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Stimulus Competition Between a Discrete Cue and a Training Context: Cue Competition Does Not Result From the Division of a Limited Resource

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Abstract

Several associative learning theories explain cue competition as resulting from the division of a limited resource among competing cues. This leads to an assumption that behavioral control by 2 cues competing with each other should always reflect a tradeoff, resulting in apparent conservation of total reinforcer value across all competing cues. This assumption was tested in 3 conditioned lick suppression experiments with rats, investigating the effects of changing the conditioned stimulus (CS) duration (Experiment 1), administering pretraining exposures to the CS (Experiment 2), and presenting nonreinforced CSs during the intertrial interval (Experiment 3) on Pavlovian conditioned responding to both the CS and the conditioning context. Fear conditioned to the context and to the CS decreased when the CS was of longer duration, massively preexposed before being paired with the reinforcer, or presented alone during the intertrial interval. These observations are problematic for the theories that explain cue competition as the division of a limited resource and suggest that the total reinforcer value across competing cues is not always fixed for a given reinforcer.

Keywords

total error reduction; context; CS-duration effect; latent inhibition; partial reinforcement effect

For several decades, one of the central topics in the field of associative learning has been the study of how multiple cues trained together with an outcome (e.g., food or footshock) interact in their control over behavior. The main finding from this work has been that multiple cues often appear to compete with each other for behavioral control. For example, when a compound of two cues is trained with an outcome, each element of the compound usually elicits weaker responding than when that element is trained alone (i.e., overshadowing; Pavlov, 1927). This class of phenomena, called cue competition, attracted great attention from researchers for both practical and theoretical reasons. One of the significant implications of cue competition is that it cannot be explained by a class of theories that explains acquired behavioral control exclusively on the basis of the intensities of target cue and the outcome and the contiguity between them.

Many learning theories assume that in a cue competition situation, the total behavioral control by all members of the compound cue reflects the physical properties of the outcome and that

the weaker behavioral control elicited by an element that was trained in compound is the result of a division of a limited resource. For example, the well-known Rescorla and Wagner (1972) model explains cue competition as a division of the outcome's associative reserve among simultaneously presented cues, which is determined by the physical properties of the outcome (e.g., intensity). Specifically, in the framework of the Rescorla–Wagner model, pairing a set of cues and an outcome results in a decrease in the discrepancy between the total associative strength with respect to that outcome of all cues present on that trial and λ , the total associative strength that the outcome can support. Thus, when only one cue is present, the associative strength of that cue approaches λ as the training continues, whereas when a compound of two cues is conjointly paired with the outcome, the summed associative strength of the two cues approaches λ , resulting in weaker associative acquisition to each member of the compound than when they are trained elementally. This explanation of simple cue competition effect is shared by a modification of the Rescorla–Wagner model proposed by Van Hamme and Wasserman (1994). Wagner's (1981) SOP model, which hypothesizes that more complex mechanisms explain the cue competition effect, also includes a similar division-of-limited-resource mechanism. We defer consideration of the SOP model until the General Discussion.

In this division-of-limited-resource framework, associative strength acquired by a cue varies according to whether other competing cues are present and what associative status they have. The total associative strength acquired by all cues inevitably approaches the value determined by the limited resource, regardless of how many cues are competing. Because the lack of behavioral control by one cue in a cue competition situation is directly caused by an increase in behavioral control by the other cue, behavioral control by two cues competing with each other should always reflect a tradeoff. The tradeoff relationship predicted by the division-of-limited-resource accounts is congruent with several empirical findings. For example, when two cues are trained in compound, responding to one cue is known to become weaker if the other member of the compound has been previously trained with the outcome (blocking; Kamin, 1968). Similarly, responding to a cue is known to become stronger when (presumably) negative associative value (i.e., conditioned inhibition) has been acquired by the other member of the compound (superconditioning; Rescorla, 1971). The division-of-limited-resource account successfully predicts and explains these various cue competition phenomena through a simple presupposition.

Recently, however, findings have been reported that challenge the division-of-limited-resource account. Several studies found counteractive effects between overshadowing, which is a prototypic stimulus competition effect, and other basic phenomena of learning, which are commonly viewed as cue competition between a discrete cue and the context. For example, Urcelay and Miller (2006) investigated the interaction of two treatments, conditioning a cue in compound with another salient cue (i.e., overshadowing treatment) and presenting an unsignaled unconditioned stimulus (US) interspersed with the cue–outcome pairings (i.e., degraded contingency treatment). It is well known that exposure to the US alone during intertrial intervals (ITIs) causes retardation of conditioned responding to the cue (Rescorla, 1966). This phenomenon is viewed by most learning theories as a type of cue competition between the discrete cue and the conditioning context, resulting from the context's acquiring greater associative strength with the outcome as the result of outcome-alone exposures (i.e., added pairings of the context and the outcome) during the ITI. Urcelay and Miller found that conditioned responding to a target cue was stronger when these two treatments were combined than when either was administered alone. This contradicts the prediction of the division-of-limited-resource account because in this account, when the number of cues competing for an outcome increases, the behavioral control by each cue should decrease. Thus, when a target cue is competing at the same time with two cues (i.e., the context and the overshadowing cue), behavioral control by the target cue is expected to be weaker than when it is competing with

either the context or the overshadowing cue alone. Other studies have found that the trial massing effect (Stout, Chang, & Miller, 2003) and the US–preexposure effect (Urushihara & Miller, 2006) also counteract overshadowing. These results cast doubt on the presupposition that cue competition is the result of a division of some limited resource.

There exist several theories that explain cue competition phenomena through means other than the division of a limited resource. For example, the comparator hypothesis (Miller & Matzel, 1988; Miller & Shachtman, 1985) explains cue competition as a result of interaction at the time of behavioral expression (i.e., testing) among multiple associations formed during training. In a situation in which two conditioned stimuli (CSs; e.g., X and A) are paired with a US, three associations are supposed to be formed. Each cue forms its own association with the US (i.e., X–US and A–US), and in addition, an association is formed between the two cues (i.e., X–A). At test, conditioned responding to a cue is assumed to reflect a comparison between the US representations directly activated by the target cue and indirectly activated by that cue through the competing cue. For example, when X is tested, excitatory responding to X is positively correlated with the strength of the directly activated representation of the US, that is, the association between X and the US (Link 1 in Figure 1) and inversely related to the indirectly activated representation of the US, that is, the product of the strengths of the association between X and the companion cue A (Link 2) and the association between A and the US (Link 3). Likewise, when A is tested, responding to A is directly related to the strength of the A–US association and inversely related to the product of the strengths of the A–X and X–US associations. It is important to note that the comparator hypothesis does not explain the stimulus competition as a division of a limited resource. That is, in the framework of the comparator hypothesis, the relationship among competing cues is not always a tradeoff. Specifically, at asymptote the summed total of all cue–outcome associations for cues trained together is not always the same for a given outcome.

In many cases, however, the predictions of the comparator hypothesis are similar to those of the division-of-limited-resource accounts; that is, behavioral control by two competing cues is predicted to approximate a tradeoff relationship. When the association between one cue and an outcome is changed, behavioral control by the other cue changes in the opposite direction, resulting in a seeming tradeoff relationship between the two cues. For example, suppose two cues, X and A, are conditioned in compound. When X is tested, responding to X is determined by a comparator process in which X is the target cue and A is the comparator stimulus; when A is tested, responding to A is determined by a comparator process in which A is the target cue and X is the comparator stimulus. If the association between A and the US is enhanced, responding to X should become weaker because the product of the X–A and A–US associations is enhanced (e.g., Miller & Matute, 1996). At the same time, responding to A should become stronger because the A–US association, which serves as Link 1 for A, has been enhanced. Thus, enhancement of the A–US association results in a loss of responding to Stimulus X and at the same time an enhancement of responding to Stimulus A. As a result, responding to X and A is in a tradeoff relationship, which is congruent with several well-established empirical findings such as blocking (e.g., Kamin, 1968); hence, apparent conservation of reinforcer value with respect to the US is usually observed.

