

Renewal of Comparator Stimuli

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ABSTRACT

Prior research has found a) recovery from overshadowing as a result of posttraining extinction of comparator stimuli (i.e., the overshadowing stimulus), and b) context modulation of conditioned responding to Pavlovian stimuli (i.e., renewal). The present research brought together these two findings by investigating whether comparator stimuli are subject to contextual control. In a Pavlovian conditioned suppression situation, rats were exposed to an overshadowing procedure (i.e., AX1) in one context and then received extinction of the overshadowing cue (i.e., A2) in the same or a different context. If AX1 training and subsequent extinction of A occurred in the same context, animals exhibited recovery of responding to the target cue (i.e., X) regardless of the test context. However, if AX1 training and extinction of A occurred in different contexts, behavior depended on the test context. If X was tested in the overshadowing context, overshadowing was observed. But if X was tested in the context where A had been extinguished or in a third (neutral) context, overshadowing was not observed. Thus, context modulates comparator effects in a manner somewhat similar to how it modulates simple Pavlovian responding. The notable exception was that robust responding to both A and X was observed in the neutral context, which is problematic for most contemporary theories of learning.

The comparator hypothesis (Miller & Schachtman, 1985; also see Miller & Matzel, 1988) is a response rule for Pavlovian responding. The hypothesis assumes that during training the unconditioned stimulus (US) becomes associated with the target conditioned stimulus (CS) *and* with other cues (hereafter referred to as comparator stimuli) present during training of the target CS. More precisely, comparator cues are defined as any cues that were present in close temporal (and spatial) proximity to the target CS during training (i.e., background cues and simultaneously presented, punctate CSs). Moreover, an association between the CS and its comparator stimulus is formed during training. At the time of testing, the CS is presumed to activate one representation of the US, which we call the 'direct' representation, as a result of the CS-US association, and a second representation of the US, which we call the 'indirect' representation, as a conjoint result of the CS-comparator stimulus and comparator stimulus-US associations. According to the comparator hypothesis, excitatory conditioned responding to the target CS is a direct function of the activation of the direct US representation and an inverse function of the activation of the indirect US representation.

Thus, in the framework of the comparator hypothesis, behavior at test is expected to reflect the strength of the direct CS-US association *relative* to the strength of the CS-comparator association(s) and the comparator stimuli-US association(s). As a result, any treatment conducted after training that will serve to weaken either the CS-comparator association or the comparator stimuli-US association should strengthen responding to the target CS at test. Consistent with this expectation, posttraining extinction of a CS's comparator stimulus has been found to strengthen excitatory responding and weaken inhibitory responding. For example, Kaufman and Bolles (1981) and Matzel, Schachtman, and Miller (1985) performed an overshadowing experiment in which the overshadowing stimulus (A) was extinguished following overshadowing treatment (AX+, with X representing the overshadowed stimulus and + representing the US). Those animals displayed robust responding to X (i.e., recovery from overshadowing). Thus, the overshadowing effect was attenuated without further CS-US training.

Recovery from overshadowing without further X+ training is problematic for most theories which posit that overshadowing is due to a failure to *acquire* an association between X and the US (e.g., Kamin, 1969; Rescorla & Wagner, 1972; but see Van Hamme & Wasserman, 1994). Rather, it suggests, as does the comparator hypothesis, that animals associated X with the US during training, but failed to *express* this association at test. In the framework of the comparator hypothesis, A served as the primary comparator stimulus for X. Posttraining exposure to the comparator stimulus alone resulted in extinction of the comparator stimulus-US association (and perhaps the CS-comparator association) in the Kaufman and Bolles (1981) and Matzel et al. (1985) studies, thereby facilitating expression of the X-US association. Other researchers have also reported data that, although not easily integratable into the framework of the comparator hypothesis, are consistent with its expression-failure view of overshadowing. For instance, Kasprow, Cacheiro, Balaz, and Miller (1982) demonstrated recovery from overshadowing as a result of exposing subjects to a "reminder" treatment (e.g., a few presentations of the overshadowed CS outside of the original training context).

Additionally, Kraemer, Lariviere, and Spear (1988) found spontaneous recovery from overshadowing when a long retention interval was imposed between training and testing.

We were interested in looking for analogies between the factors that control responding to conditioned stimuli and those that govern the comparator role of a stimulus. Finding or failing to find analogies between the response eliciting and comparator roles of a stimulus might better inform us about the nature of the comparator process. For example, consider the phenomenon of “renewal.” Bouton and King (1983) demonstrated the importance of the context in modulating Pavlovian responding. They found that excitatory responding was restored (or “renewal”) following excitatory conditioning of a CS in Context 1 and subsequent extinction of that CS in Context 2, if the subject was returned to Context 1 for testing. Fiori, Barnet, and Miller (1994) found a similar result with Pavlovian conditioned inhibition. Specifically, animals were given Pavlovian conditioned inhibition training (i.e., A1/AX2) in Context 1 followed by counterconditioning with the inhibitor (i.e., X1, the analogue of extinction with respect to conditioned inhibition) in Context 1 or Context 2. If the inhibitor was counterconditioned in the inhibition training context (i.e., Context 1), inhibitory control was not witnessed when the inhibitor was later assessed in a summation test in either that context or in a neutral alternate context. However, if the inhibitor was counterconditioned in Context 2, conditioned inhibition was observed on a summation test if testing occurred in Context 1, whereas conditioned excitation was observed if testing occurred in Context 2. Thus, contextual control over behavior (renewal) appears to have an important impact on both Pavlovian excitation and inhibition.

Whereas Bouton and his colleagues have shown that responding to a conditioned stimulus can be modulated by the context, we wanted to determine if this would likewise be the case for the comparator role of a stimulus. Thus, the present research investigated whether the comparator value of a CS's comparator stimulus would differ as a function of the context in which the CS is tested if the target CS and the comparator stimulus for that CS are trained in one context and then the comparator stimulus is extinguished in a second context. In the framework of the comparator hypothesis, a reciprocal relationship in conditioned responding to an overshadowed CS and its comparator stimulus (the overshadowing CS) ought obtain in each test context.

