An Inhibitory Within-Compound Association Attenuates Overshadowing

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According to the comparator hypothesis (Miller & Matzel, 1988), cue competition depends on the association between a target stimulus (X) and a competing cue (e.g., an overshadowing cue [A]). Thus, it was expected that overshadowing would be reduced by establishing an inhibitory-like relationship between X and A before compound conditioning. In three lever press suppression experiments with rats, this expectation was supported. Experiment 1 showed that establishing an inhibitory X-A relationship reduced overshadowing. In Experiment 2, degrading the inhibitory-like relationship before conditioning allowed reinforced AX compound trials to result in overshadowing. Experiment 3 replicated the results of Experiment 2 when the inhibitory relationship was degraded after compound conditioning. The results support the view that within-compound associations are necessary not only for retrospective revaluation, but also for conventional cue competition.

Keywords: overshadowing, cue competition, within-compound associations, memory expression

When two stimuli are repeatedly presented conjointly most investigators assume that a within-compound association is formed between the internal representations of the stimuli (e.g., Rescorla & Cunningham, 1978; Rescorla & Durlach, 1981). However, most traditional theories of associative learning (e.g., Mackintosh, 1975; Pearce, 1987; Pearce & Hall, 1980; Rescorla & Wagner, 1972) deny any role to within-compound associations in conventional cue competition (e.g., overshadowing or forward blocking; but see below for a discussion of Wagner's [1981] SOP model and variants of this model). That is, the within-compound association formed when a target cue and a nontarget cue are presented conjointly is considered to be of little or no consequence in accounting for conventional cue competition. For example, overshadowing treatment (Pavlov, 1927) typically consists of presentations of a compound stimulus, composed of a target conditioned stimulus (CS X) and a more salient nontarget conditioned stimulus (CS A), paired with an unconditioned stimulus (US; i.e., AX-US pairings). The presence of CS A during training of CS X impairs subsequent responding to X relative to a control condition trained with X-US pairings. Traditional theories suggest that the nontarget CS A prevents the target CS X from acquiring an appreciable amount of associative strength. Notably, traditional theories take this view regardless of the status of the within-compound association between X and A. However, relatively recent findings have suggested that the within-compound association might play an important role in cue competition (e.g., Chapman, 1991; Wasserman & Berglan, 1998; Williams, Travis, & Overmier, 1986). Kaufman and Bolles (1981) first suggested a role for the within-compound association in conventional cue competition when they conducted a posttraining manipulation of the nontarget cue in an overshadowing procedure with rats. They extinguished (i.e., associatively deflated) CS A after overshadowing treatment for some of their subjects, which resulted in increased responding to CS X at test; that is, recovery from overshadowing was observed. This phenomenon is an instance of behavioral retrospective revaluation. Retrospective revaluation more generally refers to the observation that the response-eliciting potential of a target CS can be altered (revalued) following completion of training with the target CS, even if the target CS is absent on that trial. Importantly, most studies of retrospective revaluation indicate it occurs only if the target and nontarget stimuli maintain a within-compound association. Behavioral retrospective revaluation and related findings prompted the development of new theoretical approaches to associative learning. These approaches attributed a critical role to the within-compound association between the target and companion cues in retrospective revaluation (e.g., Dickinson & Burke, 1996; Miller & Matzel, 1988; Van Hamme & Wasserman, 1994) and also in conventional cue competition (Miller & Matzel, 1988).

One of the earliest accounts concerning the influence of within-compound associations on overshadowing was the comparator hypothesis of Miller and Matzel (1988). These authors proposed that the processing responsible for cue competition occurs at test

rather than during acquisition. Specifically, they posited that pairings of a compound stimulus and a US, not only promote associations between the nontarget stimulus and the US and between the target stimulus and US, but also a within-compound association between the target and nontarget stimuli, which contributes to a reduction in conditioned responding (i.e., cue competition) on a later test of the target CS. Because the comparator hypothesis views cue competition phenomena as arising from processing that occurs at test, we shall refer to it as a performance-focused model. Importantly, the comparator hypothesis assumes that contiguity is necessary and sufficient for associative acquisition, and that conditioned responding to the target CS at the time of testing depends on the strength of the target CS-US association relative to the associative strengths of other stimuli that were present during training with the target CS (comparator stimuli; e.g., the context and/or other discrete stimuli). For example, in an overshadowing procedure, the overshadowed CS (X) forms an association with the US (i.e., the X-US association; Link 1), as well as with the overshadowing CS A (i.e., the X-A association; Link 2), which, in turn, develops its own association with the US (i.e., the A-US association; Link 3). At test, the product of the X-A association and the A-US association attenuates responding to CS X that is otherwise elicited as a result of the X-US association. Basically, the comparator hypothesis posited an essential role for the within-compound association (i.e., Link 2), not only in retrospective revaluation phenomena (e.g., recovery from overshadowing and backward blocking) but also in conventional cue competition (e.g., overshadowing and forward blocking).

More recently, two acquisition-focused accounts of retrospective revaluation have posited a role for within-compound associations in retrospective revaluation. One is Van Hamme and Wasserman's (1994) modification of Rescorla and Wagner's (1972) model, and the other is Dickinson and Burke's (1996) modification of Wagner's (1981) SOP model (hereafter MSOP). Both of these revised models assume that not only cues that are present (as postulated by their predecessors), but also cues that are absent can have their association with the US updated on a given trial, provided that they are associated with a cue that is present on that trial. Specifically, absent cues are assumed to gain associative strength if their companion stimulus is associatively deflated (i.e., extinguished) and, conversely, lose associative strength if their companion stimulus is associatively inflated (i.e., given additional pairings with the US). Importantly, the acquisition-focused models of Dickinson and Burke and of Van Hamme and Wasserman assume that within-compound association are critical for the occurrence of retrospective revaluation, but not for the occurrence of conventional cue competition.

Relevant to the present research, Miller and Matzel's (1988) model differs from the models of Dickinson and Burke (1996) and of Van Hamme and Wasserman (1994) in that it asserts that the within-compound association between the target CS and competing CS plays a necessary role in conventional cue competition. The predictions of these two types of models were examined by Melchers, Lachnit, and Shanks (2004), who showed, in several cue competition paradigms, an asymmetry in the role of within-compound associations in learning about present and absent cues. The study of Melchers et al. used a human contingency judgment task, in which participants are given, on a trial-by-trial basis, information concerning foods consumed by a fictitious patient

(candidate causes, analogous to cues or CSs), which potentially results in an allergic reaction (an outcome, analogous to a US). After such training participants are shown the target cue (food) alone and asked to rate its predictive or causal relation to the outcome (an allergic reaction). In Melchers et al.'s Experiment 1, a memory test was additionally used to assess within-compound associations after forward blocking (A-Outcome pairings followed by AX-Outcome pairings) and backward blocking (AX-Outcome pairings followed by A-Outcome pairings) as well as after prevention of overshadowing (A-alone followed by AX-Outcome) and release from overshadowing (AX-Outcome followed by A-alone). They found that retrospective revaluation was positively correlated with the participants having previously formed an A-X within-compound association. However, in conventional cue competition this correlation, although positive, was not statistically significant. These findings are supportive of acquisition-focused accounts, but inconsistent with the performance-focused account of the comparator hypothesis. Other human contingency learning studies directly manipulated acquisition of within-compound associations and reached conclusions akin to those of Melchers et al. (e.g., Aitken, Larkin, & Dickinson, 2001; Larkin, Aitken, & Dickinson, 1998; but see Vandorpe, de Houwer, and Beckers [2007] for evidence that under some conditions conventional cue competition in human contingency learning is positively correlated with the strength of the within-compound association). Importantly, the critical result of these experiments was that retrospective revaluation seemed more dependent upon within-compound associations than cue competition, leaving the possibility that within-compound associations play a role in cue competition, albeit weaker than in retrospective revaluation. Thus, the remaining question is, if we independently manipulated the strength of the within-compound association, would this impact cue competition?