The comparator hypothesis generates a counterintuitive prediction, however, concerning the relationship between competing stimuli in select situations. Specifically, when the within-compound association between two cues changes, behavioral control by one cue is predicted to change in the same direction as that of the other cue. Enhancement of the within-compound association between the two competing cues should attenuate responding to both cues simultaneously because this association serves as Link 2 for both stimuli. Thus, the total behavioral consequences caused by an unaltered US can change depending on the association between two competing cues. In other words, in a situation in which two cues are competing

with each other, when behavioral control by one cue changes because its association with the US is changed, behavioral control by the other cue is expected to change in the opposite direction, resulting in a tradeoff relationship. But when behavioral control by a cue changes because of a change in its within-compound association with its competing cue, behavioral control by both cues is expected to change in the same direction, resulting in an apparent loss or increment of reinforcer value of the US rather than a tradeoff relationship. Thus, the total amount or magnitude of conditioning caused by the US is not always expected to be identical even when the US used is unchanged.

With this theoretical background, the purpose of the present experiments was to directly contrast the predictions concerning the relationship between two competing cues generated by the division-of-limited-resource accounts with those derived from the comparator hypothesis. Unlike many other experimental studies of cue competition phenomena, our focus was not on the magnitude of responding to a specific target cue but on the relative changes in responding to a pair of competing cues in two different situations. For this purpose, we designed our experiments using the simplest possible cue competition paradigm, that is, competition between a discrete CS and its conditioning context, and tested both the CS and the context for behavioral control. This is the simplest cue competition design because most learning theories, including the Rescorla–Wagner (1972) model and the comparator hypothesis (Miller & Matzel, 1988), consider the conditioning context to be a possible competing stimulus, and conditioning must always occur in a context. This design allowed us to directly investigate the relationship between two competing stimuli and the total reinforcer value imparted by a constant US.

Some prior studies (e.g., Odling-Smee, 1975a, 1975b, 1978a, 1978b) have already investigated how fear conditioned to the context changes when a discrete cue that signals the occurrence of a US is manipulated. These prior studies generally found a tradeoff relationship between the fear to the context and that to the discrete stimulus, which is congruent with the prediction by division-of-limited-resource models. For example, Odling-Smee (1975b) manipulated the probability of an electric shock US during the CS with the numbers of the CS and the US presentations fixed and found that fear to the context was greater when the probability of CS–US co-occurrence was lower (i.e., when responding to the CS is expected to be weaker). However, the results of at least some of these experiments are largely inconclusive for our purposes because many of these results are readily explained by the comparator hypothesis as well as by division-of-limited-resource models. Specifically, when the number of CS presentations is fixed, the context–CS association (i.e., Link 2) is predicted to be identical in the framework of the comparator hypothesis regardless of the placement of the USs, and when the number of the US presentations is fixed, the context–US association should also be equal among the different conditions. The only factor that is expected to be influenced by manipulating the probability of CS–US co-occurrence is the CS–US association. When this association is changed and the other two associations are fixed, responding to the context and to the CS are predicted to change in the opposite direction because the CS–US association works as Link 1 when responding to the CS is tested and as Link 3 when responding to the context is tested.

To differentiate the predictions from the two views, we focused on three well-known phenomena in the conditioning literature, the CS duration effect (Pavlov, 1927), the CS–preexposure effect (also known as latent inhibition; Lubow & Moore, 1959), and the partial reinforcement effect (e.g., Wagner, Siegel, Thomas, & Ellison, 1964). Conditioning with a CS of longer duration, a CS that has been preexposed before conditioning, or a CS that is also presented alone during the ITI results in weaker behavioral control by that CS. Most learning theories that view cue competition phenomena as the division of a limited resource explain all response deficits as a loss or failure of acquisition of CS–US associative strength (e.g., Rescorla & Wagner, 1972). Thus, these theories predict that when a CS and a conditioning context

compete with each other, these three procedures, which are all viewed as causing a decrement in the CS–US association, should enhance conditioning to the context. The comparator hypothesis provides a different account for these three phenomena. In the framework of the comparator hypothesis, they are explained as a response deficit to the target CS resulting from its forming a stronger association with the context by either being paired with the context for a longer duration or being paired with the context more frequently either before or during the conditioning phase (see Urushihara & Miller, 2007, for further discussion). In other words, responding to the CS becomes weaker because of the strengthening of the association between the CS and the context (i.e., Link 2). It is important to note that Link 2 for behavioral control by the CS and Link 2 for behavioral control by the context are assumed to be the same CS–context bidirectional association. Thus, the comparator hypothesis predicts that each of these three procedures should decrease responding to the context and to the CS, resulting in an apparent loss of total reinforcer value of the US. We conducted three experiments in a conditioned lick suppression preparation with rats. In Experiment 1, we investigated the effect of varying the CS durations between groups. In Experiment 2, we investigated the effect of massive CS preexposure on conditioned suppression to the conditioning context and to the target CS. In Experiment 3, we investigated the effect of interspersing nonreinforced CS exposures during the ITI and also examined the effect of posttraining extinction of the CS on responding to the context, the rationale of which is explained later.

Experiment 1

The purpose of Experiment 1 was to investigate the effect of changing the duration of the CS on independent responding to the CS and its training context. It is well known that conditioning with a longer CS results in attenuated conditioned responding to that CS (Pavlov, 1927). Our interest was in investigating the effect that lengthening the CS has on responding to the context. According to the division-of-limited-resource view of cue competition, responding to the context should change in the direction opposite to its competing cue. Thus, when responding to the CS is decreased by expanding the CS duration during conditioning, behavioral control by the context should increase. In contrast, according to the comparator hypothesis, expanding the CS duration should decrease behavioral control by the context.

Method

Design—The experimental design of Experiment 1 is depicted in Table 1. Four groups of subjects received different CS–US manipulations during the conditioning phase and were tested with the CS and the context separately. The CS group received CS-alone presentations during the conditioning phase. We expected little conditioned suppression to either the CS or the context; this group served as a baseline control group for fear conditioning to both the CS and the context. The US group received US-alone presentations. We expected little suppression to the CS but strong suppression to the context; this group served as a control group for the cue competition effect of the CS on the context. The Short and Long groups received pairings with the US of either a short or a long CS, respectively. In the Short group, we expected substantial suppression to the CS and also substantial suppression to the context, but expected suppression to the context to be weaker than that in the US group because of a cue competition effect caused by the CS. In the Long group, we expected suppression to the CS to be weaker than that in the Short group because of the CS duration effect. Our focus was on behavioral control by the context in the Long group. According to the division-of-limited-resource view, suppression to the CS and the context should reflect a tradeoff. Thus, suppression to the context in the Long group should be stronger than that in the Short group. In contrast, according to the comparator hypothesis, suppression to the context in the Long group should be weaker than in the Short group because the decrement in suppression to the CS reflects a stronger association

between the CS and the context, which is expected to cause a decrement in suppression to the context as well.

Subjects—The subjects were 24 male (223–334 g) and 24 female (179–215 g) experimentally naïve Sprague-Dawley–descended rats (*Rattus norvegicus*) bred in our colony. The rats were randomly assigned to one of the four groups ($n_s = 12$), counterbalanced for sex. They were individually housed in wire mesh cages in a vivarium maintained on a 16:8-hr light–dark cycle. Experimental manipulations occurred approximately midway through the light portion of the cycle. A progressive water deprivation schedule was imposed over 4 days before the beginning of the experiment until water availability was limited to 30 min per day. All subjects were handled for 30 s three times per week from weaning until the initiation of the study.

Apparatus—The apparatus consisted of 12 experimental chambers of two different types, six identical copies of Chamber Rectangular (R) and six identical copies of Chamber V shaped (V). Chamber R was rectilinear, measuring 23.0 cm $\times$ 8.5 cm $\times$ 12.5 cm (length $\times$ width $\times$ height), and consisted of clear Plexiglas ceiling and side walls and a metal grid floor of 0.48-cm diameter stainless steel rods separated by 1.5 cm center to center. The rods were connected by NE-2 neon bulbs that allowed a constant-current footshock to be delivered by means of a high-voltage AC circuit in series with a 1.0-M Ω resistor. Each copy of Chamber R was housed in its own environmental isolation chest, which was dimly illuminated by a 2-W (nominal at 120 VAC) incandescent bulb driven at 60 VAC. The houselight was mounted on the ceiling of the environmental chest approximately 26 cm from the center of the experimental chamber.