EXPERIMENT 1

Prior research (Kaufman & Bolles, 1981; Matzel *et al.*, 1985) using an overshadowing paradigm had found that posttraining extinction of the overshadowing stimulus administered in the original training context produces a recovery of responding to the overshadowed stimulus when testing occurs in either the training context or a neutral context. Extrapolating from the renewal literature, we reasoned that if posttraining extinction of the overshadowing stimulus were conducted outside of the training context, such a recovery effect would not be seen if testing were conducted in the original

overshadowing training context. But recovery would be observed if CS testing occurred in the context in which the comparator stimulus had been extinguished. Such a pattern of results would suggest that the modulatory (comparator) role of the comparator stimulus had been “renewed” for those subjects that received posttraining extinction of the overshadowing stimulus in the alternate context and were then tested in the original training context.

TABLE 1
Experiment 1 Design Summary

Group	Conditioning	Extinction	Test
ACQ	(A-/X+) _M	() _M & () _N	(X?) _M or (X?) _N
O	(AX+) _M	() _M & () _N	(X?) _M or (X?) _N
O-S	(AX+) _M	(A-) _M & () _N	(X?) _M or (X?) _N
O-D	(AX+) _M	() _M & (A-) _N	(X?) _M or (X?) _N

Note. A represents the overshadowing CS (i.e., comparator stimulus for X); X represents the overshadowed CS (i.e., target CS); + represents the footshock US; - represents nonreinforcement. Subscripts M and N denote the context used for that phase of treatment. See text for details.

Thus, Experiment 1 was conducted in order to determine whether the comparator role of a stimulus (i.e., an overshadowing stimulus) is subject to contextual modulation (i.e., renewal) in a manner analogous to Pavlovian responding. Table 1 depicts the experimental design. Subjects in Groups O (Overshadowing), O-S (Overshadowing-Same), and O-D (Overshadowing-Different) received overshadowing conditioning (i.e., AX1) in Context M, while Group ACQ (Acquisition) received elemental conditioning of X and nonreinforced exposure to A (i.e., A2/X1) in Context M. Group O-S then received extinction of the overshadowing stimulus (i.e., A2) in the *same* context in which overshadowing conditioning had occurred (M), while Group O-D received extinction of the overshadowing stimulus in a *different* context (N). All subjects received equivalent exposure to both contexts during the extinction phase of the experiment. Animals were then tested on the target stimulus (i.e., X) in either of the two contexts (M or N).

Method

Subjects

The subjects were 72 experimentally naive, adult male and female rats of Sprague-Dawley descent. The animals were bred in our colony from Holtzman stock (Madison, WI). Weight ranges were 245–350 g for males and 170–225 g for females. Each animal was randomly assigned to 1 of 4 groups counterbalanced for sex (Group ACQ, n = 12; O, n = 12; O-S, n = 24; O-D, n = 24). All animals were individually housed in stainless-steel wiremesh cages in a vivarium that was maintained on a 16-hr light/8-hr dark cycle. Experimental manipulations occurred within four hours of the midpoint

of the light portion of the cycle. Purina Laboratory Chow was freely available in the home cages. One week prior to the start of the study, all subjects were progressively deprived of water. By Day 1 of the experiment, access to water in the home cage was limited to 10 min/day, occurring 18–22 hrs prior to any treatment scheduled for the following day. All subjects had been handled three times per week for 30 s, from the time of weaning until the initiation of the study.

Apparatus

Twenty-four experimental chambers were used. Each chamber measured 30.5 cm x 27.5 cm x 27.3 cm (l x w x h). The chambers had clear Plexiglas side walls and ceilings, and metal front and back walls. The floor consisted of stainless steel rods. Chamber floors were 4-mm grids spaced 1.7 cm apart (center-to-center), connected through NE-2 neons, which allowed constant current foot shock to be delivered by means of a high voltage AC circuit in series with a 1.0-MW resistor. The chambers could be dimly illuminated by a #1820 light bulb. The house light bulb was mounted on an inside wall approximately 14 cm from the center of the animal chamber. Background noise, mostly from a ventilation fan, was 74 dB(C) re.SPL. Each chamber was enclosed in a separate light- and sound-attenuating environmental isolation chest.

Every chamber could be equipped with a water-filled lick tube that protruded 1.5 cm into a cylindrical drinking recess at the bottom of one wall (axis perpendicular to the wall). Each recess was 5.5 cm in depth, 3.5 cm in diameter, and was set into a corner of its chamber, with its axis 6.5 cm above the chamber floor. An infrared photobeam was projected across the recess approximately 0.5 cm in front of the tip of the lick tube. In order to drink from the lick tube, subjects had to insert their heads into the recess, thereby breaking the photobeam. Time during which subjects accessed the lick tube could be recorded. Two 45-W speakers, mounted on interior walls of the environmental chest, could deliver a white noise stimulus of 6 dB (C) above background or a six per second train of clicks 10 dB (C) above background. These stimuli served as X and A, respectively. All CS presentations were 10 s in duration. The US was a 1-s, 0.7-mA footshock which was initiated at the termination of the CS.

Treatment and testing occurred in one of two contexts which were designated as Context M and Context N. For each subject, Contexts M and N were different examples of the 24 chambers. Furthermore, Contexts M and N differed with respect to illumination of the chamber (houselight on or off) and the presence or absence of an odor cue. The odor cue consisted of applying one drop of 100% methyl salicylate to a small, rectangular block of wood in each isolation chest. Contexts M and N were counterbalanced such that for half the subjects in each treatment condition, Context M consisted of houselight on and odor cue absent and Context N consisted of houselight off and odor cue present; while for the remaining subjects, this was reversed.