A problem with manipulating the strength of the within-compound association is that many treatments potentially confound changes in the strength of the within-compound association with changes in CS-US associations. The strategy we adopted in the present experiments was inspired by several recent studies using conditioned taste aversion paradigms. These studies have shown that alternating exposures to two compounds of flavors (AC and XC) sharing a common element (C) results in inhibitory learning to X when A is later reinforced (e.g., Espinet, Iraola, Bennett, & Mackintosh, 1995; for a replication with audiovisual stimuli, see Leonard & Hall, 1999; for similar findings with human subjects, see Artigas, Chamizo, & Peris, 2001). This phenomenon is considered an example of conditioned inhibition established between two neutral stimuli, X and A. This is so because each unique element (A and X) comes to predict the absence of the other element: during AC/XC training, on AC trials A signals the absence of X, and on XC trials X signals the absence of A. Notably, it has been demonstrated that this procedure produces reciprocal inhibition between the unique elements (here A and X; see Dwyer, Bennett, & Mackintosh, 2001, for assessment of such inhibition using a summation test; see Dwyer & Mackintosh, 2002, for assessment of such inhibition using a retardation test). The present experiments used a variant of this alternating exposure to compounds of neutral stimuli sharing a common element to establish an inhibitory-like relationship between the target CS X and the overshadowing cue A before the AX-US overshadowing treatment.

In summary, acquisition-focused theories, both traditional and those capable of accounting for retrospective revaluation, do not

attribute an essential role to the within-compound association in the occurrence of conventional cue competition and, consequently, predict that the establishment of an inhibitory-like relationship between A and X should have little impact on the subsequent observation of overshadowing. If the establishment of an inhibitory-like relationship between A and X were found to reduce overshadowing, these results would be suggestive of a critical contribution of within-compound associations to conventional cue competition.

Experiment 1

The purpose of Experiment 1 was to assess the role of the X-A within-compound association in conventional cue competition, specifically overshadowing. Half of the rats received treatment to establish an inhibitory-like relationship between CSs A and X (i.e., AC/XC training). The remaining half received equal exposure to X and A, but without a common element being present on the two types of trials (i.e., AD/XC). Orthogonal to this treatment, half of the rats subsequently received overshadowing treatment (i.e., AX-US pairings), whereas the other half received simple elemental conditioning of CS X (i.e., X-US pairings). Table 1 summarizes the 2×2 factorial design of Experiment 1.

Method

Subjects. The subjects were 24 male (225–340 g) and 24 female (175–225 g) adult experimentally naïve Sprague–Dawley rats, randomly assigned to one of four groups ($ns = 12$) counterbalanced for sex. They were individually housed in wire mesh cages in a vivarium maintained on 16:8-hr light:dark cycle. From the time of weaning until the start of the experiment, all subjects were handled for 30 seconds, three times per week. The experimental manipulations occurred approximately midway through the light portion of the diurnal cycle. A progressive water deprivation schedule was imposed over the week before the beginning of the experiment until water availability was limited to 30 minutes per day.

Apparatus. The apparatus consisted of 12 chambers, each measuring $30 \times 30 \times 27$ cm (l $\times$ w $\times$ h). The sidewalls of the chamber were made of stainless steel sheet metal, and the front wall, back wall, and ceiling of the chamber were made of clear

Table 1
Design of Experiment 1

Group	Preexposure	Phase 1	Phase 2	Test
Inhib-OV	2 A / 2 X	32 AC / 32 XC	4 AX-US	8 X
NoInhib-OV	2 A / 2 X	32 AD / 32 XC	4 AX-US	8 X
Inhib-Con	2 A / 2 X	32 AC / 32 XC	4 X-US	8 X
NoInhib-Con	2 A / 2 X	32 AD / 32 XC	4 X-US	8 X

Note. 'Inhib' and "NoInhib" denote, respectively, the occurrence and nonoccurrence of inhibition treatment between CSs X and A during Phase 1. "OV" and "Con" denote, respectively, overshadowing treatment (X being reinforced in compound with A) and overshadowing-control treatment (X being reinforced elementally) during Phase 2. The numbers preceding the letters indicate the total number of presentations of the stimuli in that phase. Slashes separate interspersed trials. Stimuli A and X were a complex tone and a click train, respectively. Stimuli C and D were a buzzer and a flashing light, counterbalanced.

Plexiglas. Each chamber was dimly lit by a #1820 incandescent house light. On one metal wall of each chamber, there was an operant lever and adjacent to it a niche (4.5 × 4.0 × 4.5 cm) centered 3.3 cm above the floor through the top of which a solenoid-driven valve could deliver 0.04 ml of water into a cup at the bottom of the niche. Chamber floors were stainless steel grids, 4-mm in diameter, spaced 1.7 cm a part center-to-center, connected with NE-2 neon bulbs, which allowed constant-current 0.5-s, 1.0-mA footshock US to be delivered by means of a high voltage AC circuit in series with a 1.0-MΩ resistor. All chambers were housed in sound and light attenuating environmental chests. Each environmental chest was equipped with a buzzer and three 45-Ω speakers widely separated on the inside walls of the environmental chest. Each speaker could deliver a different auditory stimulus. One speaker mounted on the right sidewall was used to deliver a complex tone stimulus (3000 and 3200 Hz), 15 dB above background, which served as CS A. A second speaker mounted on the back sidewall of the experimental chamber was used to deliver a click stimulus (6/s) 3 dB above background, which served as CS X (note that A was more intense than X to encourage overshadowing). A third speaker mounted on the left sidewall of the chamber was used to deliver a white noise stimulus 6 dB above background, which served as a 0.5-s signal for water reinforcement. The buzzer mounted on the front wall of the chambers was used to deliver a buzzing sound 6 dB above background, which served as stimuli C or D, counterbalanced within groups. A flashing visual stimulus consisted of a 75-W light (0.5-s on/0.5-s off) nominal at 120 VAC, but driven at 100 VAC, mounted on the interior back side of each environmental chest approximately 30 cm from the center of the experimental chamber also served as stimuli C or D, counterbalanced within groups. Ventilation fans in each enclosure provided a constant 74-dB background noise. All CS durations (except the white noise) were 60 seconds.