Chamber V was a 22.1-cm-long box in the shape of a vertical truncated V (25.3 cm height, 21.3 cm wide at the top, and 5.1 cm wide at the bottom). The floor and sides were stainless steel sheets, and the ceiling consisted of clear Plexiglas. The floor consisted of two parallel metal plates, each 2.0 cm wide, with a 1.1-cm gap between them, which permitted the delivery of constant-current footshock. Each V-shaped chamber was housed in its own environmental chest, which was dimly illuminated by a 7.5-W (nominal at 120 VAC) incandescent houselight driven at 60 VAC mounted on an inside wall of the environmental chest approximately 30 cm from the center of the experimental chamber. Both Chambers R and V could be equipped with a water-filled lick tube that extended 1 cm from the rear of a cylindrical niche, 4.5 cm in diameter, left–right centered in one short wall, with its axis perpendicular to the wall, and positioned with its center 4.25 cm above the floor of the chamber. Each niche had a horizontal infrared photobeam traversing it parallel to the chamber wall on which the niche was mounted, 1 cm in front of the lick tube. To drink from the tube, subjects had to insert their heads into the niche, thereby breaking the infrared photobeam. Thus, we could record when subjects had their heads in the niche with the water tube. Ordinarily, they did this only when they were drinking. Disruption of drinking by being placed in the conditioning context or by the presentation of the test CS in the nonconditioning context served as our dependent variable.

In each of the 12 isolation chests, ventilation fans provided a constant 76-dB (C-scale) background noise. Two 45- Ω speakers mounted on the interior right and left sides of each environmental chest were used to deliver a complex tone (3000 + 3200 Hz, 6 dB [C-scale] above the background) and a click train (6/s, 6 dB [C-scale] above the background), respectively. Chamber R served as Context 1 and Chamber V served as Context 2 for half of the subjects, whereas these relationships were reversed for the other half. In Experiment 1, CS X was a 2.5- or 25-s click train. The US was a 0.5-s, 1.0-mA footshock. The complex tone was used only in Experiment 2.

Procedure

Acclimation to Context 2: On Day 1, all subjects were exposed to Context 2 for 60 min with the lick tubes available. Subjects established baseline licking behavior in Context 2 during this session, and the clicks were presented alone four times to all subjects. Two of these presentations were of long duration (25 s), and two were of short duration (2.5 s). This was intended to reduce nonassociative suppression to the CS in the US group when tested.

Acclimation to Context 1: On Day 2, all subjects were exposed to Context 1 for 60 min with lick tubes available. This session established baseline licking in Context 1. No nominal stimulus was presented during this session.

Conditioning: On Days 3 and 4, conditioning treatment was conducted during daily 260-s sessions in Context 1. The lick tube was not available during these sessions. Subjects in the Long group received four pairings of the 25-s CS X and the US, with a mean US–US interval of 65 s. Subjects in the Short group received four pairings of the 2.5-s CS X and the US with the same US–US interval as the Long group; thus, the US–CS interval was 62.5 s in the Short group compared with 40 s in the Long group. In each CS–US trial, the CS and the US were coterminous. Subjects in the US group received four exposures to the US with the same US–US interval as the Long and Short groups. Subjects in the CS group received four presentations of CS X but no US presentation. For half of the subjects in the CS group, CS X was 25 s in duration; for the remaining half, CS X was 2.5 s in duration.

Testing: On Days 5–8, testing of conditioning context (Context 1) and CS X was conducted, with the order counterbalanced within groups. Half of the subjects in each group received testing of Context 1 on Day 5, recovery of baseline licking in Context 2 on Days 6 and 7, and testing of CS X in Context 2 on Day 8. The other half of the subjects in each group received recovery of licking baseline in Context 2 on Days 5 and 6, testing of CS X in Context 2 on Day 7, and testing of Context 1 on Day 8. In the test session of Context 1, subjects were left in Context 1 with the lick tube available and the time to complete the first cumulative 5 s of drinking was recorded. All subjects were left in Context 1 for 30 min; if any subject did not complete its first cumulative 5 s of drinking in Context 1, a ceiling value of 30 min was recorded. In the two recovery-of-licking baseline sessions in Context 2, subjects were left in Context 2 and allowed to access to the lick tube for a 1-hr session without any nominal stimulus presentation. The testing session for CS X was then conducted in Context 2. Exposure of CS X started for each subject at the moment it completed its first cumulative 5 s of drinking and continued for 15 min. Times to complete cumulative 5 s of drinking both before CS onset (pre-CS time) and in the presence of CS X (CS time) were recorded. Before statistical analysis, all data were converted to log (base 10) scores to better approximate a within-group normal distribution of scores, as required for the use of parametric statistical analysis.

Results and Discussion

The data of 2 subjects, 1 from the CS group and 1 from the Short group, were lost because of experimenter error. Figure 2 depicts with black bars the mean latencies to complete the first cumulative 5 s of drinking in Context 1 and with white bars the mean latencies to complete first cumulative 5 s of drinking in the presence of CS X. First, from visual comparison of the white bars, it can be seen that both the CS and the US groups showed little fear to CS X, whereas two CS–US groups showed substantial fear to CS X. Between the two CS–US groups, the Long group showed weaker fear of CS X than did the Short group, indicative of the CS duration effect. Second, from visual comparison of the black bars, the CS group showed the least fear of the training context, the US group showed the greatest fear, and the Short and the Long groups showed moderate fear. Between the two groups that received CS–US pairings during conditioning, the Long group showed weaker fear of the training context than did the Short

group. Thus, it appears that there was a decrement of contextual fear as a result of signaling the US with the discrete CS, which can be taken as evidence of cue competition between the CS and the context. Centrally, this deleterious effect of signaling the US was greater when the signal (CS X) was presented for a longer duration, which is the CS–US condition that also showed reduced responding to the CS X. The following statistical analyses supported these conclusions.

We first analyzed the pre-CS scores from CS X testing to assess any potential differences in expression of fear to Context 2. To assess whether test order (i.e., whether the CS X testing was conducted before or after the context testing) interfered with group effects, we analyzed the data with a 4 (group) $\times$ 2 (test order) analysis of variance (ANOVA). The ANOVA revealed neither a significant main effect nor an interaction, $F_s(1, 38) = 2.47, p_s > .12$. Notably, all animals completed their first cumulative 5 s of drinking in less than 60 s, thereby indicating that they had largely recovered their pretraining baseline rates of initiating licking. A similar 4 $\times$ 2 ANOVA conducted on the CS scores yielded a main effect of group, $F(1, 38) = 18.39, p < .001$. Neither the main effect of test order nor the interaction was significant ($F_s < 1$). A planned comparison revealed that suppression by the Short group was stronger than by the Long group, $F(1, 38) = 16.59, p < .001$.

Concerning the results of testing the training context, the latencies to drink in Context 1 were analyzed with a 4 (group) $\times$ 2 (test order) ANOVA. The ANOVA revealed a main effect of group, $F(3, 38) = 69.71, p < .001$. Neither the main effect of test order nor the interaction was significant, $F < 1$ and $F(3, 38) = 1.47$, respectively, $p_s > .23$. Planned comparisons revealed the following differences. First, both the Short and the Long groups showed less fear to the context than the US group, $F_s(1, 38) = 6.70$ and 32.92 , respectively, $p_s < .02$, suggesting that the CS competed with the context. Second, and most important, the Short group showed more fear than the Long group, $F(1, 38) = 10.10, p < .003$.

Before drawing a conclusion from the current data, two points require some discussion. First, one might argue that the weaker responding to the context in the Long group than in the Short group emerged because responding to the context was positively mediated by the associative status of the CS, like in the case of potentiation (e.g., Clarke, Westbrook, & Irwin, 1979; Rusiniak, Hankins, Garcia, & Brett, 1979). Specifically, it is known that adding another cue on conditioning trials of a target cue sometimes results in facilitation (i.e., potentiation) rather than impairment (i.e., overshadowing) of responding to the target cue. Comparison between the Short and US groups, however, suggests that such potentiation processes were at least not dominant in this experiment. Specifically, if we suppose that the associative status of the CS supported rather than degraded responding to the context, it follows that stronger responding to the context should be observed in the Short group than in the US group, which was not the case. Nevertheless, there still remains the possibility that conditioning to the CS simultaneously facilitated (i.e., potentiated) and degraded (i.e., overshadowed) responding to the context; the latter process resulted in weaker responding to the context in the Short and Long groups than in the US group, and the former process resulted in stronger responding to the context in the Short group than in the Long group. Experiment 3 provides further evidence concerning whether the potentiation effect between the CS and the context played a critical role in the results of this and the following experiments.