Procedure

Acclimation. Context acclimation was conducted on Days 1 and 2 without any CSs or USs programmed to occur. During each 60-min session, waterfilled lick tubes were available to all subjects. On Day 1, all subjects were acclimated to Context M, and on Day 2, all subjects were acclimated to Context N.

Overshadowing training. Prior to training, all lick tubes were removed from the chambers. On Days 3 and 4, subjects from Groups O, O-S, and O-D received 4 compound stimulus presentations of AX immediately followed by the US, per day. Group ACQ received 4 nonreinforced presentations of A intermingled with 4 reinforced presentations of X per day (i.e., A2/X1). These conditioning sessions were conducted in Context M for all subjects and were 60 min in duration.

Extinction. Prior to this phase, lick tubes were reinserted into each chamber. On Days 5, 7, 9, and 11, subjects from Group O-S received extinction of the overshadowing cue (i.e., A) in Context M (the overshadowing training context), while subjects from Groups ACQ, O, and O-D received exposure to Context M with no programmed stimulus presentations. On Days 6, 8, 10, and 12, subjects from Group O-D received extinction of the overshadowing cue in Context N, while subjects from Groups ACQ, O, and O-S received exposure to Context N with no programmed stimulus presentations. During each extinction session, animals were exposed to 54 A- trials. All sessions were 135 min in duration.

Testing. On Day 13, all subjects were tested on X in either Context M or N, thereby forming eight Training Group x Test Context conditions (i.e., ACQ.M, ACQ.N, O.M, O.N, O-S.M, O-S.N, O-D.M, and O-D.N). The test CS was presented after each subject had been placed in its test chamber and had completed 5 cumulative seconds of drinking (which for all subjects took less than 60 s). Thus, all subjects were drinking at the time of CS onset. Time to complete an additional 5 cumulative seconds of licking in the presence of the test CS were recorded with an imposed limit of 10 min. The data from one subject in Condition O.M was deleted from all analyses due to an equipment failure while this subject was being tested. Suppression times ordinarily yield distributions with a strong positive skew. In order to better approximate a normal distribution and thereby justify the use of parametric statistics, a log (base 10) transformation was performed on each suppression score. An alpha level of .05 was adopted for all tests of statistical significance.

Results and Discussion

Conditioned responding to X was observed to be greater in Group ACQ than Group O, indicating the basic overshadowing effect. Additionally, greater conditioned responding to X in Group O-S than Group O indicated that posttraining extinction of A in the overshadowing training context produced a recovery from the overshadowing response deficit. More importantly,

a renewal effect for the comparator role of A was observed in Group O-D. Specifically, subjects in Group O-D exhibited behavior indicative of overshadowing when tested on X in the overshadowing training context, whereas they did not exhibit behavior indicative of overshadowing when tested on X in the context in which A (the overshadowing stimulus) had been extinguished, a result indicative of context specific control of the overshadowing response deficit. The following analyses support these findings.

Times to complete an initial 5 cumulative seconds of drinking prior to CS onset on Day 13 were analyzed first. A 4 (Group: ACQ, O, O-S, or O-D) x 2 (Test Context: Context M or Context N) ANOVA failed to reveal main effects or interactions in the propensity to lick prior to the onset of the target CS, $F_s < 1$. This analysis indicates that the groups did not differ appreciably with respect to fear of the test context.

A 4 (Group: ACQ, O, O-S, or O-D) x 2 (Test Context: Context M or Context N) ANOVA was conducted. Group means are illustrated in Figure 1. A main effect of Group, $F(3, 63) = 16.20$, $p < .01$, and a Group X Test Context interaction, $F(3, 63) = 5.46$, $p < .01$, was observed. Planned comparisons were then conducted across test conditions within groups. These revealed no difference in responding to X between Test Conditions ACQ.M and ACQ.N, $F(1, 63) < 1$, O.M and O.N, $F(1, 63) = 1.49$, and O-S.M and O-S.N, $F(1, 63) < 1$, all $p_s > .10$. But a difference was detected between Test Conditions O-D.M and O-D.N, $F(1, 63) = 20.58$. Specifically, greater responding to X by Group O-D was seen in Context N (where A had been extinguished) than in M (where overshadowing had occurred). Thus, these analyses found that for Groups ACQ, O, and O-S responding to X was not dependent on the context in which testing took place. However, for Group O-D responding to X was greater in Context N than in Context M, indicating that one or both of the test contexts had a modulatory effect on the behavior of this group.

Due to the absence of significant differences between the pairs of test conditions corresponding to Groups ACQ, O, and O-S, data for these subjects was pooled across test contexts, that is, Test Conditions ACQ.M and ACQ.N were pooled to form Group ACQ, Test Conditions O.M and O.N were pooled to form Group O, and Test Conditions O-S.M and O-S.N were pooled to form Group O-S. Additional planned comparisons were conducted on these pooled means to assess the basic overshadowing deficit and recovery from this deficit. Evidence for overshadowing was supported by the greater responding in Group ACQ than in Group O, $F(1, 63) = 30.89$, $p < .01$. Recovery of responding to X as a result of posttraining extinction of A (without a context shift between training and extinction phases) was evidenced by greater responding in Group O-S than in Group O, $F(1, 63) = 11.81$, $p < .01$. Notably, only a few animals (3 out of 71) suppressed drinking for the maximum of 10 min. Consequently, our conclusions were not likely influenced by ceiling effects masking real differences in associative status.