Procedure

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

Preexposure. On Day 6, all subjects were exposed to two nonreinforced presentations of CS A and two nonreinforced presentations of CS X. The nonreinforced presentations of CS X occurred at 10 and 50 minutes into the 60-min session. The nonreinforced presentations of CS A occurred at 25 and 35 minutes into the 60-min session. The intent of these presentations was to reduce any possible configuring during later compound stimulus presentations.

Inhibition training. On Days 7 through 14, two different schedules (1 and 2) were used on alternate days. Schedule 1 was used on Days 7, 9, 11, and 13 and Schedule 2 was used on Days 8, 10, 12, and 14. During both schedules, all subjects received four daily nonreinforced presentations of the XC compound interspersed with either four daily nonreinforced presentations of the AC compound (Groups Inhib-OV and Inhib-Con) or four daily nonreinforced presentations of the AD compound (Groups NoInhib-OV and NoInhib-Con) during a 60-min daily session. In Schedule 1, AC or AD compound presentations occurred at 11, 26, 35, and 50 minutes into the sessions, whereas the XC compound presentations occurred at 5, 19, 30, and 44 minutes into the sessions. In Schedule 2, the AC or AD compound presentations occurred at 8, 23, 33, and 47 minutes into the sessions, whereas the XC compound presentations occurred at 15, 28, 40, and 54 minutes into the session. The number of exposures given during this phase of the experiment was borrowed from Leonard and Hall (1999).

Overshadowing training. On Days 15 and 16, Groups Inhib-OV and NoInhib-OV received two daily reinforced presentations of the AX compound and Groups Inhib-Con and NoInhib-Con received two daily reinforced presentations of CS X alone. The AX presentations or CS X presentations occurred at 15 and 45 minutes into the 60-min session, with the US being presented immediately after termination of AX or X.

Reacclimation. On Days 17 and 18, all groups experienced daily 60-min sessions that allowed uninterrupted lever pressing. This served to restabilize baseline lever pressing which might have been disrupted by the footshocks. Animals that registered less than 50 responses on Day 17 were given an extra 30-min session later on that day.

Test. On Days 19 and 20, subjects were tested for conditioned suppression of lever pressing in the presence of CS X within a 30-min test session. In each session, there were four presentations of X alone, each 60 seconds in duration. The presentations of X occurred 8, 15, 23, and 28 minutes after placement in the operant chamber. A single suppression ratio (Annau & Kamin, 1961) was calculated for each test day combining all four of the daily test trials to determine conditioned suppression to the CS. The number of lever presses emitted during the four 120-s intervals immediately before the onset of the test trial CS and during the four 60-s test trial CS presentations were recorded. The suppression ratio for each subject consisted of the total number of lever presses made during the presentations of the CS divided by the sum of that number plus half the total number of lever presses made during the 120-s intervals that immediately preceded the 60-s CSs (i.e., lever press$_{CS}$/ [lever press$_{CS}$ + 0.5 lever press$_{Pre-CS}$]). We used a 120-s baseline measure as opposed to a 60-s measure based on the assumption that a larger sample of time would better assess baseline rates of responding.

Results and Discussion

The results of Experiment 1 are depicted in Figure 1. Inspection of this figure suggests that the inhibitory-like treatment attenuated overshadowing. This impression was confirmed by the following analyses. A 2 (OV vs. Con) × 2 (Inhib vs. No Inhib) × 2 (Test Day) analysis of variance (ANOVA) was used to assess baseline lever pressing just before onset of CS X during the test sessions. The number of lever presses emitted during the four 120-s inter-
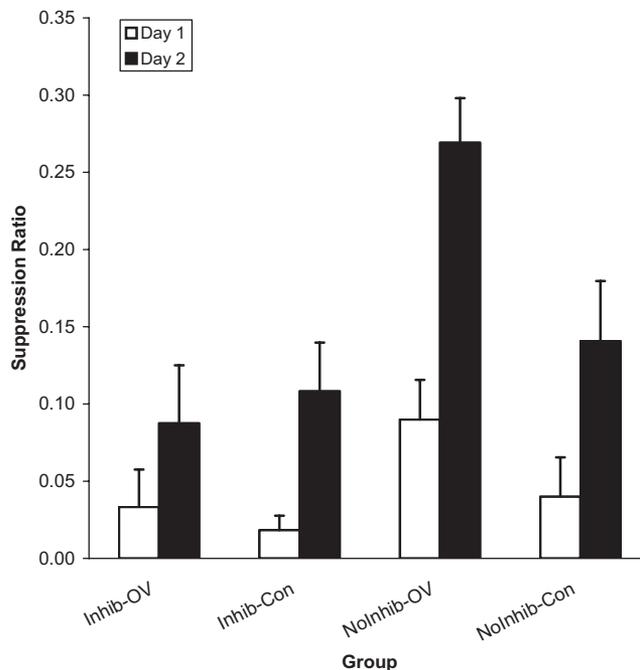
Figure 1. Mean suppression ratio in Experiment 1 for each of the two days of testing of Cue X (i.e., blocks of four trials per day). Groups Inhib-OV, Inhib-Con, and NoInhib-Con were those in which strong suppression to cue X was expected (see Table 1). Group NoInhib-OV was the group in which weak responding to X was expected because of overshadowing of Cue X by Cue A if overshadowing depends on an excitatory within-compound association between X and A. The brackets represent the standard error of the means.

vals immediately before the onset of the test trial CS was divided by eight to calculate the baseline response rate. The means on the first test day for Groups Inhib-OV, Inhib-Con, NoInhib-OV, and NoInhib-Con were 21.88, 23.71, 26.20, and 17.37 lever presses per minute, respectively. The means on the second test day for Groups Inhib-OV, Inhib-Con, NoInhib-OV, and NoInhib-Con were 21.75, 17.27, 25.00, and 17.77 lever presses per minute, respectively. The analysis of these means revealed no main effects or interactions, all $ps > .27$. A similar ANOVA was used to assess conditioned suppression of lever press responding during the presentations of CS X across the 2 days of testing. This analysis revealed a main effect of inhibition treatment, $F(1, 44) = 7.87$, $MSE = 0.13$, $p < .01$, a main effect of test day, $F(1, 44) = 70.37$, $MSE = 0.27$, $p < .001$, an Inhibition Treatment × Test Day interaction, $F(1, 44) = 7.22$, $MSE = 0.03$, $p < .05$, and a three-way interaction, $F(1, 44) = 5.10$, $MSE = 0.02$, $p < .05$. The three-way interaction suggested that test day influenced the potential interaction between overshadowing and inhibition treatment. Examination of the day-by-day data revealed a floor effect on the first test day that vanished on the second test day presumably because of partial extinction of associations to X on the first test day. Hence, an ANOVA was performed on the data from Test Day 2 alone, which appeared justified because all subjects received exactly the same exposure to X on Test Day 1. This ANOVA detected an Overshadowing Treatment × Inhibition Treatment interaction, $F(1, 44) = 4.70$, $MSE = 0.01$, $p < .05$, on the second test day. Pairwise