Second, one might argue that the difference in responding to the CS between the Long and the Short groups was explicable in terms of inhibition of delay (Pavlov, 1927). Specifically, conditioning with a CS of long duration gradually results in loss of responding during the early part of each CS presentation. Thus, weaker responding to the CS observed in the Long group than in the Short group might not result from a difference in the degree of cue competition between the CS and the context, but might simply reflect weakened responding in the early

part of the CS presentation rather than weakened response-eliciting potential of the overall CS. However, it seems difficult to accept this explanation. The parameters used in this experiment were not favorable for inhibition of delay. Two previous studies using almost the same set of parameters, CS of 25 s and eight CS–US trials (Urushihara & Miller, 2007; Urushihara, Stout, & Miller, 2004), demonstrated not only impairment of responding to the CS in the elemental conditioning situation but also facilitation of responding by extending the CS duration when the CS was trained in compound with the other CS, which strongly suggests that this set of parameters is not suitable for observing inhibition of delay. Furthermore, even if we explain weaker responding to the CS in the Long group as the result of inhibition of delay, it does not explain why responding to the context in the Long group was also weaker than in the Short group. The following two experiments used a CS of the same length across groups, which we expected would allow a clearer conclusion as to whether a process such as inhibition of delay could play any role in the phenomena we observed.

One might point out that the results of Experiment 1 are incongruent with the findings of Odling-Smee (1975a), in which the duration of a discrete CS signaling each presentation of a shock US was manipulated with the numbers of US presentations and duration of context exposure fixed. Using different CS durations of 3.3, 6.6, 10.0, 42.0, and 90.0 s, Odling-Smee found that the use of a 10-s CS as a signal of US presentation was most effective to decrease the fear to the context when a delay conditioning procedure was used. Although he did not test conditioned fear of the CS in his own study, he pointed out that Yeo (1974) had investigated the conditioned fear to a discrete CS as a function of CS duration and had reported that the fear to the CS was strongest when a CS of 10-s duration was used. He concluded that responding to the discrete CS and the context appeared in a tradeoff relationship when the duration of the CS was changed, which is opposite to the conclusion of this experiment. It is difficult to draw an unequivocal conclusion about how and why the relationship between responding to the CS and the context found in Odling-Smee's and Yeo's studies and that in Experiment 1 differ, for there are many differences in procedures between Odling-Smee's and our experiments, and even between Odling-Smee's and Yeo's experiments. However, we acknowledge that our finding of a nontradeoff relationship in this experiment might be limited to situations in which relatively short CSs and ITIs are used, and there is a possibility that contrary results might be obtained with greater timescales, as suggested by Odling-Smee's and Yeo's studies.

The results of Experiment 1 are a serious challenge to some acquisition-focused theories such as the Rescorla–Wagner (1972) model and its modification by Van Hamme and Wasserman (1994), which explain cue competition phenomena as a division of a limited resource. Experiment 1 clearly showed that the total amount of conditioned fear supported by a US does not always appear to be identical. Specifically, despite the fact that the Short and the Long groups received physically identical shocks, expanding the CS duration in the Long group resulted in a decrement of fear to the context as well as the CS. The fear conditioned to both CS X and the context was weaker in the Long group than in the Short group. This violation of a tradeoff relationship between the two competing cues is problematic for the division-of-limited-resource view, even though it might be limited to situations in which relatively short intervals are used. In contrast, the result of Experiment 1 was consistent with the prediction of the comparator hypothesis. The comparator hypothesis explains the CS duration effect as a deficit in responding to the CS caused by enhancement of Link 2 (i.e., CS–context association), which is expected to cause a decrement of responding to the context as well.

Experiment 2

In Experiment 2, we investigated the effect of preconditioning exposures of the CS alone on responding to the CS and to the context under conditions in which the CS and the context might be expected to compete with each other. Nonreinforced preexposure to a to-be-conditioned cue

is known to cause a retardation of behavioral control by the CS (the CS–preexposure effect; Lubow & Moore, 1959). Our focus was on whether this procedure enhances or decreases subsequent behavioral control by the context resulting from CS–US pairings. In the framework of the division-of-limited-resource view of cue competition, responding to the context is expected to be inversely related to behavioral control by its competing cue, that is, the CS. Thus, when conditioned responding to the CS is retarded by CS preexposure, responding to the context should be enhanced. In contrast, in the framework of the comparator hypothesis, preexposure of the CS should result in the formation of a stronger association between the CS and the context because the CS and the context are paired more times. The CS–context association serves as Link 2 for both the CS and the context in determining conditioned responding. Consequently, the enhanced CS–context association should result in a decrement of conditioned responding to the context as well as to the CS.

Method

Design—The design of Experiment 2 is depicted in Table 2. There were four groups of subjects. The CS and the US groups were similar to those of Experiment 1. The CS group received CS X–alone exposures during conditioning (Phase 2) and served as a control group for conditioning to both CS X and the context. The US group received US–alone presentations during Phase 2 and served as a control group for the cue competition effect of CS X on the context. Unlike Experiment 1, however, subjects in these two groups received preexposure to either CS X or CS Y in Phase 1. Both the Signal and the Signal-Pre groups received CS X–US pairings in Phase 2. These two groups differed in Phase 1 treatment. In Phase 1, the Signal-Pre group received preexposure to CS X, whereas the Signal group received preexposure to CS Y, which was irrelevant to the subsequent conditioning treatment. Thus, we expected retardation of responding to CS X in the Signal-Pre group compared with the Signal group. Concerning behavioral control by the context, in the Signal group we expected substantial responding to the context, but it should have been weaker than that in the US group because of a cue competition effect caused by CS X. Our main interest was responding to the context in the Signal-Pre group.

Subjects and Apparatus—The subjects were 48 male (279–355 g) and 48 female (189–247 g) experimentally naïve Sprague-Dawley–descended rats (*Rattus norvegicus*) bred in our colony. The animals were randomly assigned to one of the four groups ($ns = 24$), counterbalanced for sex. The experiment was conducted in two exact replications, each of which included 48 animals ($ns = 12$). Housing, deprivation, and handling conditions were the same as in Experiment 1. The apparatus was the same as described in Experiment 1 except that a click train and a tone, each of 2.5-s duration, were used as CS X and CS Y, counterbalanced within groups.

Procedure

Acclimation to Context 2: On Day 1, all subjects were exposed to Context 2 for 60 min with lick tubes available. During this session, CS X and CS Y were each presented separately four times in pseudorandom order. This was intended to reduce nonassociative suppression to the CS in the US group when it was later tested.

Acclimation to Context 1 and CS preexposure: On Day 2, all subjects were exposed to Context 1 for 60 min with lick tubes available. In addition, either CS X or CS Y was presented alone 400 times with a mean ITI of 9 s (range = 6–12 s). CS X was presented to all subjects in the Signal-Pre group and half of the subjects in the CS and the US groups, and CS Y was presented to all subjects in the Signal group and the other half of the subjects in the CS and the US groups.

Conditioning: On Day 3, a conditioning session was conducted during a 260-s session in Context 1. Lick tubes were not available during this session. Subjects in the Signal and Signal-Pre groups received four presentations of the 2.5-s CS X followed immediately by the US, with a mean US–US interval of 65 s. During these conditioning trials, the 0.5-s US coterminated with the CS. Subjects in the US group received four US exposures with the same US–US interval as the Signal and Signal-Pre groups. Subjects in the CS group received four presentations of CS X at the same time as the Signal and Signal-Pre groups but no US presentation.

Testing: On Days 4–7, testing of conditioning context (Context 1) and CS X was conducted. Half of the subjects in each group received testing of Context 1 on Day 4, recovery of baseline licking in Context 2 on Days 5 and 6, and testing of CS X on Day 7. The remaining half of the subjects in each group received recovery of licking baseline in Context 2 on Days 4 and 5, testing of CS X on Day 6, and testing of Context 1 on Day 7. Testing of the context, recovery of licking baseline, and testing of CS X were conducted in the same manner as in Experiment 1.

Results and Discussion

To assess whether test order or replication interfered with group effects, we first analyzed the data with a 2 (replication) $\times$ 2 (test order) $\times$ 4 (group) ANOVA. Unlike Experiment 1, we found the effect of test order to interact with the effect of group in the data from CS testing, $F(3, 80) = 4.94, p < .004$. The overall tendency was unchanged regardless of whether the CS testing was conducted before or after testing of the context; suppression to the CS in the Signal group was greater than that in the Signal-Pre group, which was slightly greater than that in the two control groups. However, absolute fear to the CS in the Signal group was relatively weaker when the CS testing was conducted after rather than before the context test. Perhaps this occurred because the number of CS–US pairings was reduced from eight in Experiment 1 to four in Experiment 2, thereby making suppression to the CS more vulnerable to changes in the associative status of the context that occurred during testing of the context. Consequently, although we tested all subjects on both the CS and the context, we report only the data from the test session conducted first for each subject. This effectively reduced group size by half, which is why twice the number of subjects were used in Experiment 2 than in Experiment 1.