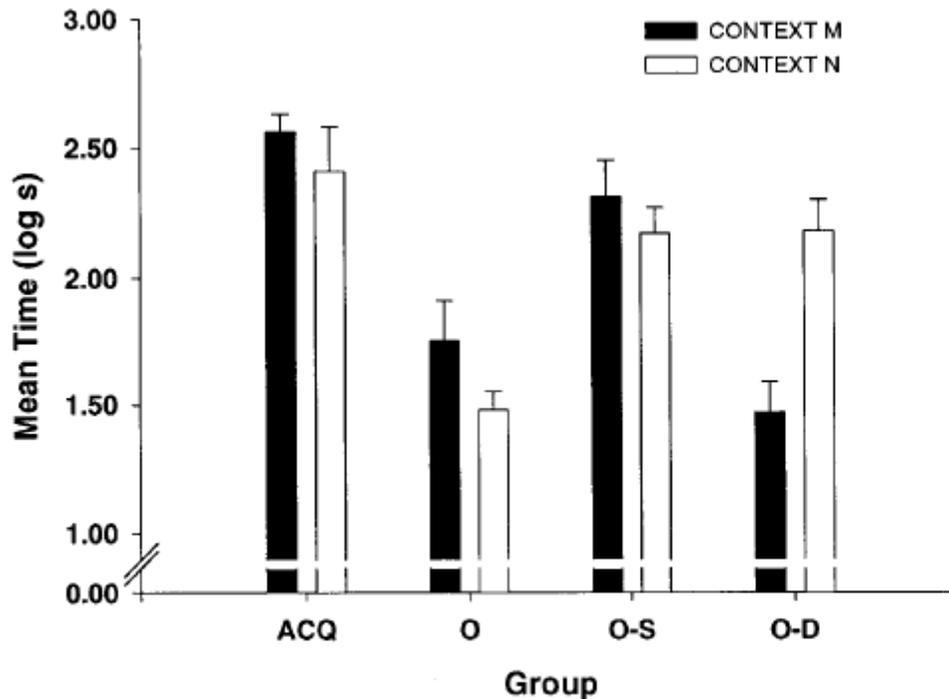


FIG. 1. Experiment 1: mean time to complete 5 cumulative seconds of licking in the presence of the target CS (i.e., X) tested either in the training context (M) or in an alternate context (N). Error bars denote standard errors of means.

To further illuminate the performance of Group O-D, a 2 (Group: O-S or O-D) x 2 (Test Context: Context M or Context N) ANOVA was conducted. This revealed a main effect of Test Context, $F(1, 43) = 5.62, p < .05$, a main effect of Group, $F(1, 43) = 12.03, p < .01$, and a Test Context x Group interaction, $F(1, 43) = 12.16, p < .01$. The results of this analysis indicate that the difference between Conditions O-D.N and O-D.M was greater than that between Conditions O-S.N and O-S.M. Thus, analogous with Pavlovian responding, renewal of the comparator role of A in attenuating responding to X was evidenced in Group O-D (i.e., subjects that received training of AX1 and extinction of A in different contexts). Subjects tested in Group O-D on X in the overshadowing training context (M) suppressed less than those tested on X in the extinction context (N) despite having received extinction of the comparator stimulus (i.e., the overshadowing stimulus) in an alternate context (N), $F(1, 43) = 20.58, p < .01$. This pattern of results was not observed in Group O-S (i.e., subjects that received training and extinction in the same context), in which responding to X was high regardless of the test location. The observed behavior of Group O-S is consistent with prior studies of target CS training and extinction of comparator stimuli in one context being followed by testing in a different context (e.g., Kaspro, Schachtman, & Miller, 1987). These studies found that testing in a neutral context does not affect this comparison.

It is worth mentioning that this experiment does not address the issue of stimulus specificity. Based on the present data, it is possible that extinction

of any excitatory stimulus (i.e., a stimulus other than A) could produce the same pattern of results witnessed in Experiment 1. However, in light of past research that concerned itself with the specificity of comparator effects, this is unlikely. Miller, Barnet, and Grahame (1992) found that in order to obtain recovery of responding to the overshadowed cue, posttraining extinction must be done with the same overshadowing cue as was used in training. In their study, overshadowing subjects received AX+ and BY+ with either subsequent extinction of both A and the training context, the training context alone, or no treatment. Results indicated that posttraining extinction of A resulted in recovery of responding to X but not to Y. These data demonstrate that the result of posttraining extinction of the A-US association was stimulus specific. Specificity of comparator cues has been found in a number of other conditioning preparations, including negative-contingency conditioned inhibition training, local context modulatory effects on excitatory conditioning (Miller *et al.*, 1992), latent inhibition (Grahame, Barnet, Gunther, & Miller, 1994), and the relative validity effect (Cole, Barnet, & Miller, 1995). In each case, the posttraining extinction manipulation that resulted in the greatest recovery of responding was extinction of the specific comparator stimulus that was present during training of the target CS.

EXPERIMENT 2

Experiment 1 demonstrated that the comparator role of an ambiguous stimulus is modulated by the contexts in which it was trained and extinguished. Dependent upon the location of testing, the comparator stimulus was either of high effective associative value (in the context in which overshadowing training had occurred) or of low effective associative value (in the context in which the comparator stimulus had been extinguished). Whether the comparator stimulus was of high or low effective value consequently determined responding to the target stimulus (X).

Bouton and his colleagues (e.g., Bouton & Bolles, 1979; Bouton & Brooks, 1993; Swartzentruber & Bouton, 1992) have investigated a CS's response eliciting potential in an associatively neutral context (Context 3) following simple Pavlovian training in Context 1 and extinction in Context 2. Of critical interest in the present experiment is a CS's modulatory (i.e., comparator) potential in an associatively neutral context (Context 3) following Pavlovian training in Context 1 and extinction in Context 2. There are at least four possibilities worthy of consideration: 1) The site in which ambiguity about a CS is established (i.e., the extinction context because during extinction the CS is for the first time paired with a second outcome, reinforcement having been the first outcome) may modulate behavior exclusively in that context, with all other contexts supporting the knowledge state existing prior to the establishment of ambiguity. In the case of renewal of excitation (i.e., excitation training with a CS in one context followed by extinction training with that CS in another context), this view would predict that behavior in the neutral context would resemble that seen in the first (training) context (i.e., vigorous conditioned responding). 2) The context where the US is presented may determine conditioned responding in a neutral context.