comparisons revealed greater overshadowing in the condition that did not receive inhibition treatment between X and A, relative to the condition that did receive inhibition treatment. That is, Group NoInhib-OV exhibited weaker suppression of lever press responding than its control group, NoInhib-Con, $F(1, 44) = 6.95, p < .05$, thereby indicating the occurrence of overshadowing in the NoInhib condition. In contrast, comparable suppression was observed in Groups Inhib-OV and Inhib-Con, $F < 1$, indicating that overshadowing did not occur in the Inhib condition. Finally, weaker suppression was found in Group NoInhib-OV than in Group Inhib-OV, $F(1, 44) = 10.45, p < .01$. These comparisons indicate that, on the second test day, the interaction arose from attenuated overshadowing in Group Inhib-OV relative to Group NoInhib-OV.

The results of Experiment 1 support the view that within-compound associations are important for conventional cue competition. An extension of the comparator hypothesis (the extended comparator hypothesis [ECH; Denniston, Savastano, & Miller, 2001]), which posits higher-order comparator effects, can account for the undermining of overshadowing in the present situation (see the General Discussion for elaboration). Basically, the extended comparator hypothesis explains the effect of pretraining on overshadowing by assuming that separately preexposing A and X with a common element reduced the potential of X to activate a representation of A at test, thereby attenuating overshadowing of X by A. However, the present results can also be accounted for by Wagner's (1981) SOP model, although not through any process that is essential for the model to explain conventional cue competition. Importantly, both the ECH and SOP explain the present results by assuming that impairing the development of within-compound associations reduced competition between A and X.

Overall, the results of Experiment 1 suggest that the establishment of an inhibitory-like relationship between the overshadowing CS (A) and overshadowed CS (X) before overshadowing treatment attenuated overshadowing. Experiment 1 did not directly assess the putative inhibitory X-A within-compound association. However, our procedure was highly similar to that of the several prior studies that found alternating AC/XC trials establishes an inhibitory-like relationship between A and X (e.g., Dwyer et al., 2001; Dwyer & Mackintosh, 2002).

Experiment 2

Based on the results of Experiment 1, it appears that an effective excitatory within-compound association must be in force for overshadowing to occur. These results are consistent with the extended comparator hypothesis, which attributes a critical role to the within-compound association at the time of testing for the occurrence of conventional cue competition phenomena. Although the results of Experiment 1 are suggestive, restoration of overshadowing achieved by posttraining attenuation of the putative inhibitory relationship between X and A would further strengthen this conclusion. Therefore, the purpose of Experiment 2 was to further test the extended comparator hypothesis' account of the results of Experiment 1. We took advantage of a prior finding by Urushihara, Wheeler, Pineño, and Miller (2005) to test this prediction. They observed that massive exposure to the common element alone (i.e., extinction of the common element) following alternating exposure of two compounds sharing the common element undermines the inhibitory-like relationship between X and A.[1] In terms of the

extended comparator hypothesis, such an effect is explained as a result of a weakening of the higher-order associations. Presenting C-alone in Phase 2 should presumably weaken both A-C and X-C associations, thereby allowing Link 2 to be better expressed at test of X. Hence, the US-representation indirectly activated by X through Links 2 and 3 should more strongly suppress the expression of the direct X-US association (Link 1). This should result in restoration of overshadowing.

In Experiment 2, the common element, C, was presented alone between inhibitory training and overshadowing treatment to determine if this manipulation would restore the potential of A to subsequently overshadow X. To achieve this objective, subjects in Experiment 2 were assigned to one of five groups (see Table 2). Groups NoInhib-OV and NoInhib-Con were compared to one another to demonstrate overshadowing. Group Inhib-OV was compared to Group NoInhib-OV to replicate the attenuation of overshadowing seen in Experiment 1 when an inhibitory-like relationship is established between X and A. The critical comparison in Experiment 2 was between Groups Inhib-OV and Inhib-Ext-OV. This comparison was critical because the extended comparator hypothesis predicts behavior indicative of restored overshadowing (i.e., less responding to the target cue X) in Group Inhib-Ext-OV. That is, according to the extended comparator hypothesis, C-alone trials should attenuate the inhibitory-like association, thereby allowing the A-X association to be expressed as the appearance of overshadowing. Finally, Groups NoInhib-Con and NoInhib-Ext-Con were compared to control for the possibility that the extinction treatment itself directly impacted responding to X.

Method

Subjects and apparatus. Subjects were 30 male (253–401 g) and 30 female (182–296 g) Sprague–Dawley rats housed and maintained as in Experiment 1, randomly assigned to one of five groups (ns = 12) counterbalanced for sex. The apparatus was the same as in Experiment 1.

Procedure

The procedure was identical to Experiment 1 except for the addition of an extinction treatment phase (Phase 2), immediately before overshadowing treatment, during which the common element (C) or an alternative stimulus (D), was presented alone (see Table 2). Specifically, subjects in Groups Inhib-Ext-OV and NoInhib-Ext-Con received 72 nonreinforced presentations of the common element, C, on each of the three days of this phase (Days 15–17). Subjects in Groups NoInhib-OV and NoInhib-Con received 72 nonreinforced presentations of A's companion stimulus (i.e., D- alone trials) each day of extinction treatment. Subjects in Group Inhib-OV also received 72 nonreinforced presentations of D each day. The nonreinforced presentations of stimuli C or D occurred every 1.2 minutes within a 90-min session. Overshadow

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[1] A similar procedure has also proven effective in reducing conditioned inhibition in other studies using preparations more similar to this present one. For example, Hallam, Matzel, Sloat, and Miller (1990) and Lysle and Fowler (1985) both found that posttraining extinction of the common element used in conditioned inhibition training attenuated behavior indicative of inhibition.

Table 2
Design of Experiment 2

Group	Preexposure	Phase 1	Phase 2	Phase 3	Test
Inhib-Ext-OV	2 A / 2 X	32 AC / 32 XC	216 C	4 AX-US	8 X
Inhib-OV	2 A / 2 X	32 AC / 32 XC	216 D	4 AX-US	8 X
NoInhib-OV	2 A / 2 X	32 AD / 32 XC	216 D	4 AX-US	8 X
NoInhib-Con	2 A / 2 X	32 AD / 32 XC	216 D	4 X-US	8 X
NoInhib-Ext-Con	2 A / 2 X	32 AD / 32 XC	216 C	4 X-US	8 X

Note. 'Inhib' and "NoInhib" denote, respectively, the occurrence and nonoccurrence of inhibition treatment between CSs X and A during Phase 1. "OV" and "Con" denote, respectively, overshadowing treatment (X being reinforced in compound with A) and overshadowing-control treatment (X being reinforced elementally) during Phase 3. "Ext" denotes the occurrence during Phase 2 of nonreinforced presentations of the common element (C) that was used to establish the inhibitory-like relationship between X and A in Phase 1. The numbers preceding the letters indicate the total number of presentations of the stimuli in that phase. Slashes separate interspersed trials. Stimuli A and X were a complex tone and a click train, respectively. Stimuli C and D were a buzzer and a flashing light, counterbalanced.

ing treatment occurred on Days 18 and 19. Reacclimation took place on Days 20 through 22, and testing with CS X occurred on Days 23 and 24.