Figure 3 depicts mean latencies to complete the first cumulative 5 s of drinking in the presence of CS X or the training context. Suppression to the context by the 12 subjects in each group tested with the context first are depicted with black bars, and suppression to CS X by the subjects tested with the CS X first are depicted with white bars. Examination of the white bars suggests that both the CS and the US groups showed little fear of CS X, whereas the Signal group showed substantial fear. Although subjects in the Signal-Pre group received the same number of CS–US pairings, fear to CS X was lower in the Signal-Pre group than in the Signal group, indicative of the CS preexposure effect. Examination of the black bars suggests that the CS group showed the least fear of the context, whereas the US group showed the greatest fear of the four groups. Both the Signal and the Signal-Pre groups showed moderate fear of the context, which fell between the two control groups, indicative of a decrement of contextual fear resulting from cue competition between the context and the discrete CS. Of central interest was that the Signal-Pre group showed weaker fear of the context than did the Signal group. Thus, a decrement of contextual fear as a result of signaling the US with a discrete stimulus was observed, which is evidence of cue competition between the CS and the context. More important, this cue competition effect was stronger when the signal (CS X) was presented before conditioning. The following statistical analyses supported these conclusions.

We first analyzed pre-CS scores gathered during testing of CS X to assess any potential differences in expression of fear to the context in which CS X was tested (Context 2). To investigate whether there was any difference between the two replications, we conducted a 2 (replication) $\times$ 4 (groups) ANOVA on pre-CS scores. The ANOVA revealed neither main effects nor an interaction, $F_s(1, 40) < 3.30$, $p_s > .07$. A similar 2 $\times$ 4 ANOVA conducted on the CS X scores (of only subjects tested first on CS X) yielded a main effect of group, $F(3, 40) = 26.53$, $p < .001$. Neither the main effect of replication nor the interaction was significant ($F_s < 1$). A planned comparison revealed that the Signal group showed stronger fear than the Signal-Pre group, $F(1, 40) = 33.55$, $p < .001$, thereby documenting a CS preexposure effect.

We also analyzed log latencies to complete the first cumulative 5 s of drinking in Context 1 with a 2 (replication) $\times$ 4 (group) ANOVA. The ANOVA revealed a main effect of group, $F(3, 40) = 10.68$, $p < .001$, whereas neither the main effect of replication nor the interaction was significant, $F(1, 40) = 1.37$ and $F < 1$, respectively. A planned comparison revealed that the contextual fear in the Signal-Pre group was weaker than that in the Signal group, $F(1, 40) = 4.96$, $p < .04$.

The results of Experiment 2 are again problematic for most theories of learning that explain cue competition as a division of a limited resource among cues. More important, Experiment 2 again clearly showed that the total amount of fear supported by a US is not always the same. Although the electric shock presented to the subjects in the Signal and the Signal-Pre groups was physically identical, fear to both the context and CS X was weaker in the Signal-Pre group than in the Signal group, contrary to the tradeoff principle among competing stimuli. Critical to this conclusion is the fact that other than the CS and context (which itself is a conglomerate of cues), no other cues were present during training. This finding, as well as that of Experiment 1, poses a serious challenge to acquisition-focused theories such as the Rescorla–Wagner (1972) model and its modification by Van Hamme and Wasserman (1994), whereas it is consistent with the prediction by the comparator hypothesis (Miller & Matzel, 1988).

Experiment 3

The purpose of Experiment 3 was twofold. First, we wanted to investigate the effect of nonreinforced exposures of the CS interspersed among the CS–US pairings, that is, the partial reinforcement procedure, on responding to the context and to the CS. Presenting CSs without the US during the ITI results in weaker responding to the CS (e.g., Wagner et al., 1964). According to the models that explain cue competition phenomena as a division of some limited resource of the outcome, when the responding to the CS is impaired by the partial reinforcement procedure, its competing cue (context) should acquire greater response-eliciting potential, resulting in apparent conservation of reinforcer value across the context and the CS. In contrast, according to the comparator hypothesis, presenting nonreinforced CSs during the ITIs should result in formation of a stronger context–CS association (i.e., Link 2), which is expected to decrease responding to the context and to the CS, at least in select situations (i.e., in relatively small timescale; see Urushihara & Miller, 2007, for further discussion). The first purpose of Experiment 3 was to compare these two opposing predictions.

The second aim of Experiment 3 was to investigate the effect of posttraining associative deflation of the CS on fear conditioned to the context, which is of interest for two reasons. First, in the previous two experiments, we found that responding to the context and to the CS became weaker when the CS signaling the US was of longer duration (Experiment 1) or when the CS was massively preexposed alone in advance of the CS–US pairings (Experiment 2). As we previously noted, these observations could readily be explained if one supposes that responding to the context was (positively) mediated by the associative status of the CS (i.e., potentiation). However, prior experiments did not seem to support this view because fear of

the context was weaker when the presentation of the US was signaled by the CS (i.e., the Long and Short groups in Experiment 1 and the Signal and Signal-Pre groups in Experiment 2) than in the groups in which the US was experienced without any signals (i.e., the US groups in Experiments 1 and 2). We expected testing the effect of posttraining deflation of the CS on responding to the context to provide further evidence concerning this issue. Previous studies that focused on cue competition between multiple discrete cues have reported that posttraining extinction of the competing cue often induces recovery from various cue competition phenomena such as blocking (Blaisdell, Gunther, & Miller, 1999), overshadowing (Kaufman & Bolles, 1981), and relative cue validity effect (Cole, Barnet, & Miller, 1995). Thus, if the CS and the context are competing with each other in the current experiments, posttraining deflation of the CS should cause recovery of fear of the context. In contrast, if responding to the context was positively mediated by the associative status of the CS, there is no reason to expect fear to the context to recover as a consequence of posttraining deflation of the CS.

The second reason for our investigating the effect of posttraining deflation of the CS on fear of the context was to further test the prediction generated by the comparator hypothesis (Miller & Matzel, 1988). The comparator hypothesis assumes that a strong within-compound association between the context and the CS will impair responding to the context at the time of testing given that there is an intact association between the context and the US. That is, responding to the context should be determined not only by the status of the context-US association (i.e., Link 1) but also by the status of the association both between the context and the CS (i.e., Link 2) and between the CS and the US (i.e., Link 3) at the time of testing. Thus, if the associative status of the CS is manipulated, it should have an effect on responding to the context regardless of whether it is conducted before or after the conditioning to the context. Specifically, if the CS is massively extinguished after conditioning, it should cause recovery of responding to the context because the CS will lose its potential to serve as an effective comparator stimulus for the context. Notably, in Experiment 3 and in the previous two experiments, the duration of context exposure (i.e., the total session duration) and the number and timing of the US presentations were equated across groups. Thus, although responding to the context differed, the hypothetical association between the context and the US should have been identical across groups because the strength of the context-US association should be determined simply by the physical intensity of the associates, their spatiotemporal contiguity, and the number of pairings. Thus, if the CS loses most of its potential to serve as the comparator stimulus for the context (which is expected to be achieved by conducting a large number of CS extinction trials), we predict that responding to the context should become identical across the conditions.

To investigate the effect of posttraining extinction of the CS on responding to the context, we modified the design and procedure of Experiment 3 from that of the previous experiments so its focus was exclusively on responding to the context rather than on both the context and the CS. The order of testing of the CS and the context were no longer counterbalanced in this experiment. The context was tested first for all the subjects and then the CS was tested. This was done to maximize the impact of posttraining CS deflation because CS testing, that is, exposure of the CS for a long duration without any US presentation in our lick suppression preparation, might cause some effect similar to posttraining deflation of the CS in all groups. This could result in diminishment of the difference among the groups caused by the intended posttraining deflation of the CS. Thus, we conducted CS testing for all subjects after context testing, which means that the results of CS testing might be contaminated by context testing. In addition, we selected the parameters used during posttraining extinction of the CS with the intent of maximizing sensitivity to changes in responding to the context. Thus, a large number of CS extinction trials were administered so that extinction of the CS would be near asymptotic. At the same time, to avoid any effect caused by the retention interval between conditioning and testing, the number of posttraining extinction sessions was minimized. As a result, as many

as 800 CS-alone trials were administered in two 1-hr sessions. On the one hand, this set of parameters is preferable for investigating the effect of posttraining deflation of the CS on responding to the context. On the other hand, this set of parameters might yield some spontaneous recovery from extinction because of the massed extinction trials conducted in a small numbers of sessions. For these two reasons, the results of the CS testing should be taken as supplemental data in this experiment. We should mention that the effect of partial reinforcement on responding to the CS with the current set of parameters has already been provided by a recent study (Urushihara & Miller, 2007).