That is, responding to the CS in the training context might generalize to all neutral contexts. In this case, the same prediction as above would prevail. One would expect to see responding similar to that seen in the first (training) context. 3) The behavior seen in a third, neutral context may represent an averaging of the two different values of X in the two treatment contexts. This alternative would predict conditioned responding somewhere between that seen in the first (training) and second (extinction) contexts. 4) The consequences of extinction might generalize to the neutral context by virtue of recency, which is equivalent to generalization (rather than context specificity) of what is learned in the context in which ambiguity arises (ambiguity is created not during initial conditioning, but during extinction). This leads to a prediction of little responding in the neutral context.

Bouton and Bolles (1979) conducted a conditioned suppression experiment with rats in which subjects received excitation training with a CS in Context 1 and extinction training with that CS in Context 2. Interestingly, they found renewed excitation in an associatively neutral, third context, and interpreted this result to support the view that extinction is specific to the context in which it occurred, whereas conditioned excitation will readily generalize to a neutral context. This corresponds to the second mechanism described above (generalization from the training context to a neutral context), but their data are equally compatible with the view that ambiguity is limited to the context in which the ambiguity was created. Furthermore, in a recent study conducted by Gunther, Denniston, and Miller (in press), subjects showed generalized excitatory behavior when tested in a neutral context following conditioning and extinction conducted in separate contexts. The main goal of their study involved other issues and the aforementioned subjects represented a control condition used in that experiment. However, the results provide us with further support of Bouton and Bolles' results.

Subsequent data from Bouton's laboratory favors the view that ambiguity is limited to the context in which the ambiguity was created. For example, Bouton and Brooks (1993) conducted discrimination training (i.e., T+ and L-) in one context (A) followed by reversal training (i.e., T- and L+) in another context (B). In other words, subjects received excitation training followed by extinction (with a context switch between phases) for one CS (i.e., T) and CS-preexposure followed by excitation training (with a context switch between phases) for another CS (i.e., L). Results showed that testing in Context A revealed robust conditioned suppression to T but not to L, and that testing in Context B revealed robust conditioned suppression to L but not to T, thereby suggesting that both contexts came to acquire the ability to modulate responding to the CSs. Behavior observed in a third, neutral context was more perplexing. Subjects exhibited weak conditioned responding to T and a modest level of responding to L; thus, it was the second (and most recent) context experienced that seemed to control responding to both T and L in the neutral context (i.e., possibility #4 from the preceding list). These data challenge the view that conditioned responding in a neutral context is determined by the context in which the CS was paired with the US.

The present study sought to examine the effects of testing both X (the overshadowed stimulus, or target cue) and A (the overshadowing stimulus, or comparator cue) in a third, neutral context (P) after presenting subjects with overshadowing training in Context M and extinction of the overshadowing cue in Context N. Let us consider what each of the four aforementioned views would predict with respect to responding to the overshadowed (X) and overshadowing (A) cues in this neutral context. First, the view stating behavior acquired in the context in which ambiguity arises will be specific to that context would predict that in the neutral context responding to both stimuli will be determined by the effective associative value of each stimulus in the first (unambiguous) context (M). Specifically, X should support little conditioned responding and A should support strong conditioned responding since, following overshadowing training, responding to the overshadowed stimulus is typically weak and responding to the overshadowing stimulus is strong. This prediction assumes that A is far more salient than X, thereby minimizing reciprocal overshadowing. Due to A being of high saliency and X being of low saliency, A presumably served as the comparator stimulus for X, whereas the context rather than X served as the comparator stimulus for A. Second, if training in the context in which the US was presented determines behavior in a neutral context, responding to the stimuli should be determined by the value of the stimuli in Context M, where training occurred. As in the preceding view, X should support little conditioned responding in Context P because it was overshadowed in the training context (M), while A should support vigorous conditioned responding in Context P concordant with that which it supports in Context M. Again, this assumes that reciprocal overshadowing is minimized by the use of an A stimulus that is much more salient than the X stimulus. Third, if behavior in a neutral context (P) is an average of the CS's response eliciting potential in the two treatment contexts, we would expect moderate conditioned responding to X because X's effective associative value is low in the training context (M) and high in the context in which A was extinguished (N), and modest responding to A because A's effective associative value is high in the training context and low in the extinction context. Fourth, if there is a recency effect, strong responding to X and weak responding to A would be expected in Context P because that is what was observed in the extinction context (N) following extinction of A in Experiment 1.

Method

Subjects

The subjects were 48 experimentally naive, adult male and female rats of Sprague-Dawley descent. The animals were bred in our colony from Holtzman stock (Madison, WI). Weight ranges were 240–325 g for males and 180–275 g for females. Each animal was assigned to 1 of 3 test conditions ($n_s = 16$), counterbalanced for sex. Subjects were housed and maintained as described in Experiment 1.

Apparatus

The apparatus was the same as for Experiment 1, except for the addition of a third context (i.e., Context P). Context P was substantially different from Contexts M and N in that (a) subjects were placed into a different example of the experimental chamber, (b) a 15-W bulb (nominal at 120 VAC but powered at 50 VAC), flashed at a rate of .2 s on/.2 s off, and (c) each chamber was equipped with a Plexiglas floorplate over the grid floor.

Procedure

Details and parameters for Experiment 2 were identical to those in Experiment 1 except where otherwise stated. Because overshadowing was clearly demonstrated in Experiment 1 and identical parameters were used, that group was not included in the present study. Contexts M and N were fully counterbalanced within groups.

Acclimation. On Days 1–3, all animals were acclimated to Contexts M, N, and P, respectively. Context acclimation was conducted as in Experiment 1.

Overshadowing training. Prior to training, all lick tubes were removed from the chambers. Subjects were randomly assigned to one of three test conditions ($n_s = 16$): M, N, or P, identified by where testing with X would subsequently occur. All subjects received 4 daily AX1 compound trials in Context M on Days 4 and 7. On Days 5 and 8, all subjects received comparable exposure to Context N, and on Days 6 and 9, all subjects received comparable exposure to Context P. On Days 5, 6, 8, and 9, no CSs or USs were programmed to occur.

Extinction. Prior to this phase, lick tubes were reinserted into each chamber. On Days 10, 13, 16, and 19, all subjects received extinction of the overshadowing cue (i.e., 54 A2 trials per day) in Context N. On Days 11, 14, 17, and 20, all subjects received comparable exposure to Context M. Finally, on Days 12, 15, 18, and 21, all subjects received comparable exposure to Context P.

Testing. The procedure used for testing was the same as was used in Experiment 1. On Day 22, all subjects, which until this time had been treated identically, were tested on X in either Context M, N, or P. On Day 23, all subjects were tested on A in one of the two contexts (counterbalanced) other than that in which they were tested on Day 22. This was done to minimize the influence on Day 23 behavior of any learning that might have occurred during testing on Day 22. We consistently tested on X before A because responding to X was of greatest interest. Because A was presumably the comparator stimulus for X, the extinction of A that would have occurred during testing of A might have influenced responding to X had we tested on A first. Due to X being of lower salience than A, X was likely a less significant comparator stimulus for A than A was for X. Hence, extinction of X during testing of X was less apt to influence responding to A. More

important, by testing all subjects on X first, any resultant change in responding to A would have occurred in all three groups because the three groups were treated identically until the test trials.

The data from one subject tested on X in Context M was eliminated from all analyses due to an error made during testing, and the data from two subjects tested on X in Context P were eliminated due to illness prior to testing.

Results and Discussion

When testing was conducted in the overshadowing context (i.e., Context M), responding to X was weak (indicative of overshadowing), despite X's comparator stimulus (A) having been extinguished (albeit in a different context). However, responding to X was robust in Context N, where A had been extinguished. Responding to A was also modulated by the context in which testing occurred. Strong conditioned responding was seen to A in Context M (where it had overshadowed X) and weak conditioned responding was seen to A in Context N (where it had been extinguished). Most interesting was responding in Context P (the neutral context). We observed robust conditioned responding to *both* X and A in Context P, a result not predicted by any of the alternative views described earlier. The following analyses confirm these conclusions.

One-way ANOVAs (Test Context: M, N, or P) were initially conducted on the pre-CS times from each of Days 22 and 23. These analyses failed to reveal any group differences in baseline responding, $F_s < 1$. Therefore, we can conclude that there were no appreciable differences in fear to the contexts across groups.

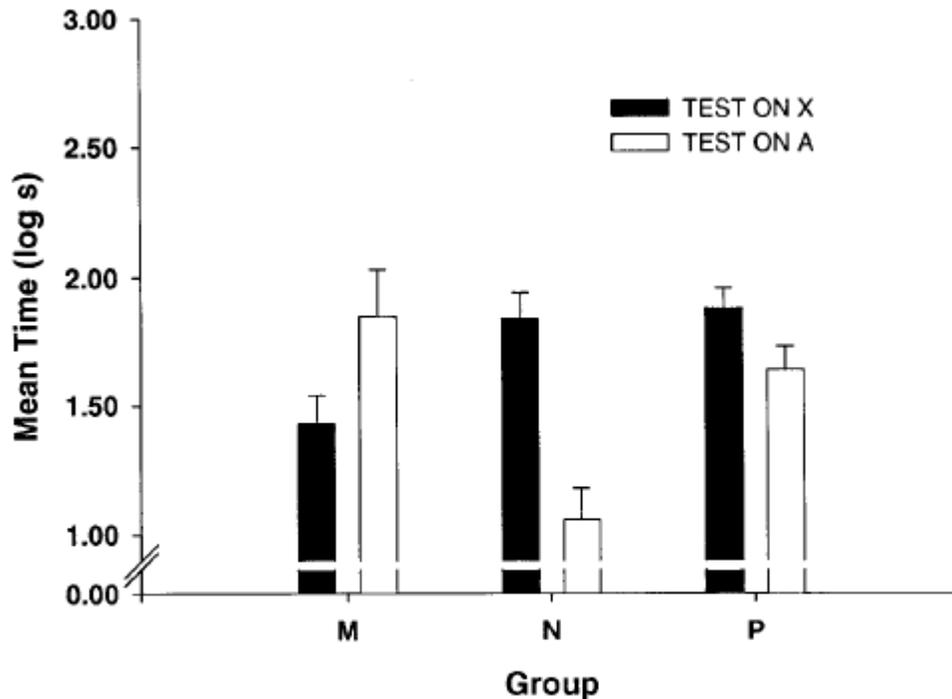


FIG. 2. Experiment 2: mean time to complete 5 cumulative seconds of licking in the presence of the target CS (i.e., X) and the overshadowing stimulus (i.e., A) tested in either the training context (M), the context in which A was extinguished (N), or a neutral context (P). Error bars denote standard errors of means.

A one-way ANOVA (Test Context: M, N, or P) was conducted on the X data and revealed a main effect of Test Context, $F(2, 42) = 5.93, p < .01$. Group means are illustrated in Figure 2. Two planned comparisons were conducted. First, greater conditioned suppression to X was observed in Condition N than in Condition M, $F(1, 42) = 8.35, p < .01$, demonstrating contextual control of A's role as a comparator stimulus (i.e., overshadowing) by the two contexts. Thus, a renewal effect for the comparator role of A was observed in Experiment 2, as it had been in Experiment 1. Second, greater suppression to X was detected in Condition P than in Condition M, $F(1, 42) = 9.41, p < .01$, indicating decreased overshadowing in the neutral test context relative to the training context. Inspection of Figure 2 indicates that responding to X in Context P was at least as robust as that seen in Context N.

In none of the three contexts was responding to A found to differ as a function of which context the prior test on X had occurred, $ps > .10$. Therefore, we pooled data across this variable. A one-way ANOVA (Test Context: M, N, or P) was then conducted on the A data, which revealed a main effect of Test Context, $F(2, 42) = 9.76, p < .01$ (see Figure 2). Two planned comparisons were then conducted. First, subjects in Condition M were found to exhibit more conditioned suppression than subjects in Condition N, $F(1, 42) = 17.67, p < .01$. This shows that context modulated responding to A. Second and most interesting was that subjects in Condition P exhibited more

conditioned responding than subjects in Condition N, $F(1, 42) = 9.86, p < .01$ indicating generalization of renewal of the associative status of A to a neutral context. Since the physical contexts serving as Contexts M and N were counterbalanced within groups, differences in responding to X or A could not be attributed to differences in stimulus generalization decrement going from Contexts M and N to Context P. In addition, one might suspect that prior testing with X decreased subsequent responding to A if extinction of X (during testing of X) generalized to A. However, this expectation was not supported in that responding to both X and A was vigorous in Context P.

Although Contexts M and N were counterbalanced within groups, Context P was not for practical reasons. In principle, this might have influenced the present results. However, baseline licking on the test days was highly similar in all three contexts, suggesting no special fear of Context P that might have yielded strong suppression to X and A. Moreover, Context P was on average within groups equally similar to Contexts M and N because Contexts M and N were counterbalanced. Thus, it is unlikely that the lack of counterbalancing of Context P could explain the present data.

Recall from the previous discussion that in three of the four alternative views concerning factors determining conditioned responding in a neutral context, responding to X and A was expected to reflect the reciprocal inequalities seen in either Context M or Context N, and in the fourth view (averaging), responding to X and A midway between that seen in Contexts M and N was expected. What was actually observed in Context P was very robust responding to both X and A. Therefore, the present results support none of the alternatives mentioned. Again, as in Experiment 1, very few subjects suppressed for the full 10 min allowed. Thus, ceiling effects could not have masked real differences in associative status.

Given the failure of each of the four previously described predictions of what might occur during testing in a neutral context, one might ponder the strategy the animals employed in this task. In Context P, both X and A are ambiguous in the sense that they are known to yield different behaviors in the training context (M) than in the extinction context (N). In other words, the animal can disambiguate the two different values of X and A by using the training or extinction context as a discriminative stimulus. However, presenting the animal with either X or A in the neutral context (P) now creates a new level of ambiguity, one that cannot be disambiguated by the use of contextual cues. Here, it may be (evolutionarily) advantageous for the subject to adopt the strategy that involves the least risk; that is, the subject uses a “default strategy” for responding in which it responds in an excitatory manner to all stimuli in potentially threatening situations that can’t be disambiguated.

GENERAL DISCUSSION

The comparator hypothesis (Miller & Matzel, 1988; Miller & Schachtman, 1985) predicts that behavior seen at test is determined by the US representation

directly activated by the CS relative to the US representation indirectly activated by associations between the CS and its comparator stimuli, and between the comparator stimuli and the US. In Experiment 1, the comparator hypothesis would suggest that A was X's primary comparator stimulus because it was consistently present during training of X and it had high predictive value with respect to the US (except for Group ACQ). While the context was also present during subjects' experience with X, the comparator hypothesis maintains that A (and not the context) was the primary comparator stimulus for X due to A's greater salience and superior contiguity with respect to the US). If the context were the primary comparator stimulus for X, then our deflation manipulation should not have revealed differences across groups in responding to X. Additionally, if the context was the primary comparator stimulus for X, Groups O-S, O-D, and O should each have exhibited high (and equivalent) responding to X in Context M as a result of each group having received posttraining deflation of Context M. Subjects in Group O-S received extinction of the comparator stimulus in the same context in which overshadowing training had previously occurred. These subjects showed recovery from overshadowing as a result of this posttraining manipulation (a replication of the findings of Kaufman & Bolles, 1981; Matzel *et al.*, 1985). It is important to note that this recovery effect was maintained even when testing was conducted in an associatively neutral context (i.e., no CSs or USs had been presented to Group O-S in Context N prior to testing in that location). This is consistent with a tenant of the comparator hypothesis (see Kasrow *et al.*, 1987; Miller & Matzel, 1988) that the critical comparison between the target CS-US association and the comparator stimulus-US association is made at the time of testing, but that the comparator stimuli are the salient cues that were present during training (not testing). Clearly, posttraining extinction of the comparator stimulus in Group O-S served to weaken the comparator stimulus-US association (and perhaps the target CS comparator stimulus association), thereby enhancing *expression* of the target CS-US association at test regardless of where testing occurred.

However, in Experiment 1, when training and subsequent extinction of the overshadowing stimulus occurred in different contexts, as was the case for Group O-D, responding to X was strongly influenced by the test location. In Group O-D, subjects received overshadowing training in Context M and extinction of the comparator stimulus (A) in Context N. When Group O-D subjects from Experiment 1 and Condition M subjects from Experiment 2 were tested for suppression to X in the overshadowing training context (M), weak responding (i.e., overshadowing) was observed, despite the fact that these subjects had received extinction of A. Apparently, a return to the original overshadowing training context "renewed" the comparator stimulus (A)-US association, thereby allowing it to attenuate the expression of the target CS (X)-US association at test in Context M such that an overshadowing effect was observed. However, when testing was conducted in the context in which extinction of the comparator stimulus had occurred (N), X elicited strong responding. This observation indicates that, in the context in which the comparator stimulus was extinguished, the effective comparator stimulus (A)-US association had been successfully weakened, thereby permitting expression of the target CS-US association at test in that context.

Van Hamme and Wasserman's (1994) model views overshadowing as an acquisition failure and can also account for the attenuation of the overshadowing deficit as a result of posttraining extinction of the overshadowing cue. According to their model, additional acquisition of excitatory value with respect to X accrues during the A2 trials. Although this explanation is able to account for the basic recovery effect in a more mechanistic manner than does the comparator hypothesis, it does not anticipate any effect of shifting contexts between training and the extinction of the overshadowing stimulus. In contrast, the comparator hypothesis anticipates that responding to a target CS ought to be modulated by the local associative value of its comparator stimulus. Thus, the present data based on testing in Contexts M and N appear more consistent with the comparator hypothesis, with its emphasis on the failure to express associations that were acquired, than with the Van Hamme and Wasserman model, with its emphasis on the failure to acquire associations.

Bouton and Swartzentruber (1986) suggested that when a CS is reinforced in one context and subsequently extinguished in another context, the contexts may be acting as positive and negative occasion setters, respectively, for the CS. An occasion setter is assumed to modulate responding to a discrete CS independently of the occasion setter's direct association with the US (Holland, 1983). Bouton and Swartzentruber exposed animals to reinforced presentations of a CS in one context, alternated with nonreinforced presentation of the same CS in an alternate context. Subjects quickly learned to modulate responding to the CS as a function of the particular context in which it was presented. A variety of tests were conducted to rule out the possibility that the contexts themselves had gained either excitatory or inhibitory strength.

In the present Experiment 1, for Group O-D, Context M (the overshadowing training context) may have set the occasion for X to elicit behavior indicative of an overshadowing deficit, while Context N (the context in which X's comparator stimulus had been extinguished) may have set the occasion for X to elicit behavior indicative of recovery from that deficit. Applying this reasoning to the comparator hypothesis, the overshadowing context (M) may have set the occasion for effective retrieval of comparator (A)-US associations that attenuated responding to X (i.e., overshadowing), whereas the comparator stimulus extinction context (N) set the occasion for nonretrieval of comparator stimulus (A)-US associations (or retrieval of an A-no US association), thereby allowing vigorous responding to X (i.e., no overshadowing). While the present study was not explicitly intended to examine occasion setting by context, the observed modulatory role of the test contexts M and N with respect to responding to X by Group O-D is consistent with the view that occasion setting by the test contexts in fact occurred.

Let us now consider the results of Experiment 2. In a study of relative stimulus validity with rats, Cole, Barnet, and Miller (1995) found results similar to those of Experiment 2. After correlated relative validity training (i.e., AX+/BX-) in one context and extinction of the more valid cue (i.e., A-) in another context, all subjects were tested for responding to X in a third (neutral) context. Subjects demonstrated strong conditioned responding to X in this neutral context. According to Bouton and his colleagues, extinction should be context specific. Thus, the results of extinguishing A (i.e.,

attenuated responding to A and with it enhanced responding to X) should be specific to the context in which extinction of A occurred, and this prediction might be extrapolated to the anticipation of weak responding to X in a neutral context; however, strong responding to X was observed. It is important to note that Cole *et al.* did not conduct their study with the intention of looking at contextual modulation of behavior. Therefore, testing was not conducted with X in the relative-validity training context or in the context in which A was extinguished. Additionally, no tests were conducted on A. It would be interesting to determine if animals in that situation would show robust conditioned responding to A in the third context in the relative validity procedure, a result that would be consistent with Bouton and King (1983) as well as with what was observed with our present overshadowing procedure.

Lovibond, Preston, and Mackintosh (1984) found a similar result using a latent inhibition procedure. Subjects received extensive nonreinforced exposure to a CS in one context prior to excitatory training with that CS in another context. Subjects exhibited weak conditioned responding to the CS when testing took place in the context where CS-preexposure had been conducted, and strong conditioned responding to the CS when testing took place in the context where conditioning had been conducted. More relevant to the issue at hand, they also observed robust responding to the CS when testing occurred in a third, neutral context. Lovibond *et al.*'s study was aimed at looking at this particular phenomenon (as opposed to the Cole *et al.*, 1995, study), and as a result included proper controls (e.g., all contexts were equated for the values of context-US associations).

Taking together the studies of Bouton (e.g., Bouton & Bolles, 1979), Lovibond *et al.* (1984), Cole *et al.* (1995), and the present Experiment 2 of this report, the following conclusion emerges: that Bouton and Bolles (1979) were correct in presuming that excitation generalizes more readily to a novel context than does extinction (or inhibition). While no contemporary model of associative learning or performance (including the comparator hypothesis) can account for this result, it is interesting in and of itself, appears to be a consistent finding in the literature, and begs for theoretical address. When contexts disambiguate the meaning of a CS, subjects use that information; but when contexts fail to resolve the ambiguity, the default strategy appears to be to respond . . . at least in aversively motivated situations.

More generally, the present experiments probed the nature of various types of associations established during a conditioning session with multiple cues present. It is important to remember that although a relatively large number of associations (with varying degrees of effective strength) are likely acquired in a given session, the associations made evident at the time of testing will greatly depend on the contextual cues present at testing. The present data further support the view that context plays a distinctly important role in the expression of learned associations. Just as test contexts can modulate simple Pavlovian excitatory responding to a CS that is trained in one context and extinguished in an alternate context, test contexts can also modulate the comparator value of a stimulus that was trained (with its companion target CS) in one context and extinguished in a different context. Alternatively stated, the renewal phenomenon, which is well established for the direct CSUS

associative strength that supports Pavlovian responding, also appears applicable to the associative strength of cues in their roles as comparator stimuli for Pavlovian CSs.

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