Results and Discussion

The results of Experiment 2 depicted in Figure 2 show two critical differences. First, as in Experiment 1, the establishment of an inhibitory-like relationship between X and A before overshadowing treatment attenuated overshadowing. Second, and of focal importance, is that nonreinforced presentations of C, the common element previously used to establish the putative inhibitory rela-
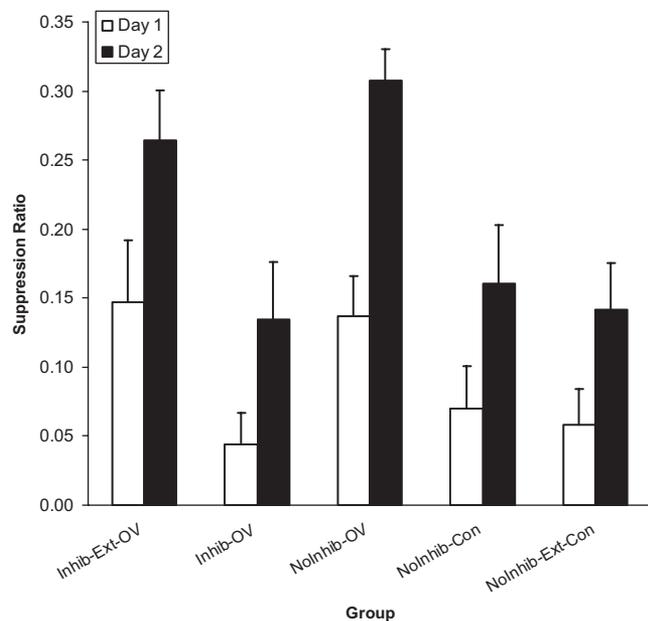

Figure 2. Mean suppression ratio in Experiment 2 for each of the two days of testing of Cue X (i.e., blocks of four trials per day). Groups Inhib-OV, NoInhib-Con, and NoInhib-Ext-Con were those in which strong suppression to Cue X was expected (see Table 2). Groups NoInhib-Ext-OV and NoInhib-OV were the groups in which weak suppression to X was expected because of overshadowing of Cue X by Cue A if overshadowing depends on a within-compound association between X and A. The brackets represent the standard error of the means.

tionship between X and A, resulted in restoration of overshadowing. These impressions were confirmed by the following analyses. A 5 (Group) x 2 (Test Day) ANOVA was used to assess baseline lever pressing just before onset of CS X on the test trials. The baseline response rate was calculated in the same manner as Experiment 1. The means on the first test day for Groups Inhib-Ext-OV, Inhib-OV, NoInhib-OV, NoInhib-Con, and NoInhib-Ext-Con were 27.25, 18.43, 17.26, 22.95, and 16.17 lever presses per minute, respectively. The means on the second test day for Groups Inhib-Ext-OV, Inhib-OV, NoInhib-OV, NoInhib-Con, and NoInhib-Ext-Con were 27.54, 21.32, 18.65, 20.26, and 15.81 lever presses per minute, respectively. Statistical analysis revealed no main effects or interactions, all $ps > .05$. A similar ANOVA was used to assess suppression ratios during the test presentations of CS X across the two days of testing. This analysis revealed a main effect of group, $F(4, 55) = 3.87$, $MSE = .09$, $p < .01$, and a main effect of test day, $F(1, 55) = 112.66$, $MSE = .37$, $p < .001$, but only a tendency toward a Group x Test Day interaction, $F(4, 55) = 2.44$, $MSE = .01$, $p < .06$, which eludes to a floor effect on the first test day similar to that observed in Experiment 1. To determine the source of these effects, pairwise comparisons were conducted. These revealed that overshadowing occurred in the condition in which inhibition treatment was not administered, but only on the second test day. That is, on Test Day Group NoInhib-OV displayed less suppression than Group NoInhib-Con, $F(1, 55) = 8.36$, $p < .01$, which indicates that overshadowing occurred. A second comparison between Groups NoInhib-OV and Inhib-OV found that overshadowing was attenuated by prior X-A inhibition training, $F(1, 55) = 11.65$, $p < .01$. Of importance is the comparison between Groups Inhib-OV and Inhib-Ext-OV, which revealed that overshadowing was restored by extinction of the common element from inhibition training, $F(1, 55) = 6.56$, $p < .05$. Finally, a comparison between Groups NoInhib-Con and NoInhib-Ext-Con showed that the extinction treatment itself did not directly impact responding to X, $p > .73$.

Overall, Experiment 2 demonstrated that overshadowing was restored when the common element used during inhibition treatment was presented alone, thereby presumably extinguishing the X-C and C-A associations. These results are consistent with the performance-focused view that the attenuated overshadowing observed when an inhibitory-like relationship exists between A and X results from information processing that occurs at test, rather

than enhanced acquisition of an X-US association. These results were anticipated by both the extended comparator hypothesis and Dickinson and Burke's (1996) MSOP, while they are inconsistent with Wagner's (1981) SOP model. According to MSOP, which provides an acquisition-focused account of Experiment 1, C-alone presentations strengthened excitatory A-X associations, functioning to reverse the processes responsible for the weak overshadowing observed in Experiment 1.

Experiment 3

The purpose of Experiment 3 was to determine whether the critical result of Experiment 2 reflects processing at the time of test or whether the C-alone presentations altered processing of A and X during compound conditioning. In Experiment 2 extinction of C occurred before overshadowing treatment. Thus, C-alone presentations could have affected processing at the time of test or during subsequent compound conditioning. As a performance-focused model, the extended comparator hypothesis makes the same prediction if extinction of C follows overshadowing treatment. In contrast, the acquisition-focused MSOP model asserts that C-alone presentations can only impact responding to X by altering processing of the stimulus during subsequent AX-US trials. Thus, in Experiment 3, extinction of C was administered after compound conditioning. Based on the extended comparator hypothesis (Denniston et al., 2001), we expected this manipulation to decrease responding elicited by the target CS at test in Group Inhib-OV-Ext, relative to Group Inhib-OV. However, extensive prior research in our laboratory has found that once the target stimulus has come to control behavior its response potential is relatively insensitive to further manipulations of comparator stimuli in the absence of the target (e.g., Miller, Hallam, & Grahame, 1990). Subsequent research found that using a sensory preconditioning procedure can circumvent this problem (e.g., Denniston, Miller, & Matute, 1996). This is because a sensory preconditioning procedure permits associative manipulations of a companion stimulus after target training has been completed, but before the phase in which a biologically significant US is first introduced. Therefore, the experimental manipulations of Experiment 3 were embedded in a sensory preconditioning procedure.