Method

Design—The design of Experiment 3 is depicted in Table 3. Unlike Experiments 1 and 2, the CS group was not included in Experiment 3 because it is obvious from the results of the prior two experiments that no responding to either the CS or the context would be observed in that condition. The experiment included six groups in a 3 (stimulus conditions: US vs. Continuous vs. Partial) $\times$ 2 (posttraining deflation of the CS or not) factorial design. During the conditioning phase, two groups in the US condition and two groups in the Continuous condition received manipulations similar to the US and Short groups in Experiment 1, that is, four daily US presentations or four daily CS X–US pairings, respectively. Two groups in the Partial condition received 36 daily CS-alone exposures as well as 4 CS X–US pairings during the conditioning phase. After the conditioning phase, one group from each stimulus condition (those in the extinction condition) received 400 daily CS X–alone exposures on each of 2 days, whereas the other three groups (those in the no-extinction condition) received no nominal stimulus exposure. Then all subjects were tested for the fear of the context, which was followed by reacclimation to the CS testing context and testing of the CS. The focus of Experiment 3 was on behavioral control by the context; in the no-extinction condition, we expected substantial responding to the context in the Continuous group, but it should have been weaker than that in the US group because of a cue competition between the CS X and the context. Our main interest in the no-extinction condition was any difference in responding to the context between the Partial and the Continuous groups. In the three groups in the extinction condition, the central issue was whether recovery of fear to the context would be observed as a consequence of extinction of the CS.

Subjects and Apparatus—Thirty-six male (256–317 g) and 36 female (181–229 g) experimentally naïve Sprague-Dawley–descended rats (*Rattus norvegicus*) bred in our colony served as subjects. The animals were randomly assigned to one of six groups ($ns = 12$)—US, Continuous, Partial, US Ext, Continuous Ext, and Partial Ext, counterbalanced for sex. Housing, deprivation, and handling were the same as in Experiments 1 and 2. The apparatus was the same as described in Experiment 1. A click stimulus of 2.5-s duration served as CS X.

Procedure

Acclimation to Context 2: On Day 1, all subjects were exposed to Context 2 for 60 min with lick tubes available. During this session, CS X was presented alone four times. This was intended to reduce nonassociative responding to CS X during testing.

Conditioning: On Days 3 and 4, conditioning manipulations were conducted during daily 260-s sessions in Context 1. Lick tubes were not available during this session. Subjects in the Continuous and Continuous Ext groups received four pairings of the 2.5-s CS X and the US in each session, with a mean US–US interval of 65 s. On these conditioning trials, the 0.5-s US coterminated with the CS. Subjects in the Partial and Partial Ext groups also received four daily CS–US pairings, and in addition they received 36 daily nonreinforced exposures to the CS. Subjects in the US and US Ext groups received four US-alone exposures with the same US–US interval as the other four groups.

Extinction: On Days 5 and 6, extinction of CS X was conducted during daily 1-hr sessions in Context 2. Lick tubes were not available during these sessions. Subjects in the US, Continuous, and Partial groups received exposure to Context 2 without any nominal stimulus presentation during each session. Subjects in the US Ext, Continuous Ext, and Partial Ext conditions received 400 daily nonreinforced exposures to CS X, with a mean ITI (CS onset–CS onset) of 9 s (range = 6–12 s).

Context testing: On Day 7, testing of the conditioning context (Context 1) was conducted for all the subjects in the same manner as in Experiments 1 and 2.

Reacclimation to Context 2 and CS testing: On Days 8 and 9, daily sessions to restabilize baseline licking in Context 2 were conducted, and on Day 10, CS X was tested in Context 2. Recovery of the licking baseline and testing of CS X were conducted in the same manner as in Experiments 1 and 2.

Results and Discussion

The results of context testing conducted on Day 7 are presented in the left panel of Figure 4. Comparison among the no-extinction groups clearly shows that conditioned suppression in the Continuous and Partial groups was weaker than in the US group, suggesting cue competition between the context and the CS. More important, suppression to the context in the Partial group was weaker than that in the Continuous group, which suggests that more CS–context time together reduced suppression to the context. This finding is similar to those found with the CS duration effect and the CS preexposure effect in Experiments 1 and 2, respectively. Turning to conditioned suppression to the context in the three extinction groups, we observed no significant difference among these groups. All three groups exhibited strong suppression. This indicates that extinction of the CS after conditioning eliminated any appreciable cue competition effect of the CS on the context, which does not support an explanation of the results in the previous two experiments that second-order conditioning mediated by the CS was responsible for the observed differences in behavioral control by the context. The following statistical analyses support these conclusions.

A 3 (stimulus condition: US vs. Continuous vs. Partial) $\times$ 2 (posttraining deflation of the CS) ANOVA conducted on log latencies to complete the first cumulative 5 s of drinking in the conditioning context yielded main effects of stimulus condition, $F(2, 66) = 5.04, p < .01$, and posttraining deflation of the CS, $F(1, 66) = 13.71, p < .001$. More important, the interaction between these two factors was also significant, $F(2, 66) = 4.09, p < .02$. Planned comparisons using the error term from the ANOVA revealed no difference among the three extinction groups ($F_s < 1$), whereas among the three groups that received no extinction of the CS, the US group showed greater suppression than the Continuous group, $F(1, 66) = 4.81, p < .04$, which showed greater suppression than the Partial group, $F(1, 66) = 4.85, p < .04$. We defer presentation of the CS data until after discussion of the context data.

The results obtained from context testing in Experiment 3 are fully consistent with predictions by the comparator hypothesis (Miller & Matzel, 1988). Concerning the three groups that received no extinction of the CS, both the Continuous and the Partial groups showed weaker responding to the context than the US group, which suggests that the CS–US association served as an effective comparator stimulus for the context. More important, responding to the context was weaker in the Partial group than in the Continuous group. This is congruent with the prediction by the comparator hypothesis, whereas it is contrary to the prediction by division-of-limited-resource models (e.g., Rescorla & Wagner, 1972). The comparator hypothesis predicts that presentations of the CS alone during the ITI should enhance the association between the CS and the context, resulting in weaker responding to the context and to the CS.

Additionally, responding to the context in the two groups that received posttraining extinction of the CS after CS–US pairings was similar to that of the US group; that is, massive extinction of the CS apparently resulted in the loss of any difference in fear to the context, regardless of the procedure used in the original training phase or responding to the context before the CS extinction. This is also consistent with the prediction of the comparator hypothesis. In the framework of the comparator hypothesis, the association between the context and the US (i.e., Link 1 when the context is tested) should be identical among the three conditions because the context and the US were treated identically. Thus, as the effectiveness of the CS as a comparator stimulus of the context was decreased, suppression to the context in the continuous and the partial conditions should have approached that in the US condition. However, one should be cautious with this conclusion because it is based on null results (i.e., no difference among three groups).

The results of CS testing conducted on Day 10 are presented in the right panel of Figure 4. Differences among the no-extinction groups indicate that the conventional partial reinforcement effect occurred, that is, the Continuous group showed the greatest suppression, the Partial group showed moderate suppression, and the US group showed the weakest suppression. However, among the extinction groups, suppression in the Continuous Ext and the Partial Ext groups are comparable and are slightly higher than the US Ext group. The results suggest that as a result of massive extinction of the CS, responding to the CS in the Continuous Ext group decreased to the same level as that in the Partial Ext group, but in both groups some small amount of responding to the CS was still observed at the time of testing, presumably as the result of spontaneous recovery from extinction. The statistical analyses revealed the following tendencies.

