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Potentiation and Overshadowing in Pavlovian Fear Conditioning

Gonzalo P. Urcelay¹ and Ralph R. Miller

State University of New York at Binghamton

Abstract

The present experiments addressed a fundamental discrepancy in the Pavlovian conditioning literature concerning responding to a target cue following compound reinforced training with another cue of higher salience. Experiment 1 identified one determinant of whether the target cue will be overshadowed or potentiated by the more salient cue, namely contiguity between compound CS termination and US presentation. Overshadowing and potentiation were observed with delay and trace procedures, respectively. Experiments 2–3 contrasted elemental and configural explanations of potentiation. Both experiments supported a configural account. Experiments 3 and 4, by manipulating prior learning experiences to bias subjects to encode the same compound elementally or configurally, demonstrated decreased potentiation and overshadowing, respectively. Overall, these experiments demonstrate potentiation with non-taste stimuli and identify one variable that determines whether overshadowing or potentiation will occur. Moreover, they show that prior experiences can determine how a compound is encoded and are compatible with the idea of flexible encoding as a principle of information processing.

Keywords

Pavlovian fear conditioning; potentiation; overshadowing; elemental encoding; configural encoding; transfer of learning; encoding flexibility

A central focus in the study of Pavlovian conditioning since the 1970s has been to understand the mechanisms that underlie cue interactions during training. By cue interactions, we mean the changes in a target cues' (X) behavioral control that occur as a function of the co-presentation during training of another cue, either simultaneously or serially. In other words, conditioned responding to X during test *changes* because a second cue (A) was trained simultaneously with X (e.g., AX→US), relative to a group that was trained in the absence of A (e.g., X→US). Importantly, much theorizing in the area of Pavlovian conditioning has been concerned with one form of cue interaction, namely cue competition. Cue competition is said to have occurred when during testing we observe *less* behavioral control by the target cue (X) because a second cue was also presented during training. The example we just provided (AX→US) is called *overshadowing*, and was documented early on by Pavlov (1927). Overshadowing is not an isolated phenomenon, but rather one of many examples in which behavioral control to a target cue is decreased by the co-presentation of a second cue during training. Blocking, the decreased responding to a target cue after it has been trained in the presence of an already established predictor of the outcome, is another example of cue competition (Kamin, 1968).

Mailing Address: Ralph R. Miller, Department of Psychology, SUNY – Binghamton, Binghamton, NY 13902-6000, USA, TEL: (607) 777-2291, FAX: (607) 777-4890, E-mail: rmiller@binghamton.edu.

¹Present address: Department of Experimental Psychology, University of Cambridge, Downing St. Cambridge, CB2 3EB. United Kingdom. gu203@cam.ac.uk

Overshadowing and blocking are two phenomena that are widely observed across tasks and species. That is, they are observed in appetitive conditioning with rats (Holland, 1999), aversive conditioning with rats (Wheeler & Miller, 2007), spatial learning with rats (Sánchez-Moreno, Rodrigo, Chamizo & Mackintosh, 1999; Roberts & Pearce, 1999; Rodrigo, Chamizo, McLaren & Mackintosh, 1997), nictitating membrane response with rabbits (Kehoe, 1982; Kehoe, Schreurs & Amodei, 1981), instrumental conditioning with rats (Pearce & Hall, 1978), human causal judgments (Beckers, De Houwer, Pineño, & Miller, 2006) and human category learning (Bott, Hoffman, & Murphy, 2007). Other phenomena also categorized under the umbrella of cue competition effects are the relative stimulus validity (Wagner, Logan, Haberlandt, & Price, 1968) and overexpectation effects (Rescorla, 1970), which are also widely observed across preparations and species. Cue competition has been well captured by traditional and contemporary models of learning. In fact, one could argue that many of these models (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981) emerged after the observation of blocking by Kamin (1968) with these effects serving as a benchmark for assessing the models.

Above, cue interaction was defined as the resultant *change* in behavioral control by the target cue X that occurs when the target is trained in the presence of another cue, A. So far, we have described several instances in which these interactions are competitive and the net result is a decrement in behavioral control by the target. However, in the late 70s, when cue competition phenomena were occupying the minds of most learning theorists, several reports documented the opposite outcome (Clarke, Westbrook, & Irwin, 1979; Galef & Osborne, 1978; Rusiniak, Hankins, Garcia, & Brett, 1979). For example, Rusiniak et al. (1979), using a flavor aversion preparation, observed that when a weak odor (X) was followed by poisoning induced by the administration of lithium chloride (LiCl), rats acquired a mild aversion to the weak odor. Notably, when the same odor was reinforced in the presence of a more salient taste (XA), behavioral control was actually enhanced relative to the elemental control condition (X). That is, these researchers reported *potentiation* rather than overshadowing of odor aversion by taste. This is surprising because operationally, they reinforced two cues of different salencies presented in compound, which is identical to overshadowing treatment, but instead of observing the more salient cue overshadow the less salient cue, they observed that it potentiated behavioral control by the less salient (target) cue.

Although we are not aware of published reports of facilitation rather than cue competition resulting from treatments such as relative stimulus validity and overexpectation, the opposite of blocking has recently been documented. In three elegant series of studies, Batsell and his colleagues (Batsell & Batson, 1999; Batsell, Paschall, Gleason, & Batson, 2001; Batson & Batsell, 2000) found that behavioral control by an odor (X) was facilitated when it was trained simultaneously in the presence of a taste (XA→US) that previously had been paired with the reinforcer (A→US). They termed this effect *augmentation* because, instead of observing that prior taste conditioning blocked behavioral control by the odor (as Kamin observed), they observed that it facilitated behavioral control by the odor.

Although most observations of potentiation have used taste as the potentiating cue (but see General Discussion), one peculiarity about the potentiation phenomenon is that the ratio of salencies between the potentiating and potentiated cue seems to be critical for the observation of potentiation. For example, Bouton and Whiting (1982) failed to reliably obtain potentiation (in fact, they saw overshadowing) when they used a to-be-potentiated odor of intermediate salience. In a subsequent series of experiments, in which a lower odor concentration was used, a reliable potentiation effect was observed (Bouton, Jones, McPhillips, & Swartzentruber, 1986). In later experiments a taste potentiated another taste as long as the potentiated taste was of low salience (Bouton et al., 1987). This is consistent with other reports that found that the relative salencies rather than the physical identities of the to-be-potentiated and potentiating

cues were critical. For example, Slotnick, Westbrook, and Darling (1997) observed that an odor potentiated a taste as long as the odor was salient and the taste less salient. Other authors have also noted that the ratio of salencies appears to be critical to the observation of potentiation (Batsell & Paschall, in press; but see Kucharski & Spear, 1985 for evidence of potentiation with cues of equal salience in preweanling rats). This is important because, as we mentioned earlier, overshadowing is also best observed when the overshadowing cue is more salient than the overshadowed cue (Mackintosh, 1976).

We have described two kind of cue interactions (competitive and facilitative) that result when two cues of different salencies are presented together and reinforced. What is paradoxical about these two kinds of interactions is that they result from the same procedures, but the reason why one kind of interaction or the other is observed is still unclear. For example, in both overshadowing and potentiation, training is conducted with compound cues which differ in salience, yet under some circumstances the more salient cue overshadows the less salient cue, and under other circumstances the more salient cue potentiates behavioral control by the less salient cue. The present series of experiments was concerned with the identification of some of the factors which favor overshadowing versus potentiation, as a mean to understand the underlying mechanisms recruited in each phenomenon. Notably, these two families of phenomena are dissociated at a theoretical level, and to our knowledge there is no theory that accounts for both kinds of observations.

The basic question that the present experiments were designed to address was the following: Why is the interaction between two cues sometimes competitive and sometimes facilitative? We started by exploring the literature to determine which circumstances favor potentiation and which favor overshadowing. It seems that potentiation is generally better observed when training is embedded in a trace conditioning procedure. This is not surprising, because, as we mentioned earlier, most research on potentiation has been conducted in flavor aversion experiments, which supports long traces between CS onset (and often termination) and US presentation. In fact, even if the US in a flavor aversion preparation is administered immediately after presentation of the CS, it normally takes several minutes for the lithium chloride to make the animal sick. That potentiation is better observed with trace conditioning is evident in one of the earliest reports on potentiation (Palmerino, Rusiniak, & Garcia, 1980). In the second experiment in that report, an odor alone or an odor plus a taste was presented to different groups of rats that then received the US at different intervals (traces) between flavor presentation and LiCl administration. With no trace interval between flavor presentation and US administration, they observed good behavioral control by the odor when it was trained alone, and no benefit of training the odor in the presence of the more salient taste. As expected, with increasing trace intervals the odor trained alone lost behavioral control, which is indicative of a trace deficit. However, when a similar trace-conditioned odor was trained in the presence of a more salient taste, the trace deficit was no longer observed, and potentiation was evident. In other words, they observed potentiation with a trace interval between compound termination and US presentation, but no potentiation (nor overshadowing) without a trace. So perhaps potentiation arises from long CS-US intervals rather than from a special information processing module for ingestion as proposed by Garcia et al. Based on these observations and the general notion that the mechanisms underlying Pavlovian and instrumental conditioning are similar (Dickinson, 1980; Rescorla, 1988), we examined the operant conditioning literature.