Method

Subjects and apparatus. Subjects were 30 male (285–396 g) and 30 female (212–260 g) Sprague–Dawley rats, randomly assigned to one of five groups (ns = 12) counterbalanced for sex, housed and maintained as in Experiments 1 and 2. The apparatus was the same as in Experiments 1 and 2 except that a 0.5-s low frequency, complex tone stimulus (500 and 600 Hz), 6 dB above background, served as the signal for water delivery and the white noise stimulus (5-s duration; 6 dB above background) served as the outcome (S) during overshadowing treatment (see Table 3). Our equipment had a limited number of audio outputs that precluded our presenting the high tone, which served as A, and the low tone, which served as the signal for water delivery, in the same session. Consequently, treatment (Phases 1–4) was administered off line (i.e., levers and water reinforcement were not available).

Procedure

Other than treatment being administered off line, treatment being embedded in a sensory preconditioning procedure (including Phase 4 in which the first-order stimulus was reinforced), and the stated changes in stimuli, the procedure was identical to that of Experiment 2 save that extinction of the common element, C, occurred after second-order overshadowing treatment (see Table 3). During Phase 2 (Days 15 and 16), Groups Inhib-OV-Ext, Inhib-OV, and NoInhib-OV received two daily AX-S trials and Groups NoInhib-Con and NoInhib-Con-Ext received two daily X-S presentations. The AX-S and X-S presentations occurred at 15 and 45 minutes into the 60-min session, with the surrogate outcome (S) being presented immediately after termination of AX or X. In Phase 4 (Days 20 and 21), all subjects were exposed to four daily S-US delay-conditioning trials within a daily 60-min session. These pairings allowed S to accrue biological significance, making assessment of the X-S association possible. During these trials, the 5-s white-noise stimulus (S) was paired with a 0.7-s, 1.0-mA footshock, which was initiated 0.7-s before the termination of the white noise; thus, the white noise and the footshock terminated at the same time. All groups were exposed to S-US presentations 11, 27, 39, and 54 minutes into each of the two training sessions. Reacclimation to lever pressing for water took place on Days 22–24, and testing with CS X occurred on Days 25 and 26.

Table 3
Design of Experiment 3

Group	Preexposure	Phase 1	Phase 2	Phase 3	Phase 4	Test
Inhib-OV-Ext	2 A, 2 X	32 AC / 32 XC	4 AX-S	216 C	8 S-US	8 X
Inhib-OV	2 A, 2 X	32 AC / 32 XC	4 AX-S	216 D	8 S-US	8 X
NoInhib-OV	2 A, 2 X	32 AD / 32 XC	4 AX-S	216 D	8 S-US	8 X
NoInhib-Con	2 A, 2 X	32 AD / 32 XC	4 X-S	216 D	8 S-US	8 X
NoInhib-Con-Ext	2 A, 2 X	32 AD / 32 XC	4 X-S	216 C	8 S-US	8 X

Note. 'Inhib' and "NoInhib" denote, respectively, the occurrence and nonoccurrence of inhibition treatment between CSs X and A during Phase 1. "OV" and "Con" denote, respectively, overshadowing treatment (X being reinforced in compound with A) and overshadowing-control treatment (X being reinforced elementally) during Phase 2. "Ext" denotes the occurrence during Phase 3 of nonreinforced presentations of the common element (C), which was used to establish the inhibitory-like relationship between X and A in Phase 1. The numbers preceding the letters indicate the total number of presentations of the stimuli in that phase. Slashes separate interspersed trials. Stimuli A and X were a complex tone and a click train, respectively. Stimuli C and D were a buzzer and a flashing light, counterbalanced. S was a white noise that served as a surrogate outcome (i.e., S, Phase 2) that was later paired with footshock (Phase 4).

Results and Discussion

Examination of the first test day scores (see Figure 3) indicates, as in Experiment 2, that nonreinforced presentations of the common element used to establish the inhibitory relationship between X and A resulted in attenuated suppression of lever pressing. A 5 (Group) × 2 (Test Day) ANOVA was used to assess baseline lever pressing just before onset of CS X on the test trials. The means on the first test day for Groups Inhib-OV-Ext, Inhib-OV, NoInhib-OV, NoInhib-Con, and NoInhib-Con-Ext were 15.20, 9.93, 17.69, 11.48, and 12.23 lever presses per minute, respectively. The means on the second test day for Groups Inhib-OV-Ext, Inhib-OV, NoInhib-OV, NoInhib-Con, and NoInhib-Con-Ext were 18.24, 11.52, 21.79, 16.03, and 12.45 lever presses per minutes, respectively. This analysis detected no Group × Test Day interaction $F(4, 55) = 1.55$, $p > .20$, on baseline levels of responding. Collapsing across Test Day, a main effect of group on baseline levels of lever pressing was detected, $F(4, 55) = 2.69$, $p < .05$. Further analysis detected a simple effect of group on baseline levels of responding on Test Day 2, $F(4, 55) = 3.19$, $p < .05$. However, no significant effect of group on baseline responding was evident on the first test day, $p > .12$. Thus, subsequent analyses of lever press suppression in the presence of the target stimulus were conducted using only data from the first test day. A one-way ANOVA among groups revealed significant differences in the lever press suppression ratios for Test Day 1, $F(4, 55) = 17.19$, $MSE = .287$, $p < .01$. Pairwise comparisons were conducted to determine the source of this effect. Lever press suppression was 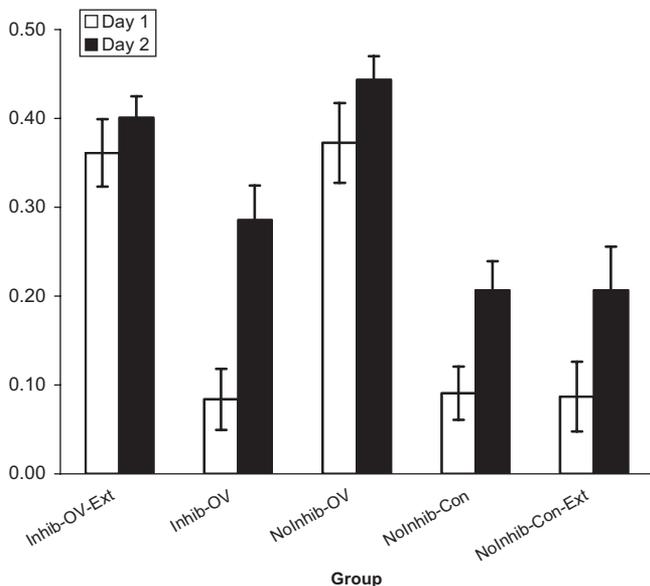found to differ between Groups NoInhib-OV and NoInhib-Con, $F(1, 55) = 28.54$, $p < .01$, suggesting that, in the absence of prior inhibitory training between X and A, the overshadowing treatment attenuated suppression relative to an elemental control group. In contrast, when overshadowing training was preceded by inhibitory pretraining (i.e., XC/AC trials), overshadowing was attenuated, which was evidenced by a reliable difference between Groups Inhib-OV and NoInhib-OV, $F(1, 55) = 29.96$, $p < .01$, thereby replicating in sensory preconditioning the critical effect observed in Experiments 1 and 2. Critically, the planned comparison between Groups Inhib-OV and Inhib-OV-Ext detected a difference, $F(1, 55) = 27.68$, $p < .01$, suggesting that nonreinforced presentations of the common element, C, following overshadowing treatment attenuated the effect of inhibitory training. Finally, a comparison between Groups NoInhib-Con and NoInhib-Con-Ext showed that the extinction treatment itself did not directly impact responding to X, $p > .83$. The critical comparison between Groups Inhib-OV and Inhib-OV-Ext is consistent with the prediction of the extended comparator hypothesis and contrary to that of MSOP.