Before the analyses of the CS scores, we conducted a 3 (stimulus condition) $\times$ 2 (posttraining deflation of the CS) ANOVA on the pre-CS scores. This ANOVA yielded no main effect or interaction ($F_s < 1.41, p > .24$). A similar ANOVA conducted on the CS scores yielded a main effect of stimulus condition, $F(2, 66) = 11.68, p < .001$. Neither the main effect of posttraining extinction nor the interaction was significant, $F < 1$ and $F(2, 66) = 1.97, p > .14$, respectively. Although the interaction was not significant because of the statistical analysis including all six groups, we conducted a planned comparison between the Continuous and the Partial groups to determine whether there was any evidence of a partial reinforcement effect when extinction of the CS was not administered. The planned comparison revealed that the suppression in the Continuous group was greater than that in the Partial group, $F(1, 66) = 10.99, p < .01$, which indicates that there was a partial reinforcement effect in the condition in which the subjects did not receive extinction of the CS during Phase 3. Overall, the results of the CS testing were not very informative. There are several reasons for this. First, the CS testing was conducted for all groups after the context testing was conducted; thus, there is a possibility that suppression to the CS in all groups was affected by the test exposure to the conditioning context. Second, and more important, the parameters for the posttraining extinction were set so as to maximize the effect of CS extinction on suppression to the context. Specifically, the 800 CS-alone exposures were conducted within two 1-hr sessions. On the one hand, such parameters should have minimized the effect of the retention interval between conditioning and testing of the context. On the other hand, such massed extinction trials might be more likely to yield spontaneous recovery by the time of the CS test. Moreover, potential spontaneous recovery was enhanced by the baseline recovery sessions, which inevitably increase the retention interval between extinction and testing of the CS. The weak responding to the CS in the Continuous Ext and Partial Ext groups was possibly because of weak spontaneous recovery from extinction caused by these factors. As previously noted, Urushihara and Miller (2007) demonstrated that the current parameters effectively produce the partial reinforcement effect between the Continuous and the Partial groups. However, in this experiment, although a nonsignificant tendency was observed, the analysis of the six groups together did not show clear statistical differences.

General Discussion

These experiments focused on the relationship between conditioned suppression to two cues that competed with each other in the simplest of cue competition situations, that is, cue competition between a discrete cue and its conditioning context. We found that conditioned suppression to these two competing cues does not always reflect an inverse relationship. That is, expanding the duration of the discrete stimulus (Experiment 1), preconditioning exposures of the discrete stimulus (Experiment 2), and adding nonreinforced presentations of the discrete stimulus during the ITI (Experiment 3) all simultaneously decreased conditioned fear to the context and to the discrete stimulus.

One might point out that the duration of the CS and the ITI during conditioning in this series was relatively shorter than those commonly used. That is, the CS duration was ordinarily 2.5 s and the US–US interval was consistently 65 s. The reason why we used these parameters was that we wanted to test conditioned suppression to the context as well as that to the CS, and it is important to keep the duration of the context exposure short to maintain behavioral control by the context at high level. A pilot experiment similar to Experiment 3 but that used longer durations of the CS (5 s) and the US–US interval (195 s on average) failed to detect clear differences in suppression to the context. To detect differences in suppression to context among conditions, relatively short ITIs (and consequently short CS duration) are favorable. In any case, with the current set of parameters well-known phenomena such as the CS duration effect, the CS preexposure effect, and the partial reinforcement effect (see also Urushihara & Miller, 2007) were observed in suppression to the CS, and the effect of these procedures on suppression to the context was also detected. Thus, the use of a relatively short timescale does not degrade the conclusions that can be drawn from the current series of experiments. However, as has been noted in the discussion of Experiment 1, there remains the possibility that our central findings of a nontradeoff relationship might be confined to situations in which a relatively small timescale is used; opposite results might be observed in a longer timescale, as has been suggested by Odling-Smee (1975a) and Yeo (1974). Further experimental work is needed to test generality of the present findings.

Similar to our findings, Barela (1999) measured fear to both the context and the CS following CS–US pairings and found that conditioned fear to these two stimuli does not always reflect an inverse relationship. He used three different ITI conditions, short (15 s), moderate (60 s), and long (900 s) and monitored freezing responses both in the training context and during the presentation of the CS in a context other than the training context to investigate the mechanism of the trial massing effect. He found that as the ITI became longer, fear to the training context did not show an inverse relationship to fear to the CS, although fear to the CS monotonically increased. Specifically, fear to the context in the moderate ITI condition was stronger than that in the short and long ITI conditions. Unfortunately, because the focus of Barela's research was different from that of the current experiments, he changed the timing of the US presentations across conditions (i.e., the USs occurred at different times for different groups). Furthermore, he made comparisons only among CS–US groups, which leaves open the possibility of positive mediation effects such as potentiation (e.g., Clarke et al., 1979; Rusiniak et al., 1979) rather than cue competition. Thus, although the results themselves are interesting and seem to be also problematic for division-of-the-limited-resource accounts of cue competition, his results are not conclusive with respect to this issue.

As mentioned in the introduction, several learning theories (e.g., Rescorla & Wagner, 1972) explain cue competition phenomena as the division of a limited resource among competing cues. These theories generate the prediction that responding to two cues competing with each other inevitably reflects a tradeoff, resulting in apparent conservation of total associative value to the US. For example, in a situation in which a discrete CS is competing with the context,

the associative strength of each stimulus changes so that at asymptote the sum of the associative strengths of the two stimuli become equal to a value determined by the US. Thus, a decrement in responding to one stimulus (e.g., the CS) should directly lead to an increment in responding to the other (i.e., the context) given that the US is physically unaltered. However, we found in our experiments violations of this tradeoff principle: Despite the fact that the US was the same for the two CS-US groups, both responding to the CS and responding to the context were weaker in the group that received conditioning with the longer CS (i.e., the Long group in Experiment 1), received CS-alone preexposure before conditioning (i.e., the Signal-Pre group in Experiment 2), or received CS-alone exposures during the ITI (i.e., the Partial group in Experiment 3) than they were in the corresponding control groups (i.e., the Short, the Signal, and the Continuous groups in Experiments 1, 2, and 3, respectively). Thus, these findings indicate that the total magnitude of conditioned responding is not determined uniquely by the physical characteristics of the outcome. That is, a reduction in responding to one cue does not always result in increased responding to the other cue. As discussed in the introduction, one alternative to the view that total associative strength to all cues conditioned in compound is conserved is provided by Miller and Matzel's (1988) comparator hypothesis, which assumes that cue competition occurs at test rather than at the time of acquisition and that conditioned responding to each of the two cues can vary directly as a consequence of manipulations of their within-compound association. In addition, the comparator hypothesis also readily explains the effect of posttraining deflation of the discrete CS on responding to the context observed in Experiment 3, whereas the simple acquisition-focused models have difficulty in explaining it.

These three experiments were originally designed to contrast the predictions of the comparator hypothesis with the view that explains cue competition as a division of some limited resource. The results of the experiments consistently supported the comparator view rather than the division-of-limited-resource account. However, this does not mean the comparator hypothesis is the only model that can explain the current results; some other theories can at least partly explain them. For example, models that explain various cue competition phenomena as a result of stimulus generalization decrement (e.g., Pearce, 1987), with minor modification, are able to explain the nontradeoff relationship found in these experiments. For example, if one assumes that responding to the context and to the CS are both determined by the amount of stimulus generalization to each from the compound stimulus of the CS and the context and that the use of CSs of longer duration, massive preexposure to the CS alone, and presentation of the CSs during the ITI all decreased conditioning to the CS-context compound, responding to both the context and the CS should be decreased simultaneously by these procedures. However, a problem of this line of reasoning is that these models cannot readily explain the recovery of responding to the context as a consequence of posttraining extinction of the CS observed in Experiment 3. Additionally, there are several contemporary learning models that explain the effect of posttraining deflation as the result of mechanisms other than the comparator process, such as an acquisition of an association between a physically absent target cue and the US (e.g., Dickinson & Burke, 1996; Van Hamme & Wasserman, 1994) or a recovery of attention to the target cue (e.g., Schmajuk & Larrauri, 2006) caused by manipulation of the competing cue.