In instrumental learning, there are numerous demonstrations of deficits in instrumental performance that result from the introduction of a trace between response emission and reinforcer delivery. For example, Schachtman, Reed, and Hall (1987) observed a decrement in pigeon key pecking when a 3-s trace was interposed between the emission of an operant response and presentation of the reinforcer (note that these pigeons were on a variable interval [VI] 60-s) relative to a 0.5-s trace. However, under these circumstances, the addition of a tone

presented simultaneously with the emission of the operant response facilitated operant behavior. Notably, a similar tone disrupted (overshadowed) operant behavior when there was a short trace (0.5 s) between operant responding and reinforcer delivery. In other words, with a short trace, presentation of a tone simultaneously with the operant response overshadowed the response-reinforcer association, but when a longer trace (3 s) was introduced between response emission and reinforcer delivery, a similar tone facilitated the instrumental behavior that was otherwise decreased by the introduction of the trace. The parallel between this observation of facilitated operant behavior and the original observations of potentiation by Garcia and colleagues suggested that perhaps a trace interval between stimulus presentation (or response emission) and the presentation of the reinforcer is important for the observation of potentiation.

The first experiment of this series was designed to investigate the possible non-additive interaction between compound reinforced training (e.g., overshadowing treatment) and trace conditioning in a Pavlovian fear-conditioning procedure. Based on the above-mentioned empirical results, we hypothesized that with strong contiguity (0 trace between CS termination and US presentation) the addition of a salient cue (**AX**-US) would impair behavioral control by the target (X), relative to a group that experienced target alone (X-US) reinforced presentations during training. We further hypothesized that similar training but embedded in a trace conditioning procedure would show the opposite pattern. That is, in trace conditioning, the target CS alone (X-----US) would display less behavioral control (a trace deficit), and under those circumstances the addition of a more salient cue (**AX**-----US) would increase behavioral control by the target cue.

Experiment 1

In Experiment 1 we used a 2×3 factorial design in which subjects experienced elemental (X) or compound (**AX**) reinforced training with a trace interval between CS termination and US presentation that was 0, 10, or 20 s in duration. The design of Experiment 1 is summarized in Table 1. In the 0-trace conditions, we expected that responding to the target (X) would be higher when it was trained alone relative to a group that experienced compound (**AX**) training which would permit overshadowing. The parameters used for these two groups were those that we have typically employed in our laboratory to observe robust overshadowing in delay conditioning situations (e.g., Amundson, Witnauer, Pineño, & Miller, 2007; Blaisdell, Denniston, & Miller, 1999; Wheeler & Miller 2007; Urushihara & Miller, 2006; 2007). Thus, we used as the target cue X a soft clicker (5 dB) and as the more salient cue **A** a more intense complex tone (3000 & 3200 Hz; 10 dB). The question was whether these stimuli would result in the opposite interaction (i.e., a synergistic effect) when training was embedded in a trace conditioning procedure. We expected groups in the elemental condition to show less behavioral control as the trace was made longer (i.e., a trace deficit). Critically, our interest was to see if there was an interaction between compound training and trace conditioning, such that in the trace groups (i.e., 10 and 20 s) the addition of the more salient cue (**A**) would actually potentiate rather than overshadow behavioral control by the target (X).

Method

Subjects—Subjects were 36 female (190 – 250 g) and 36 male (295 – 355 g), experimentally naïve, Sprague-Dawley descended rats obtained from our own breeding colony. Subjects were individually housed and maintained on a 16-hr light/8-hr dark cycle. Experimental sessions occurred roughly midway through the light portion. Between weaning and the initiation of the experiment, all animals were handled for 30 s three times a week. Subjects had free access to food in the home cages. Prior to initiation of the experiment, water availability was progressively reduced to 10 min per day, provided approximately two hours after any scheduled treatment.

Apparatus and stimuli—The apparatus consisted of 12 operant chambers each measuring $30 \times 30 \times 27$ cm ($l \times w \times h$). All chambers had clear Plexiglas ceilings and side walls and metal front and back walls. On one metal wall of each chamber there was a 3.5-cm wide operant lever on the left side (4-cm above the floor), and a niche ($2.5 \times 4.5 \times 4$ cm) on the right side, the bottom of which was 2 cm above the floor, where there was a cup into which a drop (0.04 ml) of distilled water could be presented by a solenoid valve. The floor was constructed of 0.3-cm diameter rods, spaced 1.3 cm center-to-center, and 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 chamber was housed in its own environmental isolation chest which could be dimly illuminated by a 1.12-W incandescent houselight mounted on the front wall of the experimental chamber. Ventilation fans in each enclosure provided a constant 76-dB (C-scale) background noise. A 60-W incandescent bulb was mounted on the back wall of each environmental chest 26 cm from the center of the floor of the conditioning chamber. This bulb could be flashed (0.25 s on/0.25 s off) to serve as a visual stimulus. Three 45- Ω speakers mounted on the interior right, left and back sides of each environmental chest were used to deliver a complex tone (3000 and 3200 Hz, 10 dB [C-scale] above the background), a click train (6 / s, 5 dB [C-scale] above the background), and a white noise (8 dB [C-scale] above the background), respectively. In Experiment 1, the target cue (CS X) was a 30-s click train and the overshadowing cue (CS A) was a 30-s complex tone. The tone was 5 dB louder than the click train to encourage overshadowing of the clicks. The white noise was used to make delivery of water more conspicuous, thereby facilitating shaping of lever pressing. Thus, a 0.5-s white noise accompanied delivery of each drop of water reinforcement. The US was a 0.5-s, 0.7-mA footshock.

Procedure—Subjects were randomly assigned to one of six groups based on whether the target CS was trained elementally (Elem) or in compound (Comp) with the more salient A, and depending on the trace interval (0, 10 or 20), counterbalanced for sex ($ns = 12$). Phase 1 of training was conducted in one context [Train] and all other treatments in another context [Test]. This was done to minimize differential fear of the test context summing with fear of the CS because different trace intervals might be expected to result in differential fear to the training context. The two distinct contexts differed in visual, tactile, and odor cues. In Context Test, the houselight was illuminated, the operant lever protruded through the wall, and the grid floor was covered by a clear Plexiglas plate. In Context Train, the houselight was turned off, the operant lever was retracted, the grid floor was not covered, and an odor stimulus was presented. The odor was produced by two drops of 98% methyl salicylate (a mint odor) placed on the top surface of a wooden cube located inside the environmental isolation chest but outside of the experimental chamber. Moreover, the physical chamber used as Context Train for each subject was different from that used as Context Test for that subject.

Shaping: A 5-day acclimation to Context Test and shaping of lever-press behavior were conducted in daily 60-min sessions. Subjects were shaped to lever-press for water on a variable-interval-20-s schedule in the following manner. On Days 1 and 2, a fixed-time 120-s schedule of noncontingent water delivery was in force simultaneously with a continuous reinforcement schedule. On Day 3, noncontingent reinforcers were discontinued and subjects were trained on the continuous reinforcement schedule alone. Subjects that made less than 50 responses on this day experienced a hand-shaping session later in the same day. On Days 4 and 5, a VI 20-s schedule was imposed. This schedule of reinforcement prevailed throughout the remainder of the experiment except for Phase 1. Water presentation was always accompanied by 0.5-s of the white noise.

Phase 1: During Day 6, subjects experienced elemental or compound conditioning in Context Train in a 45-min long session. Subjects in the elemental condition received four reinforced

trials of X alone. The difference between these three groups was the contiguity between the CS and US. For Group Elem-0 the US was presented immediately after CS termination. For Group Elem-10, the US was presented 10 s after CS termination, and for Group Elem-20 the US was presented 20 s after CS termination. Similar treatments were received by groups in the Compound condition, but all X presentations were accompanied (simultaneously) by the more salient A. Trials (US presentation) occurred at 11, 18, 32 and 40 min into the 45 min session.

Reshaping: On Days 7 and 8, all subjects experienced one 60-min session to restabilize lever-pressing on the variable-interval 20-s schedule in Context Test.

Test X: On Day 9 in Context Test, suppression of baseline lever-pressing during presentation of CS X was assessed in all groups. Each subject received four nonreinforced 30-s presentations of CS X during a 20-min session with the onsets occurring at 6, 10, 14, and 18 min into the session. The response rates (number of lever-presses/min) during each 30-s period preceding each CS exposure (pre-CS score) and that during each 30-s CS exposure (CS score) was recorded.

Test A: On Day 10 in Context Test, suppression of baseline lever-pressing during presentation of the Tone (A) was assessed in all groups in a similar way as was done with X on the previous day. Note that in the compound groups, responding to A could illuminate the underlying processes of potentiation.

Data Analysis—A suppression ratio (Annau & Kamin, 1961) of each subject was calculated by the formula $A/(A+B)$, where A is the pooled rate of lever-pressing during the four 30-s CSs and B is the pooled rate of lever-pressing during the four 30-s pre-CS periods. This ratio was used as an index of fear elicited by presentations of the target CS. Ratios range from 0 (maximal fear) to 0.5 (no fear). Ratios were analyzed with a 2×3 analysis of variance (ANOVA) with type of training (Elem vs. Comp) and trace duration (0, 10, and 20) as factors. When appropriate, we report effect size calculated using the algorithm provided by Myers and Well (2003, p. 210).

Results and Discussion

The results of Experiment 1 for CS X are depicted in Figure 1. As it can be observed, subjects that experienced elemental training of the target alone (X) showed robust suppression when there was no trace interval between CS termination and US presentation and less suppression when there was a 20-s trace. This decrease in conditioned suppression as a function of increasing the trace represents a trace deficit. Importantly, this relationship was inverted in the groups that received training with the compound (AX) and testing with the target CS alone (X). In these groups, conditioned suppression was minimal with a 0-s trace between compound CS termination and US presentation, replicating the basic overshadowing effect we typically observe with the use of these parameters (e.g., Urushihara & Miller, 2006). Moreover, the group that received compound training (AX) with a 20-s trace interval showed enhanced behavioral control by X relative to its elemental control group. In other words, we observed both potentiation and overshadowing in Pavlovian fear conditioning with the same compound of stimuli. These observations were corroborated by the following statistics.

A 2 (Training: Elemental vs. Compound) $\times$ 3 (Trace: 0 vs. 10 vs. 20) factorial ANOVA conducted on the number of lever presses emitted during 60 seconds immediately before the first test presentation of the target did not reveal any main effects or interaction (smallest $p = .24$), suggesting that there were no appreciable baseline differences in lever pressing. A similar ANOVA conducted on the suppression ratios revealed no main effects, but there was a significant interaction, $F(1, 66) = 8.06, p < 0.01, MSE = 0.012$, Cohen's $f = 0.44$. A series of

planned comparisons using the overall error term from the ANOVA were used to ascertain the source of the interaction. A comparison between Groups Elem-0 and Comp-0 showed less suppression in Group Comp-0, $F(1, 66) = 8.51, p < 0.01, MSE = 0.012$, Cohen's $f = 0.32$, demonstrating an overshadowing deficit when the reinforcer was presented immediately after compound termination. A similar comparison between the two conditions trained with a 10-s trace between CS termination and US presentation revealed a nonsignificant trend towards overshadowing $F(1, 66) = 2.85, p = 0.09, MSE = 0.012$. Moreover, a comparison of the two groups in Condition 20 showed a reliable potentiation effect, $F(1, 66) = 6.24, p < 0.05, MSE = 0.012$, Cohen's $f = 0.27$. That is, with a 20-s trace the addition of a more salient cue A during training facilitated, rather than decreased, behavioral control by the target. A final comparison between Groups Elem-0 and Elem-20 demonstrated that suppression was lower in Group Elem-20s, $F(1, 66) = 5.04, p < 0.05, MSE = 0.012$, Cohen's $f = 0.24$, revealing a trace deficit.

Figure 2 shows the pattern of suppression to the salient cue A. Overall, suppression to A was much lower than to X, perhaps reflecting generalized extinction from the previous session involving nonreinforced presentations of X during testing. However, Figure 2 shows that conditioned suppression to A in the Compound groups increased with the trace between compound termination and US presentation, which is similar to the pattern of responding observed to X in the same groups. These observations were supported by the following statistics.

The A data was analyzed in a manner similar to X. We used a 2 (Training: Elemental vs. Compound) $\times$ 3 (Trace: 0 vs. 10 vs. 20) ANOVA to determine if there were baseline differences in number of lever presses emitted during the 60 s immediately before the first test presentation of the target cue A. This analysis did not reveal any appreciable differences between groups (smallest $p = .29$). A similar ANOVA conducted on the suppression ratios revealed a main effect of training, $F(1, 66) = 10.92, p < 0.01, MSE = 0.009$, and an interaction, $F(1, 66) = 4.88, p < 0.05, MSE = 0.009$, Cohen's $f = 0.32$. Conditioned suppression to A in the conditions that received compound training was stronger in Group Comp-20 than in Group Comp-0, $F(1, 66) = 4.01, p < 0.05$.

The results of the present experiment indicate that when compound training is conducted with a trace interval, better behavioral control by the less salient cue (X) is observed than if it was trained alone, which by definition is a potentiation effect. Notably, we identified one variable that determines whether the addition of a salient cue A during training will increase or decrease behavioral control by the target cue X. This is important because overshadowing and potentiation are both inferred from an elemental control, but these two controls were not similar. That is, overshadowing was observed when training was conducted with a delay procedure, which resulted in strong behavioral control by X in the elemental control group relative to the compound group. In contrast, when a trace interval was imposed, potentiation was observed relative to an elemental control group, which displayed weak behavioral control by X. However, it should be noted that a low baseline alone does not necessarily predict the observation of potentiation. In our Experiment 1, the lowest level of conditioned suppression to X was still in the upper third of our (inverted) fear scale, which indicates robust behavioral control.

Experiment 2

Experiments 2 and 3 focused on alternative sources of the potentiation effect because most cue interaction research conducted in fear conditioning has reliably observed overshadowing. Fear conditioning provides a unique opportunity to study potentiation because it avoids problems associated with flavor aversion and allows for several manipulations that can not be readily implemented in flavor aversion. For example, when many reinforced trials are administered in

a flavor aversion experiment, subjects generalize the aversion to almost any novel flavor that they encounter. A second problem with flavor aversion experiments is that, as training proceeds, subjects drink less of the target solution, which makes it more difficult to equate groups in exposure to the stimuli being studied. The third problem with flavor aversion is that the CSs and USs are necessarily long in duration. Fear conditioning is exempt from these disadvantages.

In Experiment 2, we contrasted two explanations that have already received some attention in the potentiation literature. The first explanation is the within-compound association account (Durlach & Rescorla, 1980), which is an elemental approach that assumes that subjects represent all stimuli on a given trial as separate units that are linked by associations. This explanation assumes that three associations are formed during compound conditioning: 1) an $X \rightarrow US$ association, which is similar to that established in a control group and does not contribute to potentiation. 2) an $A \rightarrow US$ association, which is critical for the observation of potentiation; this association is relatively strong because **A** is often more salient than **X** and because the salient **A** leave aftereffects that facilitates its being conditioned even in the presence of long trace intervals. 3) an $X \rightarrow A$ within-compound association, which, like the $A \rightarrow US$ association, is critical for potentiation. The $X \rightarrow A$ within-compound association has been shown to be strengthened by simultaneous presentations of the compound (Coburn, Garcia, Kiefer, & Rusiniak, 1984; Holder & Garcia, 1987). Moreover, Rescorla (1981b; also see Cheate & Rudy, 1978; Holland 1980) has observed that within-compound associations are better formed when the US is omitted. In our laboratory, we have found that compound training of CSs similar to those used here but of long duration (125s) also result in a strong within compound association, which seems to eliminate the overshadowing effect (Sissons et al., 2008), presumably due to a configuration of the two stimuli. With respect to the present research, one may think that with trace conditioning procedures, delaying the presentation of the US should favor the formation of within-compound associations, particularly because the two cues are presented simultaneously, which presumably should facilitate potentiation. Importantly, this approach accounts for potentiation in terms of general principles of learning that date back to the British associationist tradition. However, this explanation depends upon a number of assumptions that are not so straightforward. For example, it assumes that the subject discriminates both **A** and **X** as separate entities from the compound. As we will see in the General Discussion, this assumption should not be taken for granted.

An alternative to this approach that does not necessitate the construct of an association linking the two conditioned stimuli is provided by configural association theory. This approach, tested and supported by Kucharski and Spear (1985), has its roots in work by Rescorla (Rescorla, 1981a; Rescorla & Durlach, 1981), Asch (Asch, Ceraso, & Heimer, 1960), Gibson and Gibson (1955), and the German Gestalt psychologists (Wertheimer, 1938). The configural view assumes that subjects simply form a unitary representation of the **AX** compound; the individual elements are not separately represented. At test, subjects are presented with one element of the compound (**X**) and retrieve a representation of the entire **AX** compound, with little generalization decrement occurring going from the compound to one of the elements. In other words, at test subjects treat one element as the entire compound, and respond as if they were being presented with the compound. Configural theory has largely been associated with Pearce's (1987) influential model, which also assumes that subjects represent the compound **AX** as whole. What differentiates Pearce's model from the above mentioned configural view is that Pearce's model assumes generalization decrements when a compound is trained and only one element tested (in fact, that is the mechanism by which the model explains overshadowing, the opposite to potentiation), whereas the above mentioned view assumes perfect generalization between the compound and one of the elements. In other words, at test the element is treated as if it were the compound (Rescorla, 1981). Preliminary evidence opposing the within-compound explanation was provided by the test of **A** in Experiment 1 (see Figure

2). In the groups that received training with the compound, conditioned suppression to **A** increased directly with the trace interval between compound termination and US presentation. If subjects' suppression to **A** were related to the trace between compound termination and US presentation, as would be predicated by the within-compound association approach, then conditioned suppression to **A** should have decreased rather than increased as a function of the trace interval. We return to the implications of this in the General Discussion.

Notably, these two approaches agree in predicting that potentiation should be attenuated if the more salient cue is extinguished after compound reinforced training (Davis, Best, Grover, 1988; Durlach & Rescorla, 1980; Kucharski & Spear, 1985; Westbrook, Homewood, Horn, & Clarke, 1983; von Kluge, Perkey, & Peregord, 1996). However, they make this prediction for different reasons. In the case of the within-compound association approach, posttraining extinction of the more salient cue should attenuate potentiation because of weakening of 1) the within-compound association between the two cues (**X** and **A**) and 2) the association between the more salient cue (**A**) and the US. Thus, the within-compound association approach predicts that extinction of **A** should reduce conditioned suppression regardless of whether one tests the less salient cue (**X**) or the compound (**AX**) because potentiation depends on the integrity of the **A**→US association (Durlach & Rescorla, 1980). In the case of the configural approach, extinction of the salient cue **A** should give subjects enough experience for them to distinguish the elements (**A**, **X**) from the compound (**AX**) and therefore attenuate potentiation. That is, experience with one of the stimuli alone will prevent subjects from retrieving the compound **AX** at the time of testing when they are presented with the less salient cue (**X**). However, if subjects are tested with the compound, they should respond strongly because the test compound **AX** is similar to the training compound **AX**. In this situation, extinction of **A** does not generalize to the compound **AX** because when subjects are tested with the compound, they retrieve the memory of the compound that was originally encoded as a unique cue. In fact, Kucharski and Spear (1985) conducted an experiment testing these divergent predictions in preweanling rats and obtained results consistent with a configural approach. That is, extinction of the salient cue **A** decreased conditioned suppression when subjects were tested with the less salient cue (**X**), but not when they were tested with the compound (**AX**). It may be noted that they did not see potentiation in adult rats, but this is consistent with Spear's contention that infant rats have a tendency to configure stimuli based on amodal properties and that this tendency decreases during development. Thus, the fact that they did not see such an effect in adult rats probably is the result of their choice of parameters being sensitive to ontogenetic differences and not favoring potentiation in adult rats.

Experiment 2 was conceptually similar to that conducted by Kucharski and Spear (1985) except for the following: 1) our potentiation effect was assessed in adult rats instead of preweanlings, and 2) instead of using a flavor aversion preparation, we used fear conditioning. Notably, this type of configural approach has received little attention in the associative literature other than by Kucharski and Spear (see Batsell & Blankenship, 2002). To date, the prediction that posttraining extinction of the more salient cue **A** will attenuate potentiation (i.e., conditioned suppression to **X**) has received mixed support in the literature. Some studies have found attenuated potentiation after this manipulation (Davis et al., 1988; Durlach & Rescorla, 1980; von Kluge et al., 1996; Kucharski & Spear, 1985; Westbrook et al., 1983), but other studies have failed to find such attenuation (Droungas & LoLordo, 1991; Lett, 1984). Thus, the present experiment also aimed to further clarify these discrepancies by using a preparation other than flavor aversion. Because, in the face of a null result, we would have not been able to determine whether this was the result of a bad choice of parameters or support for an elemental view on potentiation, and because we have previously seen that increasing the number of trials facilitates extinction (Denniston, Chang & Miller, 2003), we administered a large number of trials (i.e., 210) during the extinction treatment.

In Experiment 2 we used a 2×2 factorial design in which four groups of subjects received compound conditioning embedded in a trace conditioning procedure, which was expected to produce potentiation. During a second phase, two groups experienced massive extinction of the salient cue **A**, and the two remaining groups received comparable handling. At the time of testing, these groups were orthogonally tested either with the target cue alone (**X**) or with the compound (**AX**). Table 2 depicts the critical aspects of the design. If the within-compound approach better explains potentiation, conditioned suppression after extinction of **A** should be attenuated regardless of whether testing is of the target alone or the compound. If a configural explanation better explains potentiation, subject should display attenuated suppression to the target alone (**X**) but not to the compound (**AX**).

Method

Subjects and apparatus—The subjects were 24 female (205 – 270 g) and 24 male (330 – 390 g), experimentally naïve, Sprague-Dawley descended rats obtained from our own breeding colony. Subjects were randomly assigned to one of four groups ($ns = 12$), counterbalanced within groups for sex. The apparatus and stimuli were identical to those used in Experiment 1.

Procedure

Shaping: On Days 1-5 subjects were shaped to lever press for water on a variable-interval 20-s schedule in the same manner as in Experiment 1.

Acquisition: During Day 6, all subjects experienced reinforced compound **AX** trials in the Context Train in a single 45-min long session. All subjects received four **AX-US** pairings with a 20-s trace between termination of the compound CS and presentation of the US. Trials (US presentation) occurred 5, 18, 32 and 40 min into the 45 min session.

Extinction and exposure: On Days 7-9, subjects in condition Extinction received 70 daily nonreinforced presentations of **A** within a 59.5 min session. The mean ITI (from CS termination to CS presentation) was 21 s (range 7 - 35). Subjects in condition Control received equal handling and exposure to the training context during these days.

Reshaping: On Days 10 and 11, all subjects experienced one 60-min session to restabilize leverpressing on the variable-interval 20-s schedule in Context Test.

Test: On Day 12 in Context Test, suppression of baseline leverpressing during presentation of the test stimulus was assessed in all groups. Subjects in Condition Element were tested on **X** alone. Subjects in Condition Compound were tested with the compound **AX**. Each subject received four nonreinforced 30-s presentations of the CS during a 20-min session with the onsets occurring at 6, 10, 14, and 18 min into the session.

Results and Discussion

The results of Experiment 2 are depicted in Figure 3. Subjects that did not experience the extinction treatment suppressed to the target cue (**X**) robustly, in a way similar to what was observed in Experiment 1. Moreover, extinction of the more salient cue **A** decreased conditioned suppression to the target alone (**X**), indicative of the extinction treatment being effective in decreasing potentiation. Interestingly, subjects tested on the compound (**AX**) did not differ as a function of the extinction treatment. This suggests that the attenuated response to the target (**X**) after the extinction treatment resulted from an increased discrimination of the element (**X**) from the compound after the extinction treatment rather than from a weakening of the **A**→US association. Thus, this pattern of results suggests that the configural approach

provides a more accurate description of the present potentiation effect. The following statistics confirm these impressions.

A 2×2 ANOVA with Phase 2 (Extinction vs. Control) and Test (X vs. AX) as factors was conducted on the baseline lever presses during the 60 s immediately before the first CS presentation. This ANOVA did not reveal any main effects nor interactions, smallest $p = .13$. A similar ANOVA conducted on the suppression ratios revealed a main effect of Phase 2 training, $F(1, 44) = 10.48, p < 0.01, MSE = 0.014$, a main effect of test stimulus $F(1, 44) = 14.31, p < 0.01, MSE = 0.014$, and an interaction, $F(1, 44) = 13.43, p < 0.01, MSE = 0.014$, Cohen's $f = 0.50$. The significant interaction suggests that the effect of the extinction treatment was different depending on the test situation. To assess this, we conducted planned comparisons using the overall error term from the omnibus ANOVA. A comparison between Groups Control-Element and Extinction-Element proved significant, $F(1, 44) = 23.82, p < 0.01, MSE = 0.014$, Cohen's $f = 0.68$, suggesting that extinction of the salient cue alleviated conditioned suppression to X alone. This result is anticipated by both the elemental and configural approaches, and consequently does not differentiate between these explanations. The critical comparison between Groups Extinction-Element and Extinction-Compound also proved significant, $F(1, 44) = 27.73, p < 0.01, MSE = 0.014$, Cohen's $f = 0.74$, suggesting that, as predicted by the configural approach, extinction of the salient cue had differential effects depending on the test stimulus. When only the target cue (X) was tested, subjects showed reduced suppression (decreased potentiation). But this did not happen when the compound (AX) was tested, suggesting that the memory for the compound was intact even after 210 extinction trials of A.

The pattern of results in the present experiment supports a configural explanation of the potentiation effect. That is, similar to Experiment 2 of Kucharski and Spear (1985), we observed attenuated conditioned suppression to the target X when the salient element A underwent posttraining extinction, but suppression to the compound AX was not influenced by extinction of A. Both groups showed strong suppression to AX. Although this experiment is conceptually similar to that of Kucharski & Spear, these data are more than a replication because we used adult rats and nonflavor stimuli.

There are, however, two alternative explanations for the results of this experiment that we cannot ignore. In our effort to test subjects in an associatively neutral context, we switched all animals for testing purposes to a context different from that of training and extinction. Because memory of extinction is better retrieved (and expressed) in the extinction context relative to outside the extinction context (Bouton, 1993), it is possible that suppression to the compound was robust despite extinction of A due to renewal (Bouton & Bolles, 1979). Renewal occurs when testing is conducted in a context different from that of extinction. Although the present example represents the weakest form of renewal (AAB), which sometimes does not result in any renewal at all (e.g., Laborda, Witnauer, & Miller, 2008), we cannot categorically reject this possibility. In other words, it could be possible that we failed to observe attenuated suppression to the AX compound because we conducted testing in a context different from that of extinction treatment.

A second alternative explanation for the pattern of results observed in Experiment 2 is summation of residual fear after extinction. That is, Reberg (1972) reported that conditioned responding to two stimuli elementally trained and then extinguished to asymptote recovered when they were tested in compound, as opposed to when they were tested elementally. In other words, Reberg observed residual excitation to a compound even though the individual stimuli had been extinguished to asymptote (i.e., no responding). Applied to our case, it is possible that, although the potentiating cue (A) received 210 extinction trials, some residual excitation may have summated with that of the target cue at the time of testing. Because of these alternative

explanations, we decided to conduct another experiment that further contrasted these two explanations of the potentiation effect.

Experiment 3

Because elemental and configural accounts of potentiation anticipate the same results of many manipulations involving either preexposure or posttraining nonreinforced exposure to the potentiating cue, we decided to approach the problem through an indirect treatment that did not involve manipulating the potentiating (A) cue. One such treatment involves administering training with a distinctly different set of cues that will presumably change the way subjects encode the compound of cues (AX). The reasoning behind this approach is that prior experience (with a different set of cues) can bias the way subjects encode subsequent information. This approach has the advantage of being more realistic because, in a real word situation, behavior is not solely determined by the information encoded on a given situation, but also by prior experiences that may shape current information encoding. The mechanism might be viewed as a learning rule to configure or elementally process simultaneous cues, at least in the experimental context. This approach has received support largely in the human literature (Mehta & Williams, 2002; Melchers, Lachnit, & Shanks, 2004; Melchers, Lachnit, Unger, & Shanks, 2005; Melchers, Shanks, & Lachnit, 2008; Williams & Braker, 1999; Williams, Sagness, & McPhee, 1994) but evidence in rats has been contradictory. Whereas Alvarado and Rudy (1992) observed in rats that prior training with a problem that required a configural solution transferred to a new problem that was otherwise solved in an elemental manner, Williams and Braker (2002) failed to find this effect in rats.

In a human contingency learning task, Williams and colleagues (Williams et al., 1994) consistently failed to observe a cue selection effect such as blocking, and hypothesized that this failure was due to their subjects configuring the two predictors in the second phase of their blocking design. Consequently, they administered prior training with a different set of cues that they hypothesized would encourage subjects to adopt an elemental strategy. Specifically, they administered stimulus relative validity pretraining (BY+ / CY-; Wagner et al., 1968), in which two compounds of cues with a common element are differentially reinforced. This prior training presumably encourages subjects to attend to only one feature of the compound (B or C), which informs them whether the US will be presented. Consistent with their expectations, they observed reliable blocking only when they administered relative validity pretraining. However, this was not seen when they administered an irrelevant treatment in which none of the elemental cues in the pretraining compounds were informative.

In Experiment 3 we used a similar strategy to differentiate elemental and configural explanations of the potentiation effect. We hypothesized that if potentiation results from subjects' encoding the compound as a configuration, prior relative validity pretraining should encourage subjects to treat the compound as separate elements and thus decrease the potentiation effect. In contrast, irrelevant pretraining (control) should not alter the way subjects encode the compound, thus leaving the potentiation effect unaltered. In the former group, an elemental explanation of potentiation predicts either no change or enhanced potentiation because subjects encouraged to process elementally might better discriminate the cues from the compound and consequently link them through a within-compound association.

In Experiment 3 we administered relative validity pretraining (BY+ / CY-) to two groups whereas the remaining two groups received an irrelevant treatment (Control; BY±/ CY±, where ± indicates 50% partial reinforcement) in which no cue is more or less informative than another regarding presentation of the US (see Table 3 for the experimental design). Thus, the control groups received exposure to the two compounds and to the US equal to the relative validity groups, but both compounds were reinforced 50% of the time. Then one group from each of

these conditions was assigned to an elemental trace conditioning treatment (X---US) and the other was assigned to a compound trace conditioning treatment (AX---US) during a second phase. Note that the cues used in the relative validity (or control) treatment were different from the target X and potentiating stimulus A. Finally, all subjects were tested on X. According to an elemental explanation, prior relative validity pretraining should have no impact upon subsequent potentiation training, or might even enhance potentiation training by increasing discriminability of the two cues that compose the compound. In contrast, a configural explanation of potentiation anticipates that relative validity pretraining would encourage subjects to process the compound elementally, thereby decreasing the potentiation effect.

Method

Subjects and apparatus—Twenty four female (189 – 236 g) and 24 male (281 – 366 g) Sprague-Dawley rats similar to those used in Experiments 1-2 were used in this experiment. Subjects were randomly assigned to one of four groups ($n_s = 12$), counterbalanced within groups for sex. The apparatus and stimuli were identical to those used in Experiments 1, and 2, except that the three speakers could now deliver a complex low frequency tone (400 and 420 Hz, 8 dB [C-scale] above the background), and a complex high frequency tone (3000 and 3200 Hz, 10 dB [C-scale] above the background), a click train (6 / s, 5 dB [C-scale] above the background), and a white noise (8 dB [C-scale] above the background). Additionally, a buzzer mounted on each environment chest was able to deliver a buzzing sound at 8 dB (C) above the background sound level. In this experiment, the target cue (CS X) was a 30-s click train and the overshadowing cue (CS A) was a 30-s high frequency complex tone. Stimulus Y was the flashing light. Stimuli B and C were the low frequency tone and the white noise, counterbalanced within groups. The buzzer was used to make delivery of water more conspicuous, thereby facilitating shaping of lever pressing. Thus, a 0.5-s buzzer presentation accompanied delivery of each drop of water reinforcement.

Procedure

Shaping: On Days 1-5 subjects were shaped to lever press for water on a variable-interval 20-s schedule in the same manner as in the prior experiments.

Phase 1: During Days 6-11, all subjects experienced pretraining conditioning in the Train context in daily 100-min long sessions. Subjects in condition Control received daily two reinforced and two nonreinforced trials of both the BY and CY compounds (50% partial reinforcement). Subjects assigned to condition Relative Validity (Rel-Val) received four BY-US trials and four CY-no US trials. Thus, all subjects received four reinforced trials and four nonreinforced trials. The order of these trials was R-R-N-R-N-N-R-N on even days (Days 6, 8, and 10) and N-R-R-N-N-R-R-N on odd (Days 7, 9, and 11) days. The mean ITI for all groups was 12 min (range 6 – 18). On reinforced trials, the US was presented immediately after compound termination (0 trace interval).

Phase 2: On Day 12, subjects in condition Elemental received four reinforced presentations of X with a 20-s trace interval between cue termination and US presentation. Subjects in condition Compound also experienced four trace conditioning trials, but instead of training X alone, they received training of the compound AX. Trials (US presentation) occurred at 5, 18, 32 and 40 min into the 45 min session which occurred in the Train context.

Reshaping: On Days 13 and 14, all subjects experienced one daily 60-min session to restabilize lever-pressing on the variable-interval 20-s schedule in Context Test.

Test: On Day 15 in Context Test, suppression of baseline lever-pressing during presentation of the target CS (X) was assessed in all groups in a manner similar to Experiments 1 and 2.

Results and Discussion

Figure 4 depicts the results of Experiment 3. As can be seen in the figure, subjects that received irrelevant pretraining (Control) behaved exactly like their counterparts in Experiment 1. That is, control subjects that experienced elemental trace conditioning (X----US) displayed less suppression than subjects that experienced compound trace conditioning (AX----US). In other words, these two groups replicated the trace deficit and potentiation effects observed in Experiment 1. This pattern was not observed after relative validity pretraining. Subjects that experienced relative validity pretraining showed attenuated potentiation, consistent with a configural explanation of potentiation in which prior elemental pretraining reduces the extent to which subjects encode the compound as a unique stimulus during potentiation training. Surprisingly, subjects that received relative validity pretraining showed enhanced suppression after elemental trace conditioning, as if the pretraining facilitated the encoding of the X----US trace relationship. Thus, it seems that relative validity pretraining had opposite effects upon compound and elemental training. These impressions were confirmed by the following statistics.

A 2×2 ANOVA with pretraining (Rel-Val vs. Control) and Phase 2 (Elemental vs. Compound) as main factors conducted on the number of lever presses during the 60 s immediately before the first CS presentation did not reveal any main effects nor an interaction, smallest $p = .25$, suggesting that there were no appreciable baseline differences in lever pressing before the presentation of the target CS. A similar ANOVA conducted on the suppression ratios revealed a main effect of Phase 2 training, $F(1, 44) = 8.39$, $p < 0.01$, $MSE = 0.022$, Cohen's $f = 0.39$, and an interaction, $F(1, 44) = 8.45$, $p < 0.01$, $MSE = 0.022$, Cohen's $f = 0.39$. Planned comparisons using the overall error term from the ANOVA revealed that relative validity pretraining attenuated potentiation, in that Group Rel-Val-Compound suppressed less than Group Control-Compound, $F(1, 44) = 4.38$, $p < 0.05$, Cohen's $f = 0.37$. This is consistent with a configural explanation of the potentiation effect. Surprisingly, relative validity pretraining also increased elemental trace conditioning, as Group Rel-Val-Elemental suppressed more than Group Control-Elemental, $F(1, 44) = 4.07$, $p < 0.05$, Cohen's $f = 0.35$. We further discuss this effect in the general discussion.

Overall, the pattern of results from the present experiment supports a configural explanation of potentiation (Kucharski & Spear, 1985; Rescorla, 1981a). That is, these results support the view that subjects encode the compound of cues as a single, configured cue, and, when at the moment of testing they are presented with the less salient cue, they retrieve a representation of the entire compound. In line with this position, pretraining subjects on an elemental problem decreased the potentiation effect. An elemental approach to potentiation such as the within-compound association account of Durlach and Rescorla (1980) anticipates no change or increased responding to the potentiated target X under these circumstances. This prediction was not supported by our results.

Experiment 4

The results of Experiment 3 are surprising because they not only dissociated between different explanations of potentiation, but because they did so by using an indirect manipulation with a set of stimuli different from those of the target task that presumably changed how subjects encoded the compound of cues during potentiation training. One important question that remains to be answered is why the same compound of cues (AX) results in overshadowing when no trace is interposed between compound termination and US presentation (Experiment 1). According to some acquisition-focused models (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981) and some expression-focused models (Gallistel & Gibbon, 2000; Miller & Matzel, 1988), cue competition phenomena like overshadowing result from elemental encoding of the compound with a competitive (or selective) constraint during

learning or retrieval, respectively. If these models are correct and overshadowing does result from elemental encoding of the compound, one could ask whether prior configural training would decrease the degree to which one observes overshadowing. In other words, is it possible to teach subjects to encode in a configural way and decrease the overshadowing deficit? According to Melchers et al. (2008), subjects are capable of both elemental and configural encoding and this depends on stimuli properties, task demands, prior instructions and prior experience. Here we extend their analysis and propose that subjects encode the compound elementally or configurally based in part on contiguity with an outcome. With good contiguity (i.e., no trace), subjects are prone to encode the compound elementally and cue competition phenomena such as blocking and overshadowing are observed. With the introduction of a trace interval, we saw potentiation and the results of Experiments 2 and 3 both suggest that subjects encoded the compound as a configuration.

In Experiment 4 we asked whether prior negative patterning training, which presumably requires configuring, would decrease the overshadowing deficit. During negative patterning training, subjects experience two cues that are reinforced separately but not when presented in compound ($Y \rightarrow US / B \rightarrow US / YB-$). What is important is that, for the subjects to anticipate whether or not the reinforcer will be presented, they need to learn that the compound is different from the sum of the separate elements, or adopt a nonlinear solution (e.g., Shanks, Lachnit, & Melchers, 2008). Conceptually, our experiment is similar to those reported by Melchers et al. (2004) in which they observed less relative validity discrimination ($BY \rightarrow US / CY-$), like the one we used as pretraining in Experiment 3, after two different tasks that required a configural solution. We used a factorial design (see Table 4) in which subjects were assigned to one of four groups based on pre training (Negative patterning vs. Control) and target training (Elemental versus Compound). We hypothesized that if during overshadowing subjects encode the compound elementally, then prior configural ($Y \rightarrow US / B \rightarrow US / YB-$) but not control ($Y \rightarrow US / B \rightarrow US / YC-$) training should decrease overshadowing.

Method

Subjects and apparatus—Twenty-four female (205 - 235 g) and 24 male (295 - 360 g) Sprague-Dawley rats similar to those used in Experiments 1-4 were used. Subjects were randomly assigned to one of four groups ($ns = 12$), counterbalanced within groups for sex. The apparatus and stimuli were identical to those used in Experiments 3, including the stimuli used for Phase 1 of training. That is, Stimulus Y was the flashing light. Stimuli B and C were the low frequency tone and the white noise, counterbalanced within groups. As in all prior experiments, the target cue (CS X) was a 30-s click train and the companion cue (CS A) was a 30-s high frequency complex tone.

Procedure—Phases 1 and 2 were conducted in one [Train] context and all other treatments in the remaining [Test] context in a counterbalanced manner within groups.

Shaping: A 5-day acclimation to Context Test and shaping of lever-press behavior were conducted in daily 60-min sessions like in the prior experiments.

Phase 1: During Days 6-10, all subjects experienced pretraining conditioning in the Train context in daily 120-min long sessions. Subjects assigned to the Control condition received nonreinforced compound presentations of one of two reinforced cues (Y) and a second cue (C; YC-trials), whereas subjects in the Neg-Pat condition experienced nonreinforced compound presentations of the two cues that were elementally reinforced (YB-; see Table 5 for details). On Day 6, all subjects experienced 4 reinforced elemental trials of each cue alone (Y-US and B-US), and 4 nonreinforced trials of the compound (YC for the Control condition, YB for the Neg-Pat condition) in the following order Y-US, B-US, YB-, B-US, Y-US, YB-, Y-US, B-US,

YB-, B-US, Y-US, YB-. On Days 7 and 8, subjects experienced 3 reinforced trials of each cue and 6 nonreinforced trials of the compound (in the following order: Y-US, YB-, B-US, YB-, B-US, YB-, Y-US, YB-, YB-, Y-US, B-US, YB-). On Days 9 and 10, subjects experienced 2 reinforced elemental trials of each cue and 8 nonreinforced compound trials (in the following order: Y-US, YB-, YB-, B-US, BY-, BY-, B-US, BY-, BY-, Y-US, BY-, BY-). Thus, in total all subjects experienced 28 reinforced trials (14 Y-US and 14 B-US) and 32 nonreinforced trials (YB- or YC-, depending on the condition). The mean ITI for all groups was 9.5 min (+/- 4.5 min).

Phase 2: On Day 11, subjects in the Elemental condition received 4 delay X-US presentations. Subjects in the Compound condition received 4 delay AX-US presentations. The US was presented immediately after CS termination. US presentations occurred at 5, 18, 32 and 40 min. into the 45 min. session.

Reshaping: On Days 12 and 13, all subjects experienced one daily 60-min session to restabilize lever-pressing on the variable-interval 20-s schedule in Context Test.

Test: On Day 14 in Context Test, suppression of baseline lever-pressing during presentation of the CS X was assessed in all groups like in the previous experiments.

Results and discussion

The results of Experiment 4 are shown in Figure 5. In the Control condition, in which training was conducted with a delay conditioning procedure, robust behavioral control by X was observed at test after elemental training but not after compound training. That is, when the target cue X was trained in the presence of a more salient cue A, less behavioral control was observed, reflecting an overshadowing deficit. This replicates the pattern observed in Experiment 1 and was expected based on our use of typical parameters for obtaining overshadowing. No such overshadowing deficit was observed in the negative patterning condition. Consistent with our hypothesis based on representational flexibility, prior configural training in the form of negative patterning attenuated the overshadowing deficit, as if subjects no longer encoded the two cues during Phase 2 of training as separate stimuli but rather as a compound, which was fully retrieved at the time of testing. Conditioned suppression in these groups was similar. These impressions are supported by the following statistical analyses.

A 2×2 factorial ANOVA with Phase 1 training (Neg-Pat vs. Control) and Phase 2 training (Elemental vs. Compound) as factors was conducted on the lever presses emitted during the 60 s immediately prior to the first CS presentation and did not result in any main effects nor in an interaction, smallest $p = .52$. This suggests relatively uniform operant responding before any CS test presentation. A similar ANOVA conducted on the suppression ratios revealed a main effect of Phase 2 training $F(1, 44) = 4.34, p < 0.05, MSE = 0.015$, and importantly an interaction $F(1, 44) = 4.65, p < 0.05, MSE = 0.015$, Cohen's $f = 0.27$, which suggests differential effects of Phase 1 training upon Phase 2 training. Planned comparisons detected a reliable overshadowing deficit in the Control condition, as Group Control-Compound suppressed less to the presentation of X than Group Control-Elemental $F(1, 44) = 9.00, p < 0.01, MSE = 0.015$, Cohen's $f = 0.57$. Consistent with our hypothesis, prior configural training attenuated the overshadowing deficit. Group Neg-Pat-Compound suppressed more than Group Control-Compound, $F(1, 44) = 6.84, p < 0.05, MSE = 0.015$, Cohen's $f = 0.49$.

In summary, in this experiment we observed that prior training that encourages configural processing decreased the overshadowing deficit. This nicely complements the findings of Experiment 3, in which we observed that prior elemental training decreased the potentiation effect, which presumably results from subjects' configuring the two cues during trace

conditioning. Moreover, both experiments suggest that rats are capable of using prior experience to process new information in a way that is not accounted for by stimulus generalization along any physical dimension. Rather, it is as if the information contained in prior training modified the way subjects processed subsequent information in Phase 2. Melchers et al. (2004) using Pavlovian conditioning with human subjects reported a finding conceptually similar to that observed in the present experiment. They observed that prior configural training in the form of AB→US, BC-, CD→US, DA- (in Experiment 1), or in the form of A-, AB→US, C→US, CB- (in Experiment 2) retarded acquisition of a discrimination that required an elemental solution in the form of relative validity training (EX→US, FX-). We will further consider this in the General Discussion

General Discussion

The present series of studies was designed to address a major discrepancy in the Pavlovian conditioning literature. When a compound of two cues of different saliences (AX-US) is reinforced and the less salient cue (X) is subsequently tested, researchers typically see less responding to the less salient cue, which is referred to as an overshadowing deficit. Paradoxically, some studies have observed the opposite interaction when two cues of different saliences are reinforced together. That is, in some circumstances behavioral control by the less salient cue is facilitated (Clarke et al., 1979; Galef & Osborne, 1978; Rusiniak et al., 1979), which is referred to as a potentiation effect. The discrepancy is that similar training (AX→US) results in opposite results, and the cause of these opposite behavioral consequences is unknown. In Experiment 1, we assessed whether the introduction of a trace interval between CS (or compound) termination and US presentation would be a determinant of overshadowing and potentiation. With a delay procedure we observed overshadowing, but with a trace conditioning procedure we observed potentiation. This is the first demonstration of both overshadowing and potentiation in a single fear conditioning experiment. More importantly, this experiment was able to isolate one variable (contiguity) that determines the observation of overshadowing or potentiation. In Experiments 2 and 3 we assessed two explanations of why potentiation occurs. That is, we derived contrasting predictions from elemental and configural explanations of potentiation and our results are consistent with a configural account of potentiation, which we further discuss below. Of note, Experiment 3 used an indirect manipulation through which prior experience with a different set of cues presumably modified subject's ability to encode the target compound, thereby decreasing potentiation. Experiment 4 complemented these findings by showing that overshadowing, which presumably results from elemental encoding of the compound of two cues, was abolished when prior configural training was administered with a different set of cues.

As previously mentioned, the configural approach to potentiation has its roots in early writings by Robinson (1932), the Gestalt approach to perception (Wertheimer, 1938, 1958), and Gibson and Gibson's (1955) view on perceptual learning. A basic assumption of this approach is nonlinearity as a result of combining multiple sources of stimulation. Robinson adopted this view when he questioned the necessity of assuming associations between stimuli in situations in which it is perhaps better to assume lack of discrimination between the stimuli. In particular, he wrote "we may lay it down as a safe rule that two or more simultaneously occurring items are not to be called associated unless it can be shown that a present condition of connection has been preceded by a condition in which such connection was lacking, but in which definite discrimination may also have been lacking" (Robinson, 1932; p. 61). This is particularly relevant for the present discussion because the within-compound association model explicitly makes this assumption against which Robinson warned us. Although Robinson questioned some assumptions of the Gestalt psychology, he did agree with the view that the combination of two sources of stimulation might be something different for an organism than the summed stimulation provided by each stimulus separately. We see this to be in agreement with

Wertheimer's own words as a corollary to a book chapter that dealt with principles of perceptual organization. He wrote "perceptual organization occurs from above to below; the way in which parts are seen, in which subwholes emerge, in which grouping occurs, is not an arbitrary, piecemeal and-summation of elements, but is a process in which characteristics of the whole play a major determining role" (Wertheimer, 1958; p 134). Gibson and Gibson (1955) also adopted a similar view in their treatment of perceptual learning.

Applied to the potentiation data observed in the present experiments, this view suggests that during training subjects encoded only a unitary representation of the **AX** compound, and later at test processed the **X** stimulus as the entire **AX** compound, presumably due to the similarity between **X** alone and the **AX** compound. The data in Experiments 2 and 3 support this alternative because we observed: 1) that potentiated conditioned suppression to **X** decreased when subjects had experience with one element **A** of the compound, but this was not the case when the **AX** compound was tested (Experiment 2), and 2) prior experience with a problem that requires discriminating the elements of two compounds composed of *different* stimuli (**BY**→**US**/**CY**-) attenuated potentiation, presumably because this prior experience encouraged an elemental treatment of the **AX** compound (Experiment 3). One assumption implicit in this configural view that contrasts with contemporary configural views of associative learning (Pearce, 1987, 1994, 2002) is that there is little or no generalization decrement from the compound **AX** to presentations of **X** alone at test. One way to view this contradiction is to assume that generalization gradients differ based on the contiguity between **CS** and **US**. That is, it is widely acknowledged that with strong contiguity, generalization gradients are sharper than with weaker contiguity (trace conditioning; Mackintosh, 1974; p, 514).

Although the data in Experiments 2 and 3 provide convergent support for a configural explanation of potentiation, this explanation as it stands does not explain the overshadowing results of Experiment 1 in the delay condition. To account for that data, we would have to modify our interpretation and assume configural encoding with steep generalization gradients from the compound in **AX** to the element **X** at test. Although such a modification seems appealing based on the idea that generalization gradients are broader with weaker contiguity, it does not explain the effect of prior relative validity training that we observed in Experiment 3, nor the decreased overshadowing after prior negative patterning that we observed in Experiment 4. With few exceptions, most contemporary associative models of learning do not explain effects of prior training with a different set of stimuli, and those that do (McLaren & Mackintosh; 2000, 2002) appeal to the idea that prior training generalizes to new stimuli. This generalization is based on shared activation of elements by different stimuli (McLaren & Mackintosh, 2002; also see Schmajuk & Larrauri, 2006, 2008). However, it is difficult to see how these models handle the inverse (synergistic, as opposed to competitive) relationship between **X** and **AX** observed when there is a trace interval between compound termination and **US** presentation (i.e., potentiation). Moreover, these models do not provide a systematic analysis of the pattern of data collected in Experiments 3 and 4.

Thus, our entire pattern of results seems to be more consistent with the view that subjects are capable of encoding information in both elemental and configural ways, and that this depends on a number of different factors. Applied to the results of Experiment 1, and based on the evidence from Experiments 2 and 3 that potentiation results from configural encoding of the **AX** compound, we are inclined to the view that with delay conditioning subjects encode the compound **AX** elementally and display overshadowing, but that with trace conditioning subjects encode the compound as a configuration and display potentiated performance to **X**. The data of Experiments 3 and 4 provide strong support to this interpretation. Williams and his colleagues (Williams et al., 1994; Williams & Braker, 1999) originally articulated the idea of representational flexibility, and this notion has recently been reviewed by Melchers et al., (2008). Basically, Melchers and colleagues challenged current theories of learning that assume

either elemental processing or configural processing by reviewing evidence suggesting that both types of processing could be used depending on stimuli properties, task demands, prior instructions, and prior experience. Within that framework, our data suggest that contiguity (i.e., trace interval) can also determine whether elemental or configural processing occurs, which in turn results in overshadowing and potentiation, respectively. Of particular relevance for the present discussion are the effects of experience prior to target learning.

Evidence from one series of rodent studies suggests that prior training in an instrumental task that requires a configural solution can influence subsequent performance on configural discriminations (Alvarado & Rudy, 1992). These data support the idea that encoding flexibility may be manipulated by prior seemingly unrelated experiences. Similar findings have been observed in human using contingency learning tasks (Mehta & Williams, 2002; Williams & Braker, 1999; Williams et al., 1994) and Pavlovian conditioning experiments (Melchers et al., 2004; 2005). In the recent debate fostered by this view (Melchers et al., 2008), the generality of these effects across species was questioned because, with one exception (Alvarado & Rudy, 1992), all these demonstrations of encoding flexibility have been observed with human subjects. That is, because Williams failed to obtain a pretraining effect in an experiment with rats as subjects (Williams & Braker, 2002), Livesey and Harris (2008), and Wagner and Vogel (2008) requested further tests of these pre-training effects in Pavlovian tasks such as those used in the development and testing of current associative theories of learning (Harris, 2006; Mackintosh, 1975; Pearce, 1987, 1994, 2002; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Stout & Miller, 2007; Wagner 1981; 2003). The results of Experiments 3 and 4 speak directly to this issue by adding generality to their findings across task and species.

One may argue that the pretraining treatments of Experiments 3 and 4 did not fully reverse the either configural (Experiment 3) or elemental (Experiment 4) encoding assumed to underlie potentiation and overshadowing, respectively. However, complete reversal should not be expected. Configural and elemental encoding, as Melchers and colleagues (2008) have proposed, are extremes of a continuum that depend on a number of factors, among which are stimuli properties and prior training. If trace conditioning favored configural processing of the compound, prior elemental training in Experiment 3 (which presumably biases subjects towards elemental encoding) should decrease the potentiation effect, but not fully revert it to overshadowing, because the introduction of a trace between compound termination and US presentation should still have biased subjects towards configural encoding. A similar argument stands for the outcome of Experiment 4. A second argument that could be raised is that we only used auditory cues, which should favor the operation of configural processes and thus the observation of potentiation. While this is a legitimate concern, it does not explain why we observed overshadowing when no trace was interposed between compound termination and US presentation. That is, if potentiation was observed only because we combined two auditory cues, then we should have not observed overshadowing with delay conditioning. Moreover, the two auditory cues that we used in these experiments are similar to those used in several other experiments that successfully reported overshadowing effects (Amundson, Witnauer, Pineño, & Miller, 2008; Urushihara & Miller, 2008). Further research using stimuli of different modalities will determine the generality of these findings. One interesting issue raised by our data is why a trace interval encourages configural encoding. In other words, why does introducing a trace between compound termination and US presentation cause a switch from competitive to facilitative interaction between the two cues? Although it is speculative, we are inclined to the view that the trace interval between compound termination and US presentation introduces ambiguity (or decreases informational value of each of the cues), and that under such circumstances subjects encode the compound as a unitary representation (i.e., configure the two cues). That is, when the cues are good predictors of the outcome, subjects may select between the available cues based on intensity (i.e., overshadowing), or prior training (i.e., blocking). But when these cues do not unambiguously predict the presentation of the outcome,

subjects may use the cues based on total intensity of the compound. In other words, when the compound of cues has perfect contiguity with the US (i.e., delay conditioning), subjects encode the compound elementally, which results in a competitive interaction between the cues. The data in our Experiment 4 further supports this interpretation by showing that prior configural training decreases the overshadowing deficit. On the contrary, extinction of the potentiating cue A in Experiment 2 decreased conditioned suppression to the target X (i.e., mediated extinction). This parallels several reports that also observed decreased responding to the potentiated cue X after extinction of the potentiating cue A (Davis et al., 1988; Durlach & Rescorla, 1980; von Kluge et al., 1996; Kucharski & Spear, 1985; Westbrook et al., 1983; but see Droungas & LoLordo, 1991; Lett, 1984). Moreover, recent experiments by Batsell and his colleagues on potentiation and *augmentation* (i.e., the reversal of blocking; Batsell & Batson, 1999; Batsell et al., 2001; Batson & Batsell, 2000; Batson, Watkins, Doyle, & Batsell, 2008) have also supported a configural analysis of these synergistic interactions (see Batsell & Paschall, in press, for a review). Finally, Bouton and his colleagues also favored a configural analysis of potentiation after they manipulated the manner of stimulus presentation (Bouton et al., 1986) or salience dimensions (Bouton et al., 1987).

In two recent series of experiments testing predictions based on SOCR (Stout & Miller, 2007), we have observed in delay conditioning that overshadowing vanishes with long CS durations (Sissons, Urcelay, & Miller, 2008; Urushihara, Stout, & Miller, 2004). In both series we observed that with long CSs, overshadowing decreased and a potentiation-like effect was observed. Of note, these observations are strikingly similar to that of Westbrook and colleagues in a taste aversion preparation, which was interpreted as potentiation being better observed with long cues (Westbrook et al., 1983). Moreover, recent studies conducted in the water maze have found synergistic and competitive interactions between a beacon and landmark cues in spatial learning. For example, Timberlake, Sinning and Leffel (2007; also see Graham, Good, McGregor, & Pearce, 2006; Pearce, Graham, Good, Jones, & McGregor, 2006, for further evidence of potentiation in water-maze preparations) observed augmentation of landmark cues by a hanging beacon (Exps. 1 and 4) and blocking by a pole beacon that was *connected* to the platform by a rod (Exp. 3) rather than hanging (also see Roberts & Pearce, 1999). This is consistent with our Experiment 1 data because we observed overshadowing when our compound was *connected* to the US (delay procedure) but not when there was a temporal trace between compound termination and US presentation. In other words, if one assumes that contiguity depends on both temporal and spatial dimensions, and determines whether cue interactions are competitive or facilitative, our data are consistent with this report. These results suggest that cue competition and cue facilitation effects are readily observed in spatial learning tasks, which together with our fear conditioning data, and all the available flavor aversion experiments reviewed above, suggest that these interactions are observed in widely different preparations (also see Schachtman et al., 1987, for similar observations in instrumental learning with pigeons). In addition, recent data from Batsell's laboratory has shown a similar interaction between contiguity and type of training to the one we observed in Experiment 1. Using flavors they observed overshadowing of one flavor by another flavor when they used a delay procedure and potentiation of favor by flavor when they interposed a 2-h trace between the end of compound presentation and LiCl administration (Batsell & Wakefield, 2008). Thus, this interaction has now been observed in instrumental learning, flavor aversion, and fear conditioning.

In summary, this series of experiments suggests two general conclusions. First, potentiation and overshadowing can be observed in Pavlovian fear conditioning with two auditory cues and one cause of these opposite outcomes is contiguity. When contiguity is good (i.e., delay conditioning) the two cues compete for behavioral control and overshadowing is observed. When contiguity is not good (i.e., trace conditioning), the interaction becomes facilitative presumably due to subjects configuring the two cues into a configured stimulus, which they

retrieve at test given testing with the less salient cue. Note that previous demonstrations of both overshadowing and potentiation have mostly been achieved through between-experiments comparisons in which changes in the manner of presentation or physical attributes of the stimuli were manipulated. These observations do not directly speak to the learning mechanism that governs each effect, whereas here we demonstrated with the same stimuli a determinant (contiguity) of each effect. Second, both configural and elemental encoding of the compound are malleable through prior experiences, so that prior elemental training even with different cues decreased potentiation in Experiment 3 and overshadowing in Experiment 4. This adds to the body of literature recently reviewed by Melchers et al. (2008) suggesting the possibility of flexible encoding of representations based on stimuli properties, task demands, prior instructions, and prior experience. Thus, we see that prior experience can determine the encoding of a compound under circumstances that can yield configural (i.e., trace conditioning) or elemental (i.e., delay conditioning) processing of a compound. Moreover, one could speculate that prior demonstrations of both overshadowing and potentiation in flavor aversion (Bouton et al., 1987) and in spatial learning (Graham et al., 2006; Pearce et al., 2006; Timberlake et al., 2007) were achieved by varying stimuli properties, whereas here we have demonstrated a similar effect by modifying subjects through prior experience.

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Figure 1.

Mean suppression ratios to test presentations of X in Experiment 1. See Table 1 for group treatments and procedural details. Note that lower values denote more suppression and larger values denote less suppression. Error brackets depict the standard error of the mean for each group.

Figure 2.

Mean suppression ratios to test presentations of A in Experiment 1. See Table 1 for group treatments and procedural details. Note that lower values denote more suppression and larger values denote less suppression. Error brackets depict the standard error of the mean for each group.

Figure 3.

Mean suppression ratios to test presentations of X or AX in Experiment 2. See Table 2 for details. Subjects were tested with the target X alone (Elemental) or AX (Compound). Note that lower values denote more suppression and larger values denote less suppression. Error brackets depict the standard error of the mean for each group.

Figure 4. Mean suppression ratios to test presentations of X in Experiment 3. See Table 3 for group treatments and procedural details. Note that lower values denote more suppression and larger values denote less suppression. Error brackets depict the standard error of the mean for each group.

Figure 5.

Mean suppression ratios to test presentations of X in Experiment 4. See Table 4 for group treatments and procedural details. Note that lower values denote more suppression and larger values denote less suppression. Error brackets depict the standard error of the mean for each group.

Table 1

Design of Experiment 1

Group	Shaping 5 days	Phase 1 1 day	Reshaping 2 days	Test 1 day	Expect Test X
Elem-0	Ctx	4 X-US	Ctx	X	CR
Elem-10		4 X—US			Cr
Elem-20		4 X-----US			cr
Comp-0		4 AX-US			cr
Comp-10		4 AX—US			Cr
Comp-20		4 AX-----US			CR

Note: US= footshock. Numbers next to the stimuli indicate number of trials. Stimulus X was a 30-s soft clicker and A was a 30-s complex tone. Phase 1 was conducted in one context (Train) and the rest of the treatments in a different context (Test). Group labels refer to type of training and trace interval between CS (or compound) termination and US presentation. Expectations are based on previous experiments looking at reinforced compound cue trials when trace intervals are imposed. CR = strong conditioned response; Cr = moderate conditioned response; cr = weak conditioned response.

Table 2

Design of Experiment 2

Group	Shaping 5 days	Phase 1 1 day	Phase 2 3 days	Reshaping 2 days	Test 1 day	Expect Within-Compound	Expect Config
Control-Element	Ctx	4 AX----US	Ctx alone	Ctx	X	CR	CR
Extinction-Element			210 A-			cr	cr
Control-Compound			Ctx alone		AX	CR	CR
Extinction-Compound			210 A-			cr	CR

Note: US = footshock; - = nonreinforced trial; Ctx = context. Numbers next to the stimuli indicate number of trials in that phase. Group labels refer to Phase 2 treatment (Control vs. Extinction) and Test (Element [X] vs. Compound [AX]). Phases 1 and 2 were conducted in one context (Train) and all other treatments in the remaining context (Test). Expect Within-Compound = expectations based on an elemental explanation of potentiation that assumes a strong association between A and X. Expect Config = expectations based on a configural explanation of potentiation. CR = strong conditioned response; cr = weak conditioned response.

Table 3

Design of Experiment 3

Group	Shaping 5 days	Phase 1 6 days	Phase 2 1 day	Reacc 2 days	Test 1 day	Expect Within-Compound	Expect Config
Control-Element	Cix	24BY± / 24CY±	4 X-----US	Cix	X	cr	cr
Control-Compound			4 AX-----US			CR	CR
Rel-Val-Element		24BY+ / 24CY-	4 X-----US			cr	cr
Rel-Val-Compound			4 AX-----US			CR	cr

Note: US or + = footshock; ± = 50% partial reinforcement. Numbers next to the stimuli indicate total number of that type of trials in that phase. Slashes indicate interspersed trials. Phases 1 and 2 were conducted in one context and the rest in a different context. Group labels denote treatment during Phase 1 (Control vs. Rel-Val) and during Phase 2 (Elemental vs. Compound training). Expect Within-Compound = expectations based on an elemental explanation of potentiation that assumes a strong association between A and X. Expect Config = expectations based on a configural explanation of potentiation that assumes that relative validity pretraining with unrelated cues encourages elemental encoding of the compound and attenuate the potentiation effect. CR = strong conditioned response; cr = weak conditioned response.

Table 4

Design of Experiment 4

Group	Shaping 5 days	Phase 1 5 days	Phase 2 1 day	Reacc 2 days	Test 1 day	Expect
Control-Element	Ctx	14Y+ / 14B+ / 32 YC-	4 X-US	Ctx	X	CR
Control-Compound			4 AX-US			Cr
Neg-Pat-Element		14Y+ / 14B+ / 32 YB-	4 X-US			CR
Neg-Pat-Compound			4 AX-US			CR

Note: US or + = footshock; ± = 50% partial reinforcement. Numbers next to the stimuli indicate total number of that type of trials in that phase. Slashes indicate interspersed trials. Phases 1 and 2 were conducted in one context and the rest in a different context. Group labels denote treatment during Phase 1 (Control vs. Rel-Yal) and during Phase 2 (Elemental vs. Compound training). Expect = expected stimulus control assuming negative patterning training of stimuli unrelated to the target cues encourages overshadowing. CR = strong conditioned response; cr = weak conditioned response.