General Discussion

The purpose of the present experiments was to assess the role of the within-compound association in conventional cue competition, specifically overshadowing. Experiment 1 determined that training of an inhibitory-like relationship between the overshadowing and target CSs attenuated overshadowing. Experiment 2 found that nonreinforced presentations of the common element used to train the inhibitory-like relationship before overshadowing treatment resulted in reduced suppression to the target CS, indicative of restored overshadowing. Experiment 3 replicated the effects of Experiment 2 when extinction of the common element used in the inhibitory treatment was subsequent to overshadowing treatment. The findings of Experiment 3, taken in conjunction with the findings of Experiments 1 and 2, are supportive of a performance-focused view such as the extended comparator hypothesis (Denniston et al., 2001).

Despite the lack of a necessary contribution of the within-compound association to conventional cue competition in Wagner's (1981) SOP model and its revision by Dickinson and Burke (1996), both provide an explanation of the results of Experiment 1 because within-compound associations within the SOP framework are sufficient for cue competition. Notably, the explanation of the observed attenuation of overshadowing in Experiment 1 offered by SOP and MSOP did depend upon the within-compound association between A and X. In both models, the formation of an inhibitory association between A and X (as in Experiment 1) before overshadowing treatment could allow X to be more strongly activated into A1 (i.e., by reducing the activation of X into A2 otherwise caused by A through a net A-X excitatory association). Because of its stronger activation into A1, X could more strongly enter into an association with the US, which would result in attenuation of the overshadowing effect. Wagner's (1981) SOP model cannot explain restoration of overshadowing in Group Inhib-Ext-OV as a result of C-alone presentations in Phase 2 of Experiment 2. However, Dickinson and Burke's (1996) MSOP model does so by simply considering restoration of overshadowing to result from the reduction of the X-A inhibitory association by the formation of an excitatory X-A association because of the

Figure 3. Mean suppression ratio in Experiment 3 for each of the two days of testing of Cue X (i.e., blocks of four trials per day). Groups Inhib-OV, NoInhib-Con, and NoInhib-Con-Ext were those in which strong suppression to Cue X was expected (see Table 3). Groups NoInhib-OV-Ext and NoInhib-OV were the groups in which weak suppression to X was expected because of overshadowing of Cue X by Cue A if overshadowing depends on a within-compound association between X and A. The brackets represent the standard error of the means
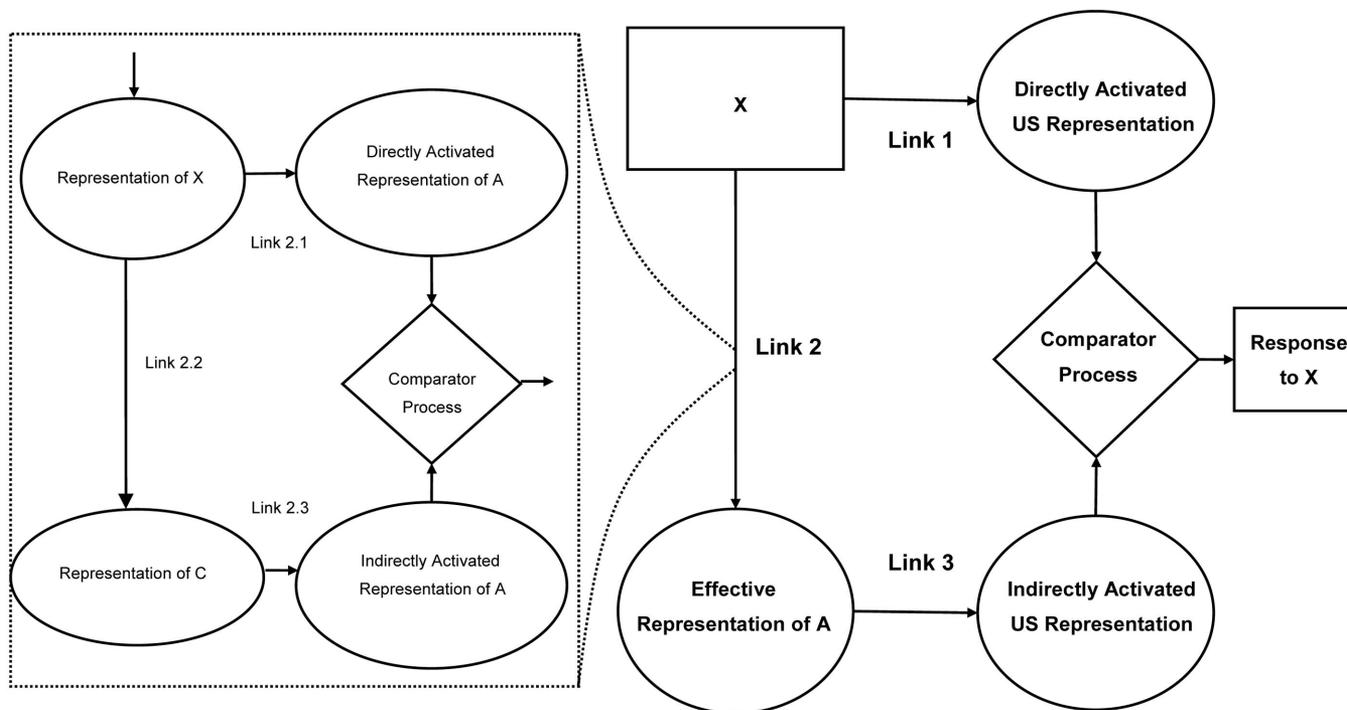
Figure 4. The extended comparator hypothesis as applied to Group Inhib-OV in Experiment 1. The strong X-C association (Link 2.2) and C-A association (Link 2.3) presumably down modulate the output based on the X-A association (Link 2.1), thereby decreasing activation of the effective representation of A. This in turn should decrease the activation of the indirectly activated US representation.

simultaneous activation of A and X into A2 during C-alone trials. Experiment 3 essentially replicated Experiment 2 with one important modification: extinction of stimulus C now followed the overshadowing treatment. Despite this change in procedure, C-alone presentations, as in Experiment 2, effectively restored overshadowing. Unlike Experiment 2, however, Dickinson and Burke's MSOP cannot account for restoration of overshadowing in Group Inhib-OV-Ext of Experiment 3 because the presumed formation of an excitatory X-A association during exposure to C should be unable to influence the status of the X-S association, which was previously formed during Phase 2.

The extended comparator hypothesis (Denniston et al., 2001; see Figure 4) anticipates attenuation of overshadowing as a consequence of the inhibitory-like training in all three experiments and the restoration of overshadowing seen in Experiments 2 and 3. Presumably in each experiment the inhibitory relationship between X and A attenuated the expression of the excitatory X-A within-compound association (i.e., Link 2; see Figure 4) formed during overshadowing treatment, relative to a condition given no prior inhibitory-like treatment.[2] That is, in each experiment the inhibitory-like treatment of Phase 1 presumably disrupted the expression of Link 2 in the OV condition by preventing Links 2 and 3 from conjointly activating a strong indirect representation of the outcome that is the basis of overshadowing according to the original and extended comparator hypothesis. Conversely, in Experiments 2 and 3 presentation of the common element C alone presumably weakened both X-C and A-C associations formed during Phase 1, thereby degrading the inhibitory-like relationship

between X and A. As a consequence of Links 2 and 3 being able to strongly suppress the expression of Link 1 (the target X-outcome association), overshadowing was restored. Moreover, in Experiments 2 and 3 the potential of stimulus C to mediate an indirectly activated representation of stimulus A through Link 2.2 was reduced because of the C-alone presentations. This was manifest in the attenuated responding observed in Groups Inhib-Ext-OV (Experiment 2) and Inhib-OV-Ext (Experiment 3) relative to Group Inhib-OV. The potential of the extended comparator hypothesis to explain the results of Experiments 2 and 3 relies on the model's assumption that the comparison process takes place at the time of testing. That is, these results are explained by the extended comparator hypothesis based on identical mechanisms because in this situation the order of the treatment phases is assumed to be irrelevant.

In addition to conventional associative learning accounts, it is possible that perceptual learning contributed to the observed effects. For example, Hall (2003) provided evidence suggesting that

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[2] Notably, the comparator hypothesis does not attribute reduced responding to X as a result of the inhibition treatment to any type of inhibitory or negatively valued association as do acquisition-focused accounts. Instead, it views reduced responding following inhibition treatment as a reduction in the effective excitatory status of the target CS, that is, a reduced behavioral impact of the directly activated outcome representation (A in this case) owing to the strength of the indirectly activated A representation produced by the X-C and C-A associations.

alternating training of two compounds of stimuli sharing a common element increases the salience of the unique elements (i.e., A and X in the current experiments). If the difference in salience between the overshadowing cue (A) and the overshadowed cue (X) is consequently reduced, then the expected magnitude of overshadowing should also be reduced, which could explain the differences in responding between the Inhib and NoInhib conditions of Experiments 1 through 3. A reduction in overshadowing would also explain the differences in responding to the target cue among all groups in Experiment 2 except for Group Inhib-Ext-OV, which demonstrated overshadowing despite intermixed preexposure. However, repeated exposure to the common element (C) might have allowed the repeated activation of the target stimulus (X) representation based on the prior pairings of X and C. In this case, the intermixed exposure to AC and XC may have raised the salience of X, but repeated activation of the representation of X could have reduced the salience of X. Stated in terms of mediated conditioning (e.g., Holland, 1990), it is possible that mediated latent inhibition may have taken place. Although this is a possible account, it seems highly speculative and data would be needed to lend it support. In any case, such a perceptual learning account fails to explain the critical result of Experiment 3.

As mentioned in the Introduction, several studies with humans have suggested that the within-compound association plays a role only in retrospective revaluation (e.g., backward blocking and recovery from overshadowing), as opposed to conventional cue competition (e.g., overshadowing and forward blocking). However, in most of those studies the critical revaluation manipulations occurred after compound treatment involving the target stimulus (e.g., Dickinson & Burke, 1996) or were interpolated between the training trials (e.g., Atiken et al., 2001), whereas in the current experiments the critical manipulation occurred before overshadowing treatment and involved the target stimulus. The only study that closely resembles the current work is one by Aitken et al. (2001), in which they used serially presented compounds on the cue competition trials and filled the interstimulus interval with a secondary task (i.e., an arithmetic task). The secondary task presumably demanded a relatively large amount of attention, thereby disrupting the formation of the within-compound association by impairing rehearsal of the cue presented first within the trial. These authors found that, when the interval was not filled on the compound trials, both blocking and retrospective revaluations were observed. However, when the interval was filled by participants performing the secondary task, only forward blocking was observed. Interpretation of their results is complicated by the fact that they did not use conventional controls for blocking; they used a reduced-overshadowing treatment as the control for forward blocking and a release-from-overshadowing treatment as the control for backward blocking. Our use of an overshadowing treatment makes the interpretation of the current results less complicated. An overshadowing procedure permits us to attribute the observed differences solely to differences in overshadowing and not to a difference between forward blocking and reduced overshadowing relative to differences between backward blocking and release from overshadowing. Moreover, our inhibition treatment occurred before any other type of training; consequently, the present results provide a somewhat clearer picture of the role of the within-compound association in a cue competition situation. Still, Aitken et al.'s data suggest that conventional cue competition is less dependent on a within-compound association than is retrospective revaluation. The present experiments did not include retrospective revaluation groups. They merely document that within-compound associations can play critical roles in conventional cue competition, at least as implemented in a preparation such as ours. Why the present data are incongruent with the previously cited studies which suggested that conventional cue competition is not particularly dependent on within-compound associations (e.g., Aitken et al.) is not obvious. Prime candidates include the differences in species (humans vs. rats) and differences in the tasks (causal judgment vs. Pavlovian fear conditioning). Currently, there is little basis for favoring one factor over the other. However, limited data indicating that causal judgment requires conscious awareness (De Houwer & Beckers, 2002) and Pavlovian conditioning (at least delay conditioning) does not (Smith, Clark, Manns, & Squire, 2005) suggests the task might be the critical factor.

In summary, the present data indicate at least two things. First, in some preparations with nonhuman subjects, within-compound associations contribute to conventional cue competition. Whether the discrepancy between the prior studies that used human participants and the present study with nonhuman subjects arose from the differences in species or the very different nature of the tasks is not clear at this time. Second, the extended comparator hypothesis (Denniston et al., 2001) is able to account for some results that remain inexplicable in terms of MSOP. That is, the extended comparator hypothesis states that a within-compound association is necessary but not sufficient for conventional cue competition, whereas MSOP says that a within-compound association is not necessary for conventional cue competition, but can be sufficient. The current data, and specifically that of Experiment 3, support the former theoretical approach.

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