It is noteworthy that Wagner's (1981) SOP model and its modification (Dickinson & Burke, 1996) provide an explanation of the present results that is competitive with that provided by the comparator hypothesis. The original SOP model hypothesizes several different mechanisms to explain cue competition phenomena, in addition to a division-of-limited-resource mechanism similar to the Rescorla-Wagner (1972) model. In the framework of SOP, the presentation of a stimulus causes an activation of its nodal elements into hypothesized memory states; the elements are first activated from an inactive memory state (I) into the most active memory state (A1), and then gradually decay over time into a relatively less active memory state (A2). Excitatory conditioning occurs only when the CS and the US nodes are activated simultaneously in the A1 state. When the CS is in the A1 state and the US is in the A2 state,

inhibitory conditioning occurs. Thus, when a CS and a US are paired, primarily excitatory but also inhibitory associations are formed between nodal elements of the CS and the US, and the resultant behavioral control by the CS is determined by the difference in excitatory and inhibitory associative effects. After the CS has formed an excitatory association with the US, presentation of the CS causes nodal elements of the US to be activated directly into the A2 state, and consequently there are fewer US elements available to be activated from the I state into the A1 state by the actual US presentation soon after the CS presentation. Behavioral control by the CS reaches asymptote when activation of the US elements activated directly into the A2 state by the CS presentation become strong enough that the new inhibitory associations formed by the US nodal elements activated into the A2 state by the CS presentation become equal to the new excitatory associations formed by the US elements activated into the A1 state by the actual US presentation. This asymptotic value does not change when a compound of multiple cues is paired with the US. The associations between the US and each member of the compound change until the total number of US elements activated directly into the A2 state by each member of the compound becomes large enough to form an inhibitory association between the compound CS and the US, which is equal to the excitatory association formed by the activation of the US elements into the A1 state. As a result, the excitatory association of the target CS with the US becomes weaker when it is paired in compound with other cues than when it is paired alone.

In addition to the division-of-limited-resource mechanism mentioned above, the SOP model includes several other mechanisms that contribute to cue competition. First, because the model assumes that the number of nodal elements that can be activated into the A1 state at one time is limited, there is a possibility that the presentation of a competing cue (i.e., the activation of its nodal elements into the A1 state) results in a smaller number of nodal elements of the target cue being activated into the A1 state. Second, similar to Miller and Matzel's (1988) comparator hypothesis, SOP assumes that simultaneous presentations of two competing cues lead to formation of a within-compound association between them. Furthermore, when a strong within-compound association is formed between two competing stimuli, the presentation of one competing cue causes activation of some of the other cue's nodal elements into the A2 state and vice versa. If nodal elements of a stimulus are activated into the A2 state, the number of the nodal elements of that stimulus available in the I state to be activated into the A1 state decreases, which results in impairment of associative acquisition between that stimulus and the US. With this latter mechanism, the SOP model can explain the central findings of the present experiments, that is, a nontradeoff relationship between a training context and a discrete cue. Specifically, when the CS is presented for a longer duration, is preexposed within the training context, or is presented alone during the ITI, the CS–context within-compound association becomes stronger because the CS and the context have more opportunity to become associated with each other. As a result, when the CS and the context are presented together, the CS activates some of the context's nodal elements into the A2 state and the context activates some of the CS's nodal elements into the A2 state. Consequently, both the CS and the context form weaker associations with the US.

A problem of the original SOP model is that it cannot readily explain the effect of posttraining manipulations such as the recovery of responding to the context caused by posttraining extinction of the CS observed in Experiment 3. SOP explains all learning phenomena as consequences of differential acquisition of the associations between each cue and the US and hypothesizes that associative strength changes only when the cue in question is physically presented (i.e., activated into the A1 state). Thus, manipulations of cues other than the target cue that take place after the completion of conditioning to the target cue should have no effect on responding to the target cue. However, there is a revision of SOP proposed by Dickinson and Burke (1996) that enabled SOP to account for the effects of many posttraining manipulations. They hypothesized that excitatory association can be formed not only when the

two associates are activated simultaneously into the A1 state but also when they are both in the A2 state. With this modification, SOP becomes capable of explaining the effects of posttraining extinction of a target CS's companion cue, including the observation of our Experiment 3 as new, indirectly learned associative formation between two absent stimuli (i.e., the target CS and the US).

As discussed above, there are several different ways to explain the results of our experiments. Therefore, these experiments are not sufficient to provide a clear conclusion concerning which model explains the cue competition effect most adequately. However, minimally it is clear that the assumption of some theories that cue competition is a result of the division of some resource is not universally correct. Inclusion of other mechanisms in addition to the division of some limited resource (e.g., Dickinson & Burke, 1996; Wagner, 1981) or a fundamentally different approach (e.g., Miller & Matzel, 1988; Pearce, 1987) seems necessary for a better accounting of cue competition phenomena.

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Figure 1.

The original comparator hypothesis. The three long arrows represent three hypothesized associations, the target cue–outcome association (Link 1), the target cue–comparator stimulus within-compound association (Link 2), and the comparator stimulus–outcome association (Link 3). Presentation of the target cue activates two representations of the outcome, the representation directly activated by the target cue through Link 1 and that indirectly activated through the comparator stimulus (through Links 2 and 3). The strengths of the outcome representation directly and indirectly activated are compared, and the strength of responding to the target cue is determined. Rectangles depict physical stimulus events and ovals depict representations of events not presented but activated by other stimuli. US = unconditioned stimulus.

Figure 2.

Results of Experiment 1. Black bars depict mean log latencies to complete the first cumulative 5 s of drinking in the context in which conditioning treatment occurred. Open bars depict mean log latencies to complete the first cumulative 5 s of drinking in the presence of Stimulus X in a neutral context. Error bars represent the standard errors of the mean. CS = conditioned stimulus; US = unconditioned stimulus.

Figure 3.

Results of Experiment 2. Black bars depict mean log latencies to complete first cumulative 5 s of drinking in the context in which conditioning treatment occurred. Open bars depict mean log latencies to complete the first cumulative 5 s of drinking in the presence of Stimulus X in a neutral context. Error bars represent the standard errors of the mean. CS = conditioned stimulus; US = unconditioned stimulus; signal-pre = signal-preexposure.

Figure 4.

Results of Experiment 3. The left panel depicts mean log latencies to complete the first cumulative 5 s of drinking in the context in which conditioning treatment occurred. The right panel depicts mean log latencies to complete the first cumulative 5 s of drinking in the presence of Stimulus X in a neutral context. Open bars represent the results of groups that did not receive extinction treatment of Stimulus X; black bars represent those of groups that received extinction treatment of Stimulus X after the conditioning phase. Error bars represent the standard errors of the mean. CS = conditioned stimulus; US = unconditioned stimulus; Ext = extinction.

Table 1

Design Summary of Experiment 1

Group	Conditioning (in Context 1)	Test context (in Context 1)	Test X (in Context 2)
CS	8 X (short) or 8 X (long)	Context 1	X
US	8 US	Context 1	X
Short	8 X (short)–US	Context 1	X
Long	8 X (long)–US	Context 1	X

Note. CS X was a click train presented for either a 25-s (long) or a 2.5-s (short) duration. The order of testing was counterbalanced within groups. In the CS group during conditioning, for half the subjects CS X was short, and for the other half it was long. CS = conditioned stimulus–alone control; US = unconditioned stimulus–alone control; short = US presentation with CS X of short duration; long = US presentation with CS X of long duration; X = target CS; US = footshock.

Table 2

Design Summary of Experiment 2

Group	Phase 1 (in Context 1)	Phase 2 (in Context 1)	Test context (in Context 1)	Test X (in Context 2)
CS	400 X or 400 Y	4 X	Context 1	X
US	400 X or 400 Y	4 US	Context 1	X
Signal	400 Y	4 X-US	Context 1	X
Signal-Pre	400 X	4 X-US	Context 1	X

Note. CS X and Y were a click train and a tone, counterbalanced within groups. The order of testing was counterbalanced within groups. In the CS and US groups, during Phase 1 half the subjects were exposed to CS X and the other half were exposed to CS Y. CS = conditioned stimulus-alone control; US = unconditioned stimulus-alone control; Signal = US presentation with CS X; Signal-Pre = US presentation with CS X, which had been massively preexposed in Phase 1; X = target CS; Y = an irrelevant stimulus; US = footshock.

Table 3

Design Summary of Experiment 3

Group	Conditioning (in Context 1)	Extinction (in Context 2)	Test context (in Context 1)	Test X (in Context 2)
US	8 US	—	Context 1	X
Continuous	8 X-US	—	Context 1	X
Partial	8 X-US / 72 X	—	Context 1	X
US Ext	8 US	800 X	Context 1	X
Continuous Ext	8 X-US	800 X	Context 1	X
Partial Ext	8 X-US / 72 X	800 X	Context 1	X

Note. CS X was a click train. US = unconditioned stimulus-alone control, Continuous = US presentation with each conditioned stimulus (CS) X; Partial = US presentation with CS X and intermingled CS X-alone exposures, consisting of 10% partial reinforcement schedule; Ext = CS-alone exposures following conditioning phase; X = target CS; US = footshock.