting the context between preexposure and conditioning is qualitatively different from shifting the context between conditioning and testing. In fact, an augmentation of the CS-preexposure effect has been observed in experiments in which subjects were preexposed and trained in one context and tested in a different context (Swartzentruber & Bouton, 1992; Westbrook et al., 2000). However, these studies did not include comprehensive control measures. Specifically, both of these studies failed to equate US exposure in each context, and Westbrook et al. did not equate overall exposure to the two test contexts. In the design below, we sought to address the confounds present in Westbrook et al. by using a mixed design that equated different

groups on exposure to the contexts and equated the different contexts in terms of S and US presentations (see Table 2).

Experiment 2 consisted of a 2 (treatment: PE vs. control) $\times$ 2 (test context: AAA vs. AAB) $\times$ 2 (stimulus: X vs. Y) mixed design; the test stimulus was manipulated within subjects, so that all subjects were tested on one cue (Y) twice and another cue only once (X; see Table 2). The context shift manipulation occurred between subjects, so that half of the subjects received an AAB context shift whereas the other half received no context shift (AAA). As in Experiment 1, CS-preexposure was manipulated between subjects. Before testing, the two cues (X and Y) were separately trained in two distinct contexts (A and B) for each subject. During Phase 1, subjects in condition PE received unpaired exposure to both X in Context A and Y in Context B, while control subjects only received comparable context exposure. In Phase 2, all of the subjects experienced X $\rightarrow$ S and Y $\rightarrow$ S pairings in Contexts A and B, respectively. Phase 3 consisted of the same S $\rightarrow$ US pairings used in Experiment 1, this time occurring in both contexts. Three days after the S $\rightarrow$ US pairings, all subjects were tested with the Y stimulus in Context B. During the following two test days, groups control-AAA and PE-AAA received tests of X and Y in their training contexts (A and B, respectively), while groups control-AAB and PE-AAB were tested on X and Y in the opposite context (B and A, respectively). The physical context shift in the PE-AAB group was expected to produce weaker responding to the X stimulus than group PE-AAA. Critical to this experiment was whether such an effect would be observed in the previously tested Y stimulus.

In the execution of Experiment 2, an experimenter error caused the loss of data from one quarter of the subjects, resulting in a loss of statistical power. Because of this, a complete replication was conducted, and the data were pooled for all analyses in order to enhance the statistical power. Thus, some counterbalancing conditions were represented twice.

Method

Subjects—Subjects remaining after the elimination of the inappropriately treated animals were 42 male and 42 female, experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Body-weight ranges were 306–374 g for males and 180–207 g for females. Subjects were randomly assigned to one of four groups, counterbalanced within groups for sex. Because of the experimenter error, group *ns* were unequal. Groups PE-AAB and control-AAB each had 18 subjects, whereas groups PE-AAA and control-AAA were composed of 24 subjects. The animals were housed, handled, and water deprived as described in Experiment 1.

Apparatus—Contexts A and B were created from the same 12 operant chambers as those used in Experiment 1, with the addition of a 45- Ω speaker that could deliver a complex tone (consisting of 3,000- and 3,200-Hz pure tones) at 8 dB (C-scale) above the ambient background sound. A 60-s presentation of the tone and click served as CSs X and Y (counterbalanced). The S stimulus was the same 5-s flashing light as that used in Experiment 1.

The identities of Contexts A and B were counterbalanced within groups. One context was illuminated by a dim (#1820) houselight, and an odour cue, supplied by two drops of mint (98% methyl salicylate, Humco Laboratory), was placed on a wooden block within the sound-attenuating environmental chamber, but outside of the operant chamber. The other context was identical, except the houselight was off, and the mint odour was replaced by an artificial banana odour (artificial banana #112, Virginia Dare Extract Co.). In both contexts, chamber assignments within the four groups, as well as the order of context exposure on each day, were counterbalanced.

Procedure

Acclimation and shaping: On Days 1–5, subjects experienced the same shaping regimen as that described in Experiment 1. In order to acclimate the subjects to each context, the subjects were given two daily 45-min shaping sessions per day, one session in each context, with the order alternated across days.

Phase 1: Phase 1 training occurred in four 60-min sessions over Days 6 and 7. For the subjects in the two PE groups, each day involved one session in Context A, during which there were six 60-s X-alone presentations separated by 9 ± 0.5 -min ITIs, and six 60-s Y-alone presentations in Context B, separated by 9 ± 4.5 -min ITIs (see Table 2). The subjects in the two control groups were exposed for 60 min to each context on each day, but received no punctate stimuli.

Phase 2: Phase 2 also consisted of four 60-min sessions, occurring over Days 8 and 9. For all groups, there was a daily X-conditioning session in Context A, which included six X $\rightarrow$ S pairings separated again by 9 ± 4.5 -min ITIs, and a similar daily Y-conditioning session in Context B, in which each subject received six Y $\rightarrow$ S pairings. X and Y were 60 s, and S was 5 s in duration. S was presented during the last 5 s of the 60-s presentations of X and Y.

Phase 3: First-order conditioning of the surrogate stimulus: On Day 10, all subjects experienced two 30-min sessions, one in Context A and the other in Context B. Each session incorporated two S $\rightarrow$ US pairings. These trials were separated by a 15-min ITI. The onset of the 0.5-s footshock US occurred 4.5 s into the 5-s presentation of S and coterminated with S.

Reshaping and Day 13: On Days 11 and 12, the animals from all groups were given daily 45-min sessions of uninterrupted bar-pressing in each context to restabilize bar-pressing. On the next day (Day 13), all subjects were tested on Y in a 30-min test session in Context A. In this session, there was one test presentation of Y alone. The test procedure and suppression ratio calculations were the same as those in Experiment 1. In addition to this test session, all subjects were given equal exposure to Context A, but experienced no nominal stimuli.

Days 14 and 15: On Days 14 and 15, all rats were tested on responding to X and Y. There was only one test session with one CS for each subject on each day, and the order of testing (X vs. Y) was counterbalanced within groups. For subjects in the AAA condition, CSs X and Y were tested in Contexts A and B, respectively. For subjects in the AAB condition, CSs X and Y were tested in Contexts B and A, respectively, so that the testing context was different from that of preexposure and training. The testing procedure for each session was identical to that used in Experiment 1.

Results and discussion

During testing, one subject from the PE–AAA group did not produce any lever presses during the X pre-CS interval and therefore was eliminated from all analyses because no suppression ratio could be calculated. Because the order of stimuli tested on Days 14 and 15 was counterbalanced within groups, the data for X on Days 14 and 15 were pooled across test order, as were the data for Y. Figure 2 shows the combined results of Days 14 and 15. Suppression to the Y stimulus was stronger in the control groups than in the PE groups, suggesting the occurrence of a latent inhibition effect in the PE condition. However, there was no clear indication of an effect of context shift on suppression to Y, presumably because Y was initially tested before the physical context shift (i.e., Day 13). In contrast, suppression to the X stimulus appeared to be markedly stronger in the PE–AAA group than in the PE–AAB group. Such a difference suggests an augmented latent inhibition effect produced by a

physical context shift between training and testing for the X stimulus, but not for the Y stimulus. Support for this observation also comes from a comparison of the first test of Y to the second test of Y (Figure 3). In all groups, suppression to CS Y appeared to get weaker with repeated testing (presumably reflecting extinction instead of enhanced conditioned responding), but there was no obvious effect of testing the Y stimulus in a different context. Statistical analyses supported these observations.

Before analysing the suppression ratio data, two 2 (treatment: PE vs. control) $\times$ 2 (test context: AAA vs. AAB) ANOVAs were conducted using the raw baseline pre-CS bar-pressing rates (immediately before the X and test presentations). These analyses yielded no main effects or interactions, indicating that there were no significant differences between the groups with regard to contextual fear. A 2 (treatment: PE vs. control) $\times$ 2 (test context: AAA vs. AAB) ANOVA of suppression to CS X detected main effects of test context, $F(1, 79) = 22.28$, and treatment, $F(1, 79) = 95.83$, and an interaction between test context and treatment $F(1, 79) = 5.58$. A planned comparison of suppression in response to X showed evidence of latent inhibition in the PE–AAA group relative to the control–AAA group, $F(1, 79) = 31.80$. A comparison of the PE–AAA and PE–AAB groups indicated weaker suppression in the PE subjects that were tested on X in the nontraining context, $F(1, 79) = 24.84$. This difference was not reliable for the control subjects, $F(1, 79) = 2.81$, $p > .09$. These analyses support the conclusion that latent inhibition was more effective when the test context of X was shifted. Another 2 (treatment: PE vs. control) $\times$ 2 (test context: AAA vs. AAB) ANOVA was conducted on suppression to CS Y. This analysis detected a main effect of treatment, $F(1, 79) = 21.36$ (denoting latent inhibition), but no interaction, $F(1, 79) = 0.08$, $p > .67$, suggesting that there was no augmentation of the latent inhibition effect.

The repeated testing of stimulus Y was also analysed using a 2 (treatment: PE vs. control) $\times$ 2 (test context: AAA vs. AAB) $\times$ 3 (test: Day 13 vs. Days 14 and 15) mixed ANOVA in order to detect any shifts in suppression in response to Y across tests. This analysis revealed an effect of treatment, $F(1, 79) = 28.90$, again indicating latent inhibition, and an effect of test, $F(1, 79) = 13.37$, demonstrating extinction from Day 13 to Days 14 and 15, but no other significant effects. The fact that extinction was apparent after repeated testing suggests that the persistence of recency observed in responding to the Y stimulus was not the result of an extinction spike (i.e., increased responding observed as a result of unexpected reinforcement omission; e.g., Dudley & Papini, 1997).

EXPERIMENT 3

Empirically, the results of Experiments 1 and 2 are straightforward. Changing the physical or temporal context between training and testing caused recency-to-primacy shifts in conditioned responding. The recency-to-primacy shifts were attenuated when subjects were exposed to the target stimulus after training, but before any shift in the physical or temporal context. Although the results of Experiments 1 and 2 are clear, the interpretation of the results is not. Here we entertain a potential account of the effect observed in Experiments 1 and 2 and test it in a third experiment.

Because the results obtained in Experiments 1 and 2 were similar to those observed by Stout et al. (2005), their interpretation should be considered as a potential account for the present results. As mentioned in the Introduction, Stout et al. interpreted their result as an instance of animals conserving cognitive effort. According to Stout et al., after their subjects evaluated and rated a cue-outcome contingency on an initial test, no further processing of that contingency was done. Thus, even after a long retention interval that normally caused a recency-to-primacy shift, subjects simply responded with their last rating of the contingency. Essentially, the initial rating allowed the subjects to reduce the contingency to a summary

statistic, and once this occurred processing of the original memories of training ceased. In the studies reported here, there was no formal contingency rating during the first test of X, but the stimulus did elicit a response that ideally should have reflected the X–S–US contingency. It is possible that the first test of X allowed the subjects to form a direct association between X and the conditioned response (R), much like Stout et al.'s subjects formed a direct association between the cue and the contingency rating. This theory is similar to Eysenck's (1968) theory of incubation of conditioned fear. Eysenck claimed that nonreinforced CS presentations might augment conditioned responding by building a strong CS–response (R) association. Therefore, processing of the full X–S–US contingency may have ceased after the X–R association was established.

Viewing the theory stated above in the framework of sensory preconditioning, it is possible that the associative structure that underlies responding to a sensory preconditioned stimulus changes when that stimulus is presented after training. Normally, responding to a sensory preconditioned stimulus is mediated by the first-order CS (in this case S). This is evident because sensory preconditioned responding to the target CS is reduced if the mediating stimulus (i.e., S) is extinguished after training (e.g., Rizley & Rescorla, 1972). In Experiments 1 and 2 of the present series, when X was first tested, conditioned responding seemed to be mediated by an X–S and an S–US association. The strength of responding to X was contingent on the expression of the X–S association, which varied based on the temporal and physical context of testing. However, after the first test of X, subsequent conditioned responding did not appear to be mediated by the X–S association. Regardless of when or where the second test took place, the subjects exhibited a recency effect. It is possible that, after a single test, the associative structure of a sensory preconditioned stimulus changed from an indirect relationship between X and the US (i.e., X–S and S–US) to a direct association between X and the conditioned response (i.e., X–R). Thus, after initial testing, the X–S association may have had no impact on responding.

Experiment 3 was designed to determine whether the X–S–US association is altered when the X stimulus is tested after sensory preconditioning (see Table 3 for the design). A simple sensory-preconditioning design was used, in which the X stimulus was always paired with the outcome (condition sensory preconditioning, SP). Also in Phase 1, unpaired (UP) controls were included that received noncontingent X and S exposures. In Phase 2, the S stimulus was paired with the footshock US. After Phase 2, one third of the subjects were exposed to a single test of X (condition ExtS–2Test). All other subjects only experienced equivalent context exposure. This initial test was followed by a third phase in which two thirds of the subjects received 30 Salone exposures (conditions ExtS and ExtS–2Test)—that is, extinction of S. Subjects in the NoExt condition experienced equivalent context exposure with no nominal stimuli presented. Finally, all subjects were tested with X. Significant responding to X was expected only in subjects that received X–S pairings (i.e., the SP condition). Furthermore, weak responding was expected for subjects that received X–S pairings followed by extinction of S. Of principal interest was whether extinction of S would affect responding to X in subjects that were previously tested with X (group SP–ExtS–2Test). According to the interpretation of Stout et al. (2005), the status of the S–US association should not affect responding to X at test, because these subjects should simply respond based on an X–R association. Thus, evidence of sensory preconditioning should be apparent in group SP–ExtS–2Test.

Method

Subjects—The subjects were 36 male and 36 female, experimentally naive, Sprague-Dawley descended rats obtained from our own breeding colony. Body-weight ranges were 316–435 g for males and 222–281 g for females. Subjects were randomly assigned to one of

six groups ($n_s = 12$), counterbalanced within groups for sex. The animals were individually housed in standard hanging stainless-steel wire-mesh cages in a vivarium maintained on a 16/8-hr light/dark cycle. Experimental manipulations occurred near the middle portion of the light phase. Water deprivation and handling occurred as in Experiments 1 and 2.

Apparatus—The apparatus was the same as that used in Experiment 1. The context was held constant throughout training and testing.

Procedure

Acclimation and shaping: Acclimation and shaping occurred as in Experiment 1.

Phase 1: Sensory preconditioning: On Days 6 and 7, training occurred in daily 60-min sessions. For the subjects in the three SP groups, each of the two sessions included six $X \rightarrow S$ pairings separated again by 9 ± 4.5 -min ITIs. The onset of the 5-s stimulus S occurred at the end of 60-s stimulus X. The UP subjects were placed in the operant chambers and were presented with six unpaired presentations of X and of S with 5 ± 5 -min ITIs between each stimulus onset.

Phase 2: First-order conditioning: On Day 8, all rats experienced four $S \rightarrow US$ pairings in a 60-min session. These pairings were separated by 15 ± 7.5 -min ITIs. The onset of the 0.5-s footshock US occurred 4.5 s into the 5-s presentation of S and coterminated with the CS.

Reshaping and Day 11: On Days 9 and 10, in order to restabilize bar-pressing all animals experienced daily 60-min sessions which allowed uninterrupted bar-pressing. The animals that registered less than 50 responses on Day 10 were given an extra 30-min session on that day. On Day 11, subjects in the 2Test condition were tested for suppression to X in a 15-min test session. During the session, there was one presentation of X alone, 60 s in duration. The onset of the stimulus occurred 4.5 min following placement in the operant chamber. All other subjects were also placed into the chambers for a 15-min session, during which no nominal stimuli were presented. The suppression ratio was calculated as in Experiments 1 and 2.

Phase 3: Extinction: On Days 12, 13, and 14, subjects in the Ext S groups received 30 S-alone exposures in each 1-hr daily session. These exposures were separated by 2 ± 1 -min ITIs. The subjects in the No Ext groups received equal exposure to the context, but no exposure to any punctate stimuli.

Day 15: On Day 15, all subjects were tested on X. The test procedure was identical to that used on Day 11.

Results

Testing on Day 11 (the first test for subjects in the 2Test condition) indicated effective sensory preconditioning in the SP group ($M = .17$, $SE = .06$) relative to the UP control group ($M = .49$, $SE = .03$). The results of testing on Day 15 are displayed on Figure 4. For subjects that were only tested once, sensory preconditioning (denoted by stronger responding in the SP condition than in the UP condition) was apparently more robust in subjects that received no extinction of S. Furthermore, a single test of X did not appear to affect the impact of S extinction. Sensory preconditioning appeared to be equally weak in groups SP-ExtS-2Test and SP-ExtS. The following statistical analyses support these observations.

The pre-CS response rates were analysed with two 2×2 ANOVAs. The 2 (contingency: SP vs. UP) $\times$ 2 (group: NoExt vs. ExtS) and 2 (contingency: SP vs. UP) $\times$ 2 (group: ExtS vs.

ExtS–2Test) ANOVAs revealed no significant effects nor any interaction. The data from the suppression ratios were also analysed with two 2×2 ANOVAs. The first 2 (contingency: SP vs. UP) $\times$ 2 (treatment: NoExt vs. ExtS) ANOVA revealed a main effect of contingency, $F(1, 44) = 39.24$, a main effect of treatment, $F(1, 44) = 24.41$, and an interaction between the two variables, $F(1, 44) = 18.24$. Planned comparisons were conducted to determine the cause of the interaction. As expected, greater responding was observed in group SP–NoExt than in group UP–NoExt, $F(1, 44) = 55.49$. Although there was a similar trend, the difference between groups SP–ExtS and UP–ExtS was not significant, $F(1, 44) = 1.99$. Furthermore, group SP–Ext suppressed significantly less than group SP–NoExt, $F(1, 44) = 42.43$. These analyses support the initial impression that extinction of S attenuated responding to X.

Another 2 (contingency: SP vs. UP) $\times$ 2 (treatment: ExtS vs. ExtS–2Test) ANOVA revealed greater responding in the SP condition than in the UP condition, $F(1, 44) = 6.43$, but no effect of treatment, $F(1, 44) = 0.04$, and no interaction, $F(1, 44) = 0.10$. This analysis shows that there was a small, yet detectable, effect of sensory preconditioning, but no effect or interaction caused by repeated testing. A planned comparison detected no difference between groups SP–ExtS and SP–ExtS–2Test, $F(1, 44) = 0.13$. Thus, initial testing did not reduce the effectiveness of S extinction, which indicates that the X–S–US contingency still guided behaviour even after X was initially evaluated. This finding seems to refute a strong version of the interpretation suggested by Stout et al. (2005).

GENERAL DISCUSSION

The results of Experiments 1 and 2 both suggest that a test trial that encourages the expression of recently acquired learning can attenuate subsequent recency-to-primacy shifts from that recently acquired association. In Experiment 1, we observed a primacy effect in subjects that were tested only after a long retention interval, relative to a recency effect (even at the long retention interval) in subjects that were tested after both a short and a long retention interval. This replicates the findings of Stout et al. (2005), but eliminates potential accounts such as experimenter demand or linguistic encoding as a result of our using nonhuman subjects. In Experiment 2, after a change in physical context, a similar attenuation of the recency-to-primacy shift was observed when subjects were initially tested prior to the context shift. Experiment 3 indicated that a single test of the target stimulus does not alter the association that drives stimulus control; responding to the target was still dependent on the associative status of S after the target was tested. While these results are consistent with the results of Stout et al. with humans, they are not expected by many accounts of latent inhibition and extinction (e.g., Mackintosh, 1975; Miller & Matzel, 1988; Pearce & Hall, 1980).

The observed attenuation of spontaneous recovery from extinction in Experiment 1 is particularly difficult to interpret theoretically. One explanation is that the test trial resulted in stronger extinction, which reduced the recovery of responding after a long retention interval. This interpretation is certainly possible, but it seems unlikely that 13 extinction trials precluded a spontaneous recovery effect that otherwise occurred when only 12 extinction trials were administered. An alternative interpretation is that the nonreinforced test trial produced an effect that was stronger or even qualitatively different from the Phase 2 extinction trials. During the Phase 2 extinction trials, the subjects had not yet been exposed to the footshock US. Because the test trial occurred after the S–US pairings, the subjects had an opportunity to make a decision concerning responding to the X stimulus based not only on the surrogate outcome, but also on the US through its indirect association. The subjects' activation of the affective value of the CS during this test trial may have produced a robust extinction effect that was resistant to spontaneous recovery.

The present research specifically poses a problem for the theoretical accounts of the super-latent inhibition effect. We discuss two such accounts in detail here: Bouton's (1993) theory of interference and Lubow's (1989; also see Lubow, Schnur, & Rifkin, 1976) conditioned attention theory (CAT). Bouton's interference theory suggests that both super-latent inhibition and spontaneous recovery from extinction arise because retrieval of first-learned memories of a CS are less dependent upon priming by the context resulting in responding that reflects the first-learned memories. This interference theory does have the potential to explain the results of Experiment 1 with regard to the extinction groups. Because the subjects in the extinction-2Test group received an extinction trial after a short retention interval, possibly an enhanced extinction effect due to this first test trial (relative to the subjects in group extinction-1Test) prevented spontaneous recovery. However, this explanation does not account for the attenuation of super-latent inhibition observed in the PE-2Test group. The short retention interval test with the target CS in Experiment 1 was an unpaired exposure, which if anything should have reduced responding to the conditioned stimulus. Instead, subjects that received this exposure suppressed more than subjects that did not receive this exposure. Thus, Bouton's (1993) interference theory would need to be adapted to explain the present results.

Lubow's (1989) CAT encounters a similar problem. According to CAT, CS preexposure produces a conditioned attentional deficit to the CS. Because the attentional deficit is conditioned, the theory anticipates that attention directed toward a stimulus is subject to the same influences as conditioned responding to a stimulus (i.e., it may be extinguished, blocked, overshadowed, etc.). Latent inhibition is observed because CS-alone presentations produce an acquired attentional deficit that later retards acquisition of the CS-US association. During the CS-US pairings, conditioned inattention is extinguished resulting in a return of attention toward the CS. Because the attentional deficit is acquired and then extinguished, the theory suggests that conditioned inattention may be spontaneously recovered after a physical or temporal context shift through the same mechanism that produces a renewal or spontaneous recovery of conditioned responding after extinction of excitatory conditioned responding. Therefore, CAT predicts the augmentation of latent inhibition observed in Experiment 1. However, much like Bouton's interference theory, CAT cannot account for the attenuation of super-latent inhibition as a result of repeated testing. CAT suggests that a nonreinforced exposure to the CS following training would reduce attention to that CS, resulting in, if anything, stronger super-latent inhibition. In both Experiments 1 and 2, after latent inhibition treatment followed by CS-US training we observed greater suppression to a CS that had been presented after a short retention interval, but prior to a physical or temporal context shift, than to the same CS if it had been presented only after a long retention interval.

In order to account for the present data, it is necessary to consider the potential effect that a single test might have after sensory preconditioning. In the Introduction, we mentioned Stout et al.'s (2005) interpretation of their protection of recency effects. Stout et al. speculated that subjects conserve cognitive effort by recalling the last (and in their case only) response to the cue when tested after a long retention interval instead of recalling the entirety of training. The present series of experiments is similar to those of Stout et al. because the training that occurs prior to first-order conditioning in Phase 3 is passive. Subjects that are tested prior to a context shift retrieve the more recent memories of the CS (this is reflected in their responding) and generate a conditioned response based on those memories. This first generation of a conditioned response should result in a CS-response (X-R) association that may dictate subsequent stimulus control instead of the X-S association. Thus, the X-S association may have ceased to impact responding after initial testing, which would explain why responding was relatively unaffected by a physical or temporal context shift, which presumably affected the expression of the X-S association.

This account, in conjunction with Pavlovian learning mechanisms (e.g., Bouton, 1997; Lubow, 1989), could explain the results of Experiments 1 and 2.

The results of Experiment 3, however, did not support Stout et al.'s (2005) interpretation. In Experiment 3, the associative status of S still affected responding to X even after initial testing. If the first test produced an X–R association that drove subsequent stimulus control, then the associative status of S would be inconsequential when X was tested a second time. Considering the results of Experiment 3, it is reasonable to reject a strong version of Stout et al.'s interpretation. The initial test of X did attenuate recency-to-primacy shifts in Experiments 1 and 2, but it did not eliminate further processing of the X–S–US associative chain in Experiment 3.

As an alternative to Stout et al.'s (2005) interpretation, we turn to a wide body of literature in psychology that examines the effects of repeated testing on memory performance. In the field of human memory research, there is a sizeable amount of research devoted to the study of hypermnesia (for a review, see Payne, 1987). Hypermnesia is said to occur when memory performance increases across repeated test trials. Recalling a memory aids the ability to recall that memory in the future. Studies of the misinformation effect in humans have also revealed a memory-facilitating effect of repeated testing. For example, Marsh, Meade, and Roediger (2003) observed a similar effect in their examination of a retroactive misinformation effect. In their study, Marsh et al. presented participants with short stories containing misinformation that conflicted with their general knowledge. The retroactive misinformation effect faded after a retention interval, but was preserved if subjects were tested prior to the retention interval. Also, studies of infant memory have shown that the forgetting that normally occurs in developing organisms can be reduced by presenting various cues associated with the original learning including the original target stimulus (e.g., Adler, Wilk, & Rovee-Collier, 2000). Although there are a number of detailed accounts of these phenomena, all share the basic common mechanism of retrieval facilitating rehearsal, thereby enhanced memory.

Memory enhanced by retrieval could also explain the results observed in Experiments 1 and 2. As mentioned in the discussion of Experiment 2, a few brief unreinforced presentations of a CS may enhance conditioned responding instead of extinguishing conditioned responding (e.g., Dudley & Papini, 1997; Rohrbaugh, Riccio, & Arthur, 1972). In the present series we did not observe enhancement of conditioned responding per se, but instead observed preservation of recency effects. Subjects that were tested repeatedly showed stable conditioned responding across the two tests regardless of whether the conditioned responding was relatively weak (extinction groups in Experiment 1), moderate (PE groups in Experiments 1 and 2), or strong (control groups in Experiments 1 and 2). This differs from the paradoxical enhancement of conditioned responding due to CS-alone exposure, but our basic design also differs. Paradoxical enhancement of conditioned responding occurs after a CS is consistently paired with a US, presumably because the CS-alone presentation allows for rehearsal or recall of the CS–US association, thus strengthening subsequent retrieval. Here, the CS was only intermittently paired with the outcome. Therefore, it is possible that we observed an enhancement in the durability or expression of the recency effect instead of a simple enhancement of conditioned responding because the subjects rehearsed or recalled their most recent relevant experience.

One question concerning the aforementioned interpretation is why the single test of X was sufficient to reduce a recency-to-primacy shift, but the eight X–S pairings were not. A possible reason for the effectiveness of the X-alone presentation is that it occurred 3 days after training during the retention interval in Experiment 1 and immediately before subsequent testing in Experiment 2, much like a reactivation treatment (i.e., a presentation of

part of an association that reactivates the memory of the association; e.g., Misanin, Miller, & Lewis, 1968). Another possible reason for the effectiveness of the X-alone presentation is that it was the first trial in which the presentation of X could cause the retrieval and rehearsal of the full X–S–US contingency. During X–S pairings, the X–S–US contingency had not yet been established. Thus, the first test of X was the first opportunity for the X representation to indirectly retrieve the US representation. The retrieval and subsequent rehearsal of the full XS, S–US associative chain may have made the more recent memories of training more easily retrievable. In the framework of Bouton's (1993) theory, the easy retrieval of recent memories of training would have rendered the more recent memories more resistant to a recency-to-primacy effect caused by a context shift.

The mechanism underlying the attenuation of recency-to-primacy shifts observed in Experiments 1 and 2 has yet to be fully understood, but the general effect can be observed under a wide variety of conditions in the field of psychology. Although associative learning theories often assume that associative strength decreases when a CS is presented alone in a way that is directly related to the strength of the initial association (e.g., Bush & Mosteller, 1951), the results presented here and elsewhere indicate that the retrieval of an association may be enhanced by stimulus-alone presentations. Under the appropriate circumstances, a single CS-alone presentation allows for rehearsal of the most recent memory, which can enhance the retrievability of that association even after a normally deleterious physical context shift, retention interval, or developmental change. Because this effect of repeated testing is observed in a number of learning and memory paradigms, it should perhaps receive greater consideration from learning theorists.

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Figure 1.

Experiment 1: Mean suppression ratios in response to X after a long retention interval. Lower ratios indicate less bar-pressing and thus better conditioned responding to the fear-invoking stimulus. Therefore, higher scores are indicative of latent inhibition and extinction. Error brackets denote the standard error of the mean for each group. PE = preexposure. See Table 1 for procedural details.

Figure 2.

Experiment 2: Mean suppression ratios in response to a test of X or Y on Day 14 or 15 after the initial test of Y on Day 13. Lower ratios indicate lower levels of bar-pressing and thus better conditioned responding to the fear-invoking stimulus. Therefore, higher scores are indicative of latent inhibition. Error brackets denote the standard error of the mean for each group. PE = preexposure. See Table 2 for procedural details.

Figure 3.

Experiment 2: Mean suppression ratios in response to Y across two tests on Day 13 and Days 14 or 15. Lower ratios indicate less bar-pressing and thus better conditioned responding to the fear-invoking stimulus. Error brackets denote the standard error of the mean for each group. PE = preexposure. See Table 2 for procedural details.

Figure 4. Experiment 3: Mean suppression ratios in response to X on Day 15. Lower ratios indicate less bar-pressing and thus better conditioned responding to the fear-invoking stimulus. Therefore, lower scores are indicative of effective sensory preconditioning. Error brackets denote the standard error of the mean for each group. SPC = sensory preconditioning condition. UP = unpaired. See Table 3 for procedural details.

Table 1

Design summary of Experiment 1

Group	Condition	Phase 1	Phase 2	Phase 3	Interval 1	Day 13	Interval 2	Day 36
PE groups	1Test	12X	12X → S	4S → US	3 days	—	23 days	X
	2Test	12X	12X → S	4S → US	3 days	X	23 days	X
PE-control subgroups	1Test	—	12X → S	4S → US	3 days	—	23 days	X
	2Test	—	12X → S	4S → US	3 days	X	23 days	X
Extinction groups	1Test	12X → S	12X	4S → US	3 days	—	23 days	X
	2Test	12X → S	12X	4S → US	3 days	X	23 days	X
Extinction-control subgroups	1Test	12X → S	—	4S → US	3 days	—	23 days	X
	2Test	12X → S	—	4S → US	3 days	X	23 days	X

Note: PE = CS-preexposure. X = click. S = flashing light. US = unconditioned stimulus (footshock). Each test consisted of one nonreinforced presentation of the target cue (X). The PE-control and extinction-control subgroups were combined for all analyses.

Table 2

Design summary of Experiment 2

Groups	Condition	Phase 1	Phase 2	Phase 3	Day 13	Days 14&15
PE	Consistent context: AAA	[12X] _A	[12X → S] _A	[2S → US] _A	[—] _A	[X] _A
		[12Y] _B	[12Y → S] _B	[2S → US] _B	[Y] _B	[Y] _B
	Changed context: AAB	[12X] _A	[12X → S] _A	[2S → US] _A	[—] _A	[Y] _A
		[12Y] _B	[12Y → S] _B	[2S → US] _B	[Y] _B	[X] _B
Control	Consistent context: AAA	[—] _A	[12X → S] _A	[2S → US] _A	[—] _A	[X] _A
		[—] _B	[12Y → S] _B	[2S → US] _B	[Y] _B	[Y] _B
	Changed context: AAB	[—] _A	[12X → S] _A	[2S → US] _A	[—] _A	[Y] _A
		[—] _B	[12Y → S] _B	[2S → US] _B	[Y] _B	[X] _B

Note: AAA = training and testing in the same context. AAB = training and testing in different contexts. PE = CS preexposure before conditioning. X and Y = click and tone, counterbalanced. S = flashing light. [—] denotes the context in which a given session takes place. Contexts A and B = banana-scented chamber without houselight and mint-scented chamber with houselight, counterbalanced. US = unconditioned stimulus (footshock). Testing consisted of one nonreinforced presentation of X or Y. The order of testing X and Y was counterbalanced.

Table 3

Design summary of Experiment 3

Group	Phase 1	Phase 2	Day 11	Phase 3	Day 15
SP-NoExt	12 X → S	4 S → US	—	—	X
UP-NoExt	12 X / 12 S	4 S → US	—	—	X
SP-ExtS	12 X → S	4 S → US	—	90 S	X
UP-ExtS	12 X / 12 S	4 S → US	—	90 S	X
SP-ExtS-2Test	12 X → S	4 S → US	X	90 S	X
UP-ExtS-2Test	12 X / 12 S	4 S → US	X	90 S	X

Note: SP = CS sensory preconditioning. UP = Unpaired control. NoExt = no extinction of the S stimulus. ExtS = extinction of the S stimulus. ExtS-2Test = extinction of the S stimulus after X has been tested once. X = click. S = flashing light. Testing consisted of one nonreinforced presentation of X.