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Conditioned suppression is an inverted-U function of footshock intensity

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Abstract

Most theories of associative learning assert that conditioned responding to a target cue is a monotonically increasing function of unconditioned stimulus (US) intensity. In a lick suppression preparation with rats, a cue was paired with either a 0.4-, 0.6-, 0.8-, 1.0-, 1.2-, or 1.4-mA footshock in Experiment 1a and either a 0.3-, 0.8-, 1.3-, or 1.8-mA footshock in Experiment 1b. Subsequent suppression to the cue was an inverted-U function of the US intensity. Experiment 2 demonstrated that massive extinction of the training context and compound conditioning can each attenuate the response decrement caused by training with a high-intensity US. The sometimes competing retrieval model (Stout & Miller, 2007) provided a better fit to the data than several other models of associative learning.

Keywords

US intensity; fear conditioning; cue competition; computational modeling

After pairings of a conditioned stimulus (CS) and an unconditioned stimulus (US), the CS often evokes a conditioned response, the strength of which is determined in large part by specific procedural parameters (Pavlov, 1927). It is often asserted that the conditioned response strength is directly affected by the number of trials, duration of the intertrial interval (ITI), CS-US contiguity, CS-US contingency, and CS and US intensities (e.g., Domjan, 2005). There is a strong empirical basis for these assertions. For example, in most situations, behavioral control by the CS is an increasing function of the magnitude of the US and the number of CS-US pairings. However, some data contradict this view. For example, Pavlov discovered that behavioral control by a CS is often attenuated when a massive amount of training is administered, relative to a moderate amount. The so-called overtraining effect is widely cited, has been replicated in several preparations, and repeatedly analyzed in detail (e.g., Urcelay, Witnauer, & Miller, 2010). The related observation that a high intensity US sometimes supports weaker conditioned behavioral control than a moderate intensity US is cited less often than the overtraining effect (e.g., Davis & Astrachan, 1978).

In aversively motivated preparations, many reports suggest that fear conditioning is a direct function of the intensity of the US. For example, Annau and Kamin (1961) measured conditioned leverpress suppression after training with 0.28-, 0.49-, 0.85-, 1.55-, or 2.91-mA footshock. Three measurements were related to the intensity of the footshock. First, subjects trained with the high intensity footshock required fewer trials to reach asymptote than

subjects trained with weaker footshocks. Second, the asymptotic levels of behavioral control were generally higher among subjects trained with a stronger footshock. Third, extinction was slower among subjects trained with a high-intensity footshock than among subjects trained with weaker footshocks. Recent experiments by Morris and Bouton (2006) investigated the effect of US intensity on several performance measurements in both aversive (i.e., fear) and appetitive conditioning paradigms. In appetitive conditioning, they administered pairings of a clicker (CS) with a US consisting of one, two, four, or eight food pellets. Critically, they observed that asymptotic performance and the rate of acquisition were directly related to the intensity of the US. Morris and Bouton conducted a similar experiment in aversive conditioning, specifically a freezing preparation. The US was a 0.2-, 0.4-, 0.6-, or 0.8-mA footshock. Morris and Bouton observed that the point in training (i.e., the number of trials) at which freezing emerged and the asymptotic amount of freezing was directly related to the intensity of the footshock. Thus, the results of Morris and Bouton as well as Annau and Kamin suggest that rate of learning and asymptotic performance are directly related to the intensity of the US, which is consistent with the overwhelming majority of models of Pavlovian conditioning.

In contrast to Annau and Kamin's (1961) and Morris and Bouton's (2006) results, there are two reports that indicate that performance in Pavlovian situations is a nonmonotonic, inverted-U function of footshock intensity. For instance, Davis and Astrachan (1978, Experiment 1) investigated the extent to which a CS potentiates a startle response after being paired with 0.2-, 0.4-, 0.8-, or 1.6-mA footshock. They observed a weak startle response after training with a 0.2-mA footshock and a robust startle response after training with a 0.4-mA footshock, which is compatible with the results of Annau and Kamin (1961). However, an attenuated startle response was observed after training with either a 0.8- or 1.6-mA footshock. Thus, fear potentiated startle seems to be an inverted-U function of the intensity of the US. Follow-up studies replicated this finding with either a 1.0- or a 3.0-mA footshock and demonstrated that it is not driven by the freezing response reducing the magnitude of the startle response because freezing also declines after training with a high intensity footshock (Leaton & Borszcz, 1985).

Towards finding a theoretical mechanism to explain the somewhat mixed literature concerning the effect of US intensity, we conducted computer simulations of the sometimes competing retrieval (SOCR) model (Stout & Miller, 2007). SOCR makes two basic assertions. First, associative learning is based on contiguity (local error reduction to be precise) rather than total error reduction as is assumed to operate in most associative models (e.g., Rescorla & Wagner, 1972). Thus, in SOCR, CSs do not compete with each other for entry into associations as they do in total error reduction models. As a result, according to SOCR, more information is encoded by animals during training. Second, the magnitude of responding at test is determined by a comparison between the strength of the US representation activated through the direct target CS (X)-US association and the strength of the US representation activated through the associative linkage of X-training context-US. A strong X-US association relative to the X-training context-US associative linkage presumably results in strong behavioral control and the opposite relationship results in weak behavioral control.

We reasoned that SOCR would be most likely to accommodate both the inverted-U results (e.g., Davis & Astrachan, 1978) and the monotonic patterns (e.g., Annau & Kamin, 1961) if the training context is less salient than the CS. In these situations, the context-US association should be more sensitive than the CS-US association to increases in US salience after the CS-US association has asymptoted. That is, the CS-US association is expected to asymptote quickly relative to the context-US association. Hence, when the context is of low salience or when the context extinguishes during the intertrial interval, increases in US

intensity (i.e., salience) should increase the strength of the contextually-mediated indirectly activated US representation (which attenuates responding) more than the strength of the directly activated US representation, assuming that the CS-US association has already reached asymptote early in training. Figure 1 depicts the results of a SOCR simulation that used Stout and Miller's (2007) parameters. See the Appendix for details of SOCR. Clearly, the model predicts that responding should be an inverted-U function of US intensity. However, it is possible that the parameters developed by Stout and Miller constitute a peculiar set of parameters, so we sought to determine how the inverted-U prediction changes as a result of systematic changes in the model's free parameters. To this end, we tried every possible combination of the parameter values that could be created by assigning each continuous parameter seven distinctly different values. SOCR anticipated the inverted-U pattern across a wide range of parameters (66% of the combinations). Also, SOCR was found to predict the inverted-U pattern only in situations that established the training context as a moderately effective comparator stimulus (e.g., when the value of the context salience parameter was moderate as opposed to high or low and when extinction of the context during the ITI was relatively small because the extinction parameter was low). Thus, based on SOCR, the inverted-U pattern should be robust in situations that encourage a strong training context-US association that is established at a slower rate than the CS-US association. In situations in which the context-US association reaches asymptote quickly, the inverted-U pattern should not be observed.

The purpose of the present experiments was twofold. First, we sought to document that conditioned lick suppression is sometimes an inverted-U function of footshock intensity. This would constitute a replication of results like those of Davis and Astrachan (1978). Second, we sought to test the predictions of SOCR concerning the effect of US intensity on suppression and the role of the context in determining the relationship between US intensity and suppression. In Experiments 1a and 1b, we replicated the finding that responding to a CS is an inverted-U function of US intensity. Experiment 2 replicated the critical result of Experiment 1 and tested specific predictions of SOCR about the interaction between training with a high intensity US and either compound conditioning or posttraining extinction of the context. Compound conditioning was expected to reduce the influence of the X-context and context-US associative linkage thereby eliminating diminished responding at high US intensities, and posttraining context extinction was expected to weaken the context-US association thereby also eliminating attenuated behavioral control at high US intensities.

Experiment 1a

SOCR's prediction that responding to a target CS is an inverted-U function of US intensity was evaluated in Experiment 1a, in which conditioned suppression to a target CS was measured after 20 pairings of the target CS (X) with a footshock US. The intensity of the footshock was 0.4-, 0.6-, 0.8-, 1.0-, 1.2-, or 1.4-mA, across different groups (see Table 1). Based on prior observation of strong suppression in our laboratory after training with a 1.0-mA footshock US (e.g., Witnauer, Urcelay, & Miller, 2008), we expected to observe strong suppression in Groups 0.8 mA, 1.0, and 1.2 mA. Based on SOCR simulations and on previous parametric studies, we expected to observe attenuated suppression in Groups 0.4 mA, 0.6 mA, and 1.4 mA. This pattern of responding would indicate that suppression is an inverted-U function of US intensity.

Method

Subjects—Subjects were 36 female and 36 male Sprague-Dawley, experimentally naïve, young adult rats, bred in our colony. Body weight range for females was 176–218 g and for males was 256–368 g. Subjects were individually housed and maintained on a 16-hr light / 8-hr dark cycle with experimental sessions occurring roughly midway through the light

portion. Subjects had free access to food in the home cage. One week prior to initiation of the experiment, water availability was progressively reduced to 20-min per day, provided soon after all scheduled treatments for that day. Subjects were randomly assigned to one of six groups: 0.4 mA, 0.6 mA, 0.8 mA, 1.0 mA, 1.2 mA, and 1.4 mA ($n_s = 12$), counterbalanced for sex. From the time of weaning until the start of the experiment, all animals were handled for 30 s three times per week.

Apparatus—Twelve identical copies of each of Chamber V and twelve copies of Chamber R were used. Chamber V was a 27-cm long box in a truncated-V shape (29.5-cm height, 21.5-cm wide at top, and 5.5-cm wide at bottom). The floor was constructed of two 27-cm long plates, 2-cm wide, with a 1.5-cm gap between the two plates. A 0.5-s constant-current footshock (the intensity of which depended on group assignment) produced by a high voltage AC circuit in series with a 1.0-M Ω resistor could be delivered through the metal walls and floor of the chamber. The ceiling was clear Plexiglas, the front and back walls were black Plexiglas, and the side walls were stainless steel. Each copy of Chamber V was housed in a separate sound- and light-attenuating environmental isolation chest. The chamber was illuminated by a 7-W (nominal at 120 VAC, but driven at 50 VAC) light bulb mounted on the inside wall of the environmental enclosure approximately 30-cm from the center of the experimental chamber. The light entered the chamber primarily by reflection from the ceiling of the environmental chest.

Chamber R was rectangular, measuring 24.0 $\times$ 9.0 $\times$ 12.5-cm (l $\times$ w $\times$ h). The walls and ceiling of Chamber R were clear Plexiglas, and the floor comprised of stainless steel rods measuring 0.5-cm diameter, spaced 1.5-cm apart (center to center). Each copy of Chamber R was housed in separate light- and sound-attenuating environmental isolation chambers. Each chamber was dimly illuminated by a 2-W (nominal at 120 VAC, but driven at 50 VAC) incandescent house light mounted on an inside wall of the environmental chest located approximately 30-cm from the animal enclosure.

Each R chamber could be equipped with a water-filled lick tube that extended 1-cm into a cylindrical niche, which was 4.5-cm in diameter, left right centered, with its bottom 1.75-cm above the floor of the apparatus and 5.0-cm deep. There was a photobeam detector 1-cm in front of the lick tube that was broken whenever the subject licked the tube. A 45- Ω speaker on the inside wall of the isolation chests could deliver a 30-s click train (6 Hz) at 6 dB above background that served as cue X. Ventilation fans in each enclosure provided a constant 76-dB background noise. All auditory cues were measured on the C-scale. The light intensities inside the two types of chambers were approximately equal due to the difference in opacity of the walls of Chambers V and R.

Procedure—Training occurred in Chamber R, whereas Acclimation, Reacclimation, and Testing occurred in Chamber V. Testing in an associatively neutral context eliminated differences between groups with respect to fear of the test context, which might otherwise summate at test with fear of the test CS.

Acclimation: On Days 1 and 2 all subjects were acclimated to the test context (i.e., Chamber V) during daily 60-min sessions. Free access to water filled lick tubes was provided in the experimental chambers and no nominal stimuli were presented.

Training: On Days 3 and 4, subjects received training consisting of 10 CS-US pairings per daily session in Chamber R. The CS and US were coterminous with the US being initiated 0.5 s before termination of the CS. Trials occurred at 9, 19, 23, 30, 42, 51, 61, 73, 81, and 92 min into each 100-min session.

Reacclimation: On Days 5 and 6, all subjects were reacclimated to Chamber V in daily 60-min sessions. Subjects had free access to the water-filled lick tubes, and no nominal stimuli were programmed to occur. The purpose of these sessions was to reestablish a stable rate of drinking behavior (which might have been differentially disrupted by the footshock US); thereby providing similar baseline behavior across the groups upon which conditioned lick suppression was to be assessed.

Testing on X: On Day 7, X was tested in Chamber V. Test sessions were 16-min in duration. Subjects completed 5 consecutive seconds of water consumption before the test stimulus was presented, ensuring that all subjects were drinking at the time of CS onset. Lick-suppression values were calculated based upon the amount of time required to complete an additional 5 s of water consumption after the presentation of the test CS. A 15-min ceiling was placed on test scores.

Data analysis: Data were normalized using a log (base 10) transformation, allowing for parametric statistical analysis. An alpha level of .05 was used on all inferential tests.

Results and Discussion

The results of Experiment 1a are depicted in Figure 2. The mean latencies to resume drinking in the presence of X were an inverted-U function of footshock intensity. Suppression in Group 0.4 mA was smaller than that in Groups 0.6 mA, 0.8 mA, and 1.0 mA. Group 1.4 mA suppressed less relative to groups that received a moderate intensity footshock. The following analysis confirmed these conclusions.

A one-way analysis of variance (ANOVA) of group on log latencies to drink for five cumulative seconds after being placed in the test context (i.e., pre-CS scores) failed to detect an effect Group, $F(5, 66) = 0.90$, $p > .48$, $MSE = 0.02$ which suggests that US intensity during training did not appreciably affect fear of the test context. A similar ANOVA on latencies to resume drinking after onset of CS X revealed an effect of group, $F(5, 66) = 5.77$, $MSE = 0.16$, Cohen's $f = 0.58$, which indicates that suppression to X was affected by the intensity of the footshock with which it was paired. A quadratic equation ($y = 1.9 * x^2 + 3.8 * x + 0.078$) provided an excellent fit to the results of Experiment 1a, which supports the prediction that suppression is an inverted-U function of US intensity. Planned comparisons were used to test specific hypotheses. Group 0.4 mA suppressed less to X than Group 0.6 mA, $F(1, 66) = 4.49$, which replicates the finding that acquired performance increases as a function of US intensity (e.g., Morris & Bouton, 2006). A comparison between Group 1.0 mA and Group 1.2 mA failed to detect a difference, $p > .78$. Suppression in Group 1.4 mA was marginally less ($.05 < p < .10$) than in Group 1.2 mA, $F(1, 66) = 3.70$. Also, Group 1.4 mA suppressed less than the pooled suppression of Groups 1.2 mA and 1.0 mA (two-tailed), $F(1, 66) = 4.25$, which indicates that suppression to a target stimulus is attenuated when the target is trained with a high intensity relative to a moderate intensity footshock.

Overall, the results of Experiment 1a support the view that suppression is an inverted-U function of footshock intensity. Responding in Group 1.4 mA was reduced relative to groups that received a moderate intensity footshock. Also, we replicated the observation that, up to a point, stronger footshocks can produce more suppression. That is, suppression was weaker among subjects that received the weak footshock than among subjects that received the intermediate footshock. A limitation to the results of Experiment 1a is that we measured suppression after a relatively narrow range of shock intensities. One consequence of this is that the decrease in behavioral control with the most intense footshock used was only moderate.

Experiment 1b

The purpose of Experiment 1b was to replicate the critical results of Experiment 1a using a broader range of footshock intensities. To this end, the experiment summarized in the lower half of Table 1 was conducted. Subjects received a 0.3-, 0.8-, 1.3-, or 1.8-mA footshock. Based on SOCR's predictions and on previous research, we expected weak responding in Groups 0.3 mA and 1.8 mA relative to 0.8 mA and 1.3 mA.

Methods

Subjects, Apparatus, and Procedure—Subjects were 24 female (160–205 g) and 24 male rats (244–311 g) that were bred and maintained in exactly the same way as in Experiment 1a. Subjects were randomly assigned to one of four groups ($n = 12$): 0.3 mA, 0.8 mA, 1.3 mA, and 1.8 mA. The apparatus was the same as Experiment 1a except for US intensity. The procedure was identical to that of Experiment 1a.

Results and Discussion

The results of Experiment 1b are depicted in Figure 3. In support of SOCR's predictions and replicating the pattern of Experiment 1a, suppression to the target stimulus was an inverted-U function of US intensity. Subjects that received pairings of X with a 0.3- or 1.8-mA footshock suppressed less than subjects that received 0.8- or 1.3-mA footshocks. The following statistical analysis supported these observations.

A one-way ANOVA using group as a between-subjects factor on log latencies to initiate drinking after being placed in the test context revealed an effect, $F(3, 44) = 3.68$, $MSE = 0.03$. The mean log latencies were 1.01 in Group 0.3 mA, 1.22 in Group 0.8 mA, 1.11 in Group 1.3 mA, and 1.02 in Group 1.8 mA. To statistically control for differences among the groups in baseline drinking, we included baseline drinking as a covariate in an analysis of covariance (ANCOVA). Group was the categorical predictor, log baseline drinking was the continuous predictor, and latency to resume drinking in the presence of X was the dependent variable. This analysis detected an effect of group, $F(3, 43) = 14.77$, $MSE = 0.13$, Cohen's $f = 0.94$. As using an ANCOVA to compensate for baseline differences is not fully justifiable, we also conducted an ANOVA. The ANOVA also revealed an effect of group $F(3, 43) = 18.92$, $MSE = 0.13$. A quadratic equation ($y = -1.4 * x^2 + 3.3 * x + 0.26$) provided an excellent fit to the data (see Figure 3). Using the error terms from the ANCOVA, planned comparisons were conducted to test specific hypotheses. Suppression among subjects that received 0.8-mA footshocks was greater than those that received 0.3-mA footshocks, $F(1, 43) = 28.67$, and those that received 1.8-mA footshocks, $F(1, 43) = 6.58$. Subjects that were trained using 0.8-mA footshocks were not reliably different from subjects that received 1.3-mA footshocks, $p > .69$. Subjects that received 1.3-mA footshocks suppressed more than subjects that received 1.8-mA footshocks, $F(1, 43) = 9.86$. Repeating the planned comparisons using the error term from the ANOVA produced higher F -values than the ANCOVA for each comparison.

The results of Experiment 1b (in conjunction with the results of Experiment 1a) suggest that conditioned suppression is an inverted-U function of footshock intensity. This confirms the prediction of SOCR and constitutes a replication of findings in fear potentiated startle. SOCR explains this finding by asserting that low responding was observed in the low intensity shock conditions (i.e., 0.3 mA) because the salience of the US in these groups was not sufficient to establish a strong X-US association. In contrast, the intermediate intensity US (i.e., 0.8 and 1.3 mA) was sufficiently salient to establish a strong, asymptotic X-US association. However, the intermediate salience was not sufficient to establish a strong context-US association because the context was of lower salience and extinguished during

the ITI. Increasing the footshock intensity to 1.8 mA had little impact on the X-US association because it was asymptotic after training with a 1.3-mA footshock. Training with a high intensity footshock was sufficient to establish an asymptotic context-US association within 20 trials, which allowed the context to compete with the target cue. These conclusions need to be qualified because of the between-group differences in baseline responding. Importantly, the critical difference observed in Experiment 1 (less responding in Group 1.8 mA than in Group 0.8 mA) was replicated in Experiment 2.

Experiment 2

The purpose of Experiment 2 was threefold. First, we sought to replicate the decrease in responding that can be observed when a target CS is trained with a high intensity footshock relative to an intermediate intensity footshock. Second, SOCR's predictions concerning the effect of extinguishing the context-US association were tested. SOCR asserts that, at the time of testing, subjects compare the strength of the US representation activated through the direct X-US association with the strength the US representation activated through the X-context and context-US associations, which, for some moderate number of trials, should be stronger after training with a high intensity US than with a moderate intensity US. This view predicts that massive posttraining extinction of the context will increase responding to a cue trained with a high intensity footshock because it will reduce the strength of the US representation activated through the X-context-US linkage. Thus, in Experiment 2 subjects received either 20 min or 480 min of context extinction towards assessing the effect of the context-US association on the response deficit observed with high intensity shocks. Third, we tested predictions of SOCR concerning the interaction between the response decrement that occurs after training with a high intensity US and the response decrement that occurs when a target cue is trained in compound with a highly salient nontarget cue (i.e., overshadowing). Specifically, SOCR anticipates that training X in compound with a highly salient nontarget cue (A) can attenuate responding by establishing strong X-A and A-US associations, which results in X indirectly activating a strong representation of the US through the X-A-US associative linkage at test. However, when compound training is administered conjointly with a high intensity footshock (which establishes a strongly excitatory context), the training context should reduce the potential of A to compete with X, and A should simultaneously reduce the potential of the context to compete with X. Thus, SOCR predicts that the response deficit that can be observed after compound training should counteract the response deficit caused by training with a high intensity footshock. The design summarized in Table 2 constitutes a $2 (0.8 \text{ vs. } 1.8 \text{ mA}) \times 3 (\text{Elemental-20 min vs. Compound-20 min vs. Elemental-480 min})$ design. Within the Elemental-20 min condition, we expected to replicate the critical finding of Experiment 1 (weaker responding in the 1.8 mA than in the 0.8 mA condition). Within the Elemental-480 condition, we expected this relationship to be minimized due to extinction of the context-US association, thereby attenuating down-modulation of the X-US association. Within the Compound-20 condition, we expected that this relationship would be reversed due to counteraction between the context and A.

Methods

Subjects and Apparatus—Subjects were 36 male (264 g–340 g) and 36 female (176 g–228 g) rats bred and maintained as in Experiment 1. Subjects were randomly assigned to one of six groups ($n = 12$): 0.8 mA-Elemental-20 min, 1.8 mA-Elemental-20 min, 0.8 mA-Compound-20 min, 1.8 mA-Compound-20 min, 0.8 mA-Elemental-480 min, and 1.8 mA-Elemental-480 min. The apparatus was the same as in Experiment 1, except that an additional 45- Ω speaker was used to present a 10-dB complex tone consisting of 1000- and 1200-Hz tones in equal parts.

Procedure—The procedure used in Experiment 2 was similar to that of Experiments 1a and 1b except for two changes. First, subjects in the Compound condition received compound (rather than elemental) training consisting of the click train (X) and the complex tone (A) being paired with footshock. Second, all subjects received either control (20 min) or experimental (480 min) Phase 2 extinction of Chamber R. Thus, Reacclimation occurred on Days 9 and 10 and Testing on Day 11.

Phase 2 (Days 5–8)—On Days 5 through 8, extinction of Chamber R occurred. Subjects in Condition 20 received daily 5-min context exposure sessions in which no nominal stimulus was programmed to occur. In Condition 480, subjects received daily 120-min context exposure sessions. Chamber doors were opened every 30 min in order to wake subjects that were sleeping during context extinction.

Results and Discussion

The results of Experiment 2 are depicted in Figure 4. Within Condition Elemental-20 min, greater suppression was observed in Condition 0.8 mA than in Condition 1.8 mA, which replicates the observation that an intense footshock US can yield weaker behavioral control by a target CS. Additionally, suppression was greater in Group 1.8 mA-Elemental-480 min relative to Group 1.8 mA-Elemental-20 min, which confirms SOCR's prediction that massive extinction of the context should increase suppression after training with an intense footshock US. Suppression was attenuated in Group 0.8 mA-Compound-20 min relative to Group 0.8 mA-Elemental-20 min, which indicates that Stimulus A overshadowed Stimulus X when they were trained in compound with a US of moderate intensity. This pattern was reversed when training involved a 1.8-mA footshock. The following statistical analysis supported these observations.

Experimenter error resulted in two subjects from Group 0.8 mA-Elemental-20 min being eliminated. A 2 (0.8 mA vs. 1.8 mA) $\times$ 3 (Elemental - 20 min vs. Elemental-480 min vs. Compound-20 min) ANOVA failed to detect any main effects or interactions on latencies to initiate drinking after being placed in the test context p s $> .22$, $MSE = 0.03$. Because baseline scores did not differ appreciably across experimental groups, a two-way ANOVA was used to analyze the data. An interaction between training and US intensity was detected in log latencies to resume drinking in the presence of X, $F(2, 64) = 29.80$, $MSE = .14$, Cohen's $f = 0.91$.

Planned comparisons tested specific hypotheses. Group 0.8 mA-Elemental-20 min suppressed more than Group 1.8 mA-Elemental-20 min, $F(1, 64) = 10.46$, which replicates the critical observation of Experiment 1 that training X with a high intensity footshock can yield lower suppression than training with a moderate intensity footshock. Subjects suppressed marginally ($.05 < p < .10$) more in the presence of X in Group 1.8 mA-Elemental-480 min than in Group 1.8 mA-Elemental-20 min, $F(1, 64) = 2.93$, which suggests that massive extinction of the training context attenuates the deficit in suppression that is caused by training with a high intensity footshock. The overshadowing effect was indexed by less suppression in Group 0.8 mA-Compound-20 min relative to Group 0.8 mA-Elemental-20 min, $F(1, 64) = 16.94$. Moreover, Group 1.8 mA-Compound-20 min suppressed more than Group 0.8 mA-Compound-20 min, $F(1, 64) = 51.81$, which suggests that overshadowing is eliminated when a high intensity footshock is used. In other words, the deficit in suppression caused by training with a high intensity footshock was eliminated by training in the presence of an overshadowing cue; suppression was greater in Group 1.8 mA-Compound-20 min than in Group 1.8 mA-Elemental-20 min, $F(1, 64) = 39.36$. Interestingly, Group 1.8 mA-Compound-20 suppressed more than Group 0.8 mA-

Elemental-20, $F(1, 64) = 7.55$, which suggests that compound training with a high intensity shock was more effective than elemental training with a moderate intensity shock.

The results of Experiment 2 support the view that competition between the context and the target cue at the time of testing is greater among subjects that receive training with a high, relative to a moderate intensity footshock. Competition between the context and the target cue in turn results in less responding to the target cue by subjects that received the high intensity footshock. This effect was eliminated when the target cue was trained in compound with a highly salient nontarget stimulus and when the training context was extinguished. In fact, compound training with a high intensity shock was more effective than elemental training with a moderate intensity shock. This last difference is anticipated by SOCR under some conditions because the model assumes that the context can influence responding to the target stimulus even in the moderate intensity condition. The overshadowing cue presumably largely eliminated the potential of the context to compete with the target stimulus. The results of Experiment 2 support SOCR's account of the response reduction observed after elemental training with high intensity shocks.

General Discussion

Experiments 1a and 1b indicated that conditioned suppression is an inverted-U function of footshock. Experiment 2 replicated this basic finding. Moreover, Experiment 2 demonstrated that the diminished responding at high US intensities is alleviated when the target is conditioned in compound with a highly salient stimulus (i.e., training with a moderate footshock is less effective than training with a high intensity footshock). Responding after training with a high intensity footshock is also increased as a result of extinguishing the training context.

Counteraction effects are said to occur when the conjoint administration of two treatments that independently attenuate responding to a target cue results in greater responding to the target cue than when either treatment alone is administered (for a review, see Wheeler & Miller, 2008). Counteractions have been demonstrated in several Pavlovian situations and using a wide-range of response reducing treatments (e.g., degraded contingency and overshadowing [Urcelay & Miller, 2006], overexpectation and trial massing [Sissons & Miller, 2008], and blocking by two independently trained blocking cues [Witnauer et al., 2008]). The results of Experiment 2, in part, constitute a counteraction between the response attenuation induced by high intensity shocks and overshadowing. That is, both the overshadowing and the high footshock treatments were shown to independently reduce suppression to the target stimulus. However, when both treatments were administered conjointly, responding was greater than when either treatment was administered alone. Thus, the depression in responding with high US intensity is part of a growing list of treatments that seem to counteract overshadowing. Additional treatments that counteract overshadowing include the CS preexposure effect (Blaisdell, Bristol, Gunther, & Miller, 1998), the US pre and postexposure effects (Urushihara & Miller, 2006), the partial reinforcement acquisition effect and the CS-duration effect (Urushihara & Miller, 2007), and the trial massing effect (Stout, Chang, & Miller, 2003). Those studies demonstrated that response decrements caused by manipulating the amount of exposure to the training context, CS, or to the US counteract overshadowing treatment. The present studies extend the observation of counteraction to a situation in which all subjects were matched on these variables.

The overtraining effect refers to the observation that responding after a massive number of trials is often weaker than responding after a moderate number of trials (e.g., Bouton, Frohardt, Sunsay, Waddell, & Morris, 2008; Pavlov, 1927; Urcelay et al., in press). For

example, Urcelay et al. used a lick suppression paradigm with rats to assess responding after 5, 10, 20, and 50 X-US pairings. They observed robust suppression after 5, 10, and 20 pairings. However, after 50 X-US pairings, little suppression to X was observed. This is similar to the present results with a high intensity US for two reasons: (1) it is paradoxical in that a treatment commonly thought to increase responding resulted in attenuated responding and (2) the effect seems to be mediated by contextual associations. That is, the overtraining effect, like the effect of training with high intensities, was attenuated when the context was extinguished and when the target was trained in compound with an otherwise competing cue (through overexpectation).

The present findings are superficially discrepant with those of Morris and Bouton (2006), who observed more behavioral control with more intense USs. The present results are somewhat limited by the lack of online acquisition data, which precludes our using the sophisticated techniques that Morris and Bouton used to analyze the rate of learning (i.e., the emergence of the conditioned response). In our lick suppression preparation, baseline drinking behavior is strongly disrupted by Pavlovian training. Thus, our procedure consisted of a predetermined amount of training followed by a test session in a neutral context, instead of training online. We elected to use this technique because our use of a wider range of footshock intensities (relative to Morris and Bouton) introduced a stronger possibility of disrupted baseline responding (which was realized in Experiment 1b). However, we feel that our results are compatible with their findings for two reasons and that the superficial dissimilarity is driven by our use of a wider range of shock intensities. First, up to a point (1.3 mA), we detected a direct effect of footshock intensity, thereby replicating part of Morris and Bouton's findings. Second, the theoretical implications of our results are congruent with those of Morris and Bouton's, who concluded that their data support the view that learning is directly related to the salience or intensity of the US.

Our results are also dissimilar to those of Annau and Kamin (1961), who ostensibly used a wider range of footshock than was used in the present studies. But there were many differences between their study and ours. First, their footshock was provided by a Grason-Stadler shock generator and mechanical scrambler. Such a device provides actual shock for only a small percentage of the specified shock duration; that is, the delivered shock was intermittent and was in fact zero between any two grids for the vast majority of the specified shock duration. In contrast, our shock circuit had a 100% duty cycle. Hence, despite our shock intensity range being below that set on Annau and Kamin's shock generator, our shocks were likely decidedly more aversive owing to the time-intensity tradeoff which occurs over short duration stimuli. Second, the difference between their results and ours may also be attributable to the very long intertrial intervals (almost 30 min) used by Annau and Kamin relative to the moderate intertrial intervals used in the present studies (10 min). Long intertrial intervals presumably resulted in context extinction during the ITIs, which in the framework of SOCR should have resulted in strong responding with a high intensity US; this is convergent with our explanation of the effect of the context extinction manipulation in Experiment 2. However, the long intertrial intervals used by Annau and Kamin could have been at least partially offset by their use of longer CSs (1 and 3 min as opposed to 10 s). Research has shown that the effectiveness of the CS is determined in part by the duration of the CS relative to the duration of the intertrial interval. Presumably, context extinction during the intertrial interval is determined by the duration of the intertrial interval relative to the CS duration, which would result in an amount of context extinction in Annau and Kamin's study that is similar to that presumably occurring in the present experiments. But Annau and Kamin also administered 10 hours of shaping in the training context, which likely resulted in latent inhibition of the training context. Such preexposure to the training context is often able to reduce the potential of the context to compete with the CS (Urcelay

& Miller, 2010). These factors might have prevented Annau and Kamin from observing that suppression is an inverted-U function of US intensity.

Less suppression after training with a high-intensity footshock, in our view, constitutes a performance (rather than a learning) deficit. SOCR was largely supported by the present studies and asserts that learning is directly affected by US intensity, but that performance can be a nonmonotonic function of US intensity due to interactions between the target CS and the training context. Figure 5 depicts the SOCR's best-fitting predictions and the results of the present experiments (see the Appendix for information about the methods used to produce these simulations). SOCR anticipated all of the between-group ordinal differences and provided a good quantitative fit to the data. Indeed, the sum of the squared differences (sum of squared error [SSE]) between predicted and observed values was low, $SSE = 0.29$ (see the Appendix for details about the simulations). SOCR anticipated the inverted-U pattern of responding observed in Experiments 1a and 1b. Moreover, SOCR anticipated the critical results of Experiment 2. Overshadowing is anticipated in the 0.8 mA condition as a result of compound training. SOCR anticipates both that the effect of compound training is reversed in the 1.8 mA condition and that suppression in Group 1.8 mA-Compound-20 is higher than in the other groups. The most important difference between SOCR's predictions and the observations was that SOCR anticipated a relatively weak effect of context extinction. This was not surprising because the group means in the Elemental-20 condition were highly similar to the analogous groups in Experiment 1b. The hillclimbing algorithm used to find the best fitting parameters was unable to find parameters that permit SOCR to accurately explain both the context extinction effect (i.e., the difference between the 20 and 480 min conditions) and the lack of an effect of the 20 min of context extinction administered in Experiment 2.

Interestingly, psychophysical research indicates that the perceived magnitude of shock is a power function shock intensity (Cross, Tursky, & Lodge, 1975), which is diametrically opposed to the inverted-U pattern observed in the present experiments. The present simulations reconcile this difference. These simulations assumed that the perceived magnitude (salience) of shock is a power function of US intensity (Stevens, 1961). Psychophysical research has revealed that the value of exponent for perceived magnitude of electric shock should be 2.26 (Cross et al., 1975). The best-fitting value for this exponent in the present simulations was 2.21, which is in strong agreement with the psychophysical research despite the observed inverted-U function between shock intensity and behavioral control of the CS. .

Importantly, the reversal of overshadowing observed in Condition 1.8 mA in Experiment 2 constitutes a replication of potentiation (Rusiniak, Hankins, Garcia, & Brett, 1979), which is most often observed in conditioned taste aversion. In conventional demonstrations of potentiation, an odor that gains weak behavioral control when elementally paired with lithium chloride can gain strong behavioral control when trained in the presence of a more salient taste. Thus, compound training with the taste potentiates behavioral control by the odor. In the 1.8 mA condition, elemental training of X resulted in weak suppression to X, but compound training resulted in potentiation of X by A. In fear conditioning, potentiation is less often observed than overshadowing. Urcelay and Miller (2009) recently reported that potentiation can be observed in fear conditioning when a long trace interval is interposed between the compound CS and the US, which illuminated an important procedural variable that determines whether potentiation or overshadowing will be observed after compound training. The present results revealed that US intensity is another procedural variable that determines whether potentiation or overshadowing will be observed.

Theoretically, the results of Experiment 1 are compatible with the view that performance is an inverted-U function of arousal (Yerkes & Dodson, 1908). Contemporary neurobiologically informed theories assume that this relationship is mediated by release of norepinephrine (Aston-Jones & Cohen, 2005). According to this view, increases in arousal are caused by a release of norepinephrine that is driven by widespread projections from the locus coeruleus. As activity in the locus coeruleus increases from low to moderate, performance increases; as activity increases from moderate to high, animals become distractible. Applied to the present experiments, moderate intensity shocks could engage moderate levels of norepinephrine release (and consequently high levels of attention during training) and high intensity shocks could result in high levels of norepinephrine release (and, consequently, low levels of attention to training). This view explains the results of Experiment 1 but not those of Experiment 2. Compound training with high intensity shock should produce weak attention, which was contradicted by the observation of high suppression in Group 1.8 mA-Compound-20.

The results of Experiment 1 are potentially compatible with the predatory imminence approach to aversively motivated behavior (Fanselow & Lester, 1988; Godsil, Tinsley, & Fanselow, 2003). According to this view, different defensive behaviors are recruited as the imminence of a predator increases. For example, freezing (which presumably drives at least some of the conditioned suppression observed in the present experiments) and conditioned analgesia occur after encounters with fear stimuli. This approach also assumes that the psychological distance between the animal and the threatening stimulus controls transitions among defensive behaviors. Psychological distance can be influenced by the perceived danger of a fear stimulus, which should increase with increases in shock intensity. Thus, the approach explains the results of Experiment 1 by assuming that increases in shock intensity causes changes in psychological distance between the rat and the predator, which causes non-monotonic changes in the strength of defensive behaviors. Depending on the behavior recruited as a result of high intensity shocks, less suppression (freezing) could be observed with greater shock intensity (predatory imminence). However, this approach fails to explain several aspects of Experiment 2, especially the reversal of the overshadowing effect observed when high intensity shocks were used during training.

The present results are also incompatible with the view that learning (or at least performance) functions to reduce total error. In simulations of the present data, SOCR distinguished itself from models based on the Rescorla-Wagner model because it rejects the view that total error across a stimulus compound drives learning. Instead, each cue's change in associative strength is driven by the discrepancy between what is expected based on that specific cue and the outcome that actually follows it. Moreover, SOCR assumes that within-compound associations in conjunction with CS-US associations influence the magnitude of the conditioned response. Our rejection of the total error reduction view is not unique. Researchers in category learning are increasingly rejecting the total error reduction view in their models (e.g., Kurtz, 2007). Moreover, research in that paradigm suggests that humans learn more information than is needed to eliminate behavioral error in categorization tasks (e.g., Bott, Hoffman, & Murphy, 2007). Similar research has amassed in the Pavlovian literature. For example, results of experiments using Rescorla's (2000) compound testing procedure consistently suggest that animals learn more information than is predicted by the total error reduction view without further modification. In summary, the present results are consistent with Pavlovian and human cognitive data suggesting that a strict total error reduction view should be abandoned.

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Appendix: Simulation methods

The present simulations assumed that the salience of the footshock in the present studies was a power function of footshock intensity (Stevens, 1961). Though we are not particularly committed to this view, it seems that it is compatible with empirical findings. Specifically, the salience of the footshock was modeled using the following equation:

$$\text{Salience}_{\text{US}} = k1 * (\text{Intensity}_{\text{US}})^{k2}$$

where $\text{Intensity}_{\text{US}}$ was the US intensity in milliamperes, $k2$ causes salience to be a power function of US intensity, and $k1$ allows perceived magnitude of shock to scale onto salience. Otherwise, simulations were conducted as in Stout and Miller (2007), except that the operator switch was not needed because it should have no effect in first-order conditioning, which was the context of the present experiments. In SOCR, $k3$ controls the rate of extinction and $k4$ dampens the activation of representations through higher-order associative linkages.

Increases in the strength of the association between two stimuli (Stim1 and Stim2; e.g., X and the US, X and A, etc.) are modeled using the following equation:

$$\Delta V_{\text{Stim1-Stim2}} = \text{Salience}_{\text{Stim1}} * \text{Salience}_{\text{Stim2}} * (\lambda - V_{\text{Stim1-Stim2}}) \quad (1)$$

where Salience is either determined by Equation 1 or a free parameter representing stimulus salience of the cue in question, λ is a fixed parameter (set at 1 by convention) that represents the maximum associative strength supportable by Stim2, and $V_{\text{Stim1-Stim2}}$ is the pretrial strength of the Stim1-Stim2 association. The update equation for SOCR in the present simulations took the form:

$$V_{\text{Stim1-Stim2}}^{n+1} = \Delta V_{\text{Stim1-Stim2}}^{n+1} + V_{\text{Stim1-Stim2}}^n \quad (2)$$

Decrements in the strength of the Stim1-Stim2 association occur when Stim1 is presented in the absence of Stim2 and are modeled by the equation:

$$\Delta V_{\text{Stim1-Stim2}} = \text{Salience}_{\text{Stim1}} * -k3 * V_{\text{Stim1-Stim2}} \quad (3)$$

where $k3$ ($0.01 < k3 < 1.0$) is a free parameter representing the rate of extinction. SOCR further assumes that responding to X (R_X) is given by the following equation:

$$R_X = V_{X-US} - k4 * ([rV_{X-Ctx} * rV_{Ctx-US}] + [rV_{X-A} * rV_{A-US}]) \quad (4)$$

where $k4$ is a free parameter that weights comparison processes so they have less impact ($0 < k4 < 1$) than the direct CS-US association (i.e., Link 1). rV_{X-Ctx} and rV_{X-A} represent X's potential to activate a representation of the context and A, respectively. rV_{Ctx-US} and rV_{A-US} represent the potential of the context and A, respectively, to activate a representation of the US. Note that $rV_{X-A} * rV_{A-US}$ only applies to the Compound condition of Experiment 2.

This response rule captures the psychological intuition that responding to X is determined by a comparison (via subtraction) between the US representation activated through the X-US association (V_{X-US}) and the US representation activated through the effective X-comparator stimulus (e.g., rV_{X-A}) and comparator stimulus-US (rV_{A-US}) associative linkage. Basically, SOCR says that responding to X is not a function of the absolute value of V_{X-US} . Rather it reflects the value of V_{X-US} relative to other cues that were present when X was trained.

Similar to the first-order processes that determine responding to X, the potential of X to activate first-order comparator stimuli (rV_{X-j}) and the potential of comparator stimuli to activate the US (rV_{j-US}) are determined by comparison processes involving second-order (j) comparator stimuli, which are other stimuli that are associated with the first-order comparator stimuli and may, but not necessarily, have an association with the target cue. Thus, the r represents higher-order comparator process. Specifically, the following equation was used to calculate X's potential to activate comparator stimuli:

$$rV_{X-i} = V_{X-i} - k4^* (V_{X-j} * V_{j-i}) \quad (5)$$

This equation captures the psychological intuition that the effective first-order comparator stimulus representation is determined by the representation of the first-order comparator activated directly through the association between X and the first-order comparator (V_{X-j}) compared to the representation of the first-order comparator activated through higher-order linkage (i.e., V_{X-j} and V_{j-i}). The strength of the effective indirectly activated representation of the US (rV_{j-US}) is determined by similar higher-order comparator processes:

$$rV_{i-US} = V_{i-US} - k4^* (V_{i-j} * V_{j-US}) \quad (6)$$

Scaling

In the present simulations, we needed to scale the predictions of SOCR to match the lick suppression scale because this allows us to compare SOCR's predictions to the results of the present experiments. The critical measurement in the present experiments was the $\log_{10}$ latency to consume water for five cumulative seconds in the presence of the test CS. Following Larrauri and Schmajuk (2008), we assumed that lick suppression multiplied by a scaling factor is equal to the response potential of X (R_X) as predicted by the models. In addition, we assumed that the lick suppression predicted by such proportional scaling is added to the scale's minimum (i.e., $\log_{10} 5$) set by our measuring latency to complete 5 s of drinking in the presence of the CS. Thus, in the present simulations, we approximated the lick suppression (LS) scale using the equation:

$$LS = \log_{10} 5 + (\text{Scaling} \times R_X)$$

where Scaling is a free parameter used to approximate the $\log_{10}$ latency scale measured in lick suppression situations.

Optimization of parameters

The predictions of most models are highly dependent on the particular values of free parameters. Thus, we used a hill climbing algorithm to optimize the parameters of SOCR. The hill climbing algorithm used was one of the built-in functions in Matlab's optimization toolbox. For any given randomly selected start in parameter space, this algorithm simulates the model using the parameter combinations corresponding to the immediately adjacent

parameters and, once the search space is exhausted, moves the search space in the direction that causes the greatest reduction in error. In the present simulations, the sum of the squared error (SSE) between predicted and observed group means was the measurement of error. The best-fitting parameters were: $k_1 = 2.21$, $k_2 = 0.27$, $k_3 = 0.01$, $k_4 = 1.00$, $\text{Salience}_X = 0.52$, $\text{Salience}_A = 1.00$, $\text{Salience}_{\text{Ctx}} = 0.09$, and $\text{Scaling} = 1.79$.

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Figure 1. SOCR's predicted responding to a target cue as a function of US salience using parameters employed in Stout and Miller (2007).

Figure 2. Group mean log latencies to drink for five cumulative seconds in the presence of X in Experiment 1a. See Table 1 and text for details. The brackets represent standard errors of the means.

Figure 3. Group mean log latencies to drink for five cumulative seconds in the presence of X in Experiment 1b. See Table 1 and text for details. The brackets represent standard errors of the means.

Figure 4. Group mean log latencies to drink for five cumulative seconds in the presence of X in Experiment 2. See Table 2 and text for details. The brackets represent standard errors of the means. The legend indicates the intensity of the footshock US.

Figure 5.
Best-fitting SOCR predictions and observations in Experiments 1 and 2.

Table 1

Design Summary of Experiment 1

Experiment	Group	Training (Ctx 1)	US Intensity (mA)	Test X (Ctx 2)
1a	0.4 mA	20 X-US	0.4	cr
1a	0.6 mA	20 X-US	0.6	Cr
1a	0.8 mA	20 X-US	0.8	CR
1a	1.0 mA	20 X-US	1.0	CR
1a	1.2 mA	20 X-US	1.2	CR
1a	1.4 mA	20 X-US	1.4	Cr
1b	0.3 mA	20 X-US	0.3	cr
1b	0.8 mA	20 X-US	0.8	CR
1b	1.3 mA	20 X-US	1.3	CR
1b	1.8 mA	20 X-US	1.8	Cr

Note: CS X was a 30-s click train. The US was a 0.5-s footshock, the intensity of which was a function of group assignment. Ctx = context. CR indicates strong expected conditioned responding, Cr indicates moderate expected conditioned responding, cr indicates weak expected conditioned responding based on SOCR simulations.

Table 2

Design Summary of Experiment 2

Group	Phase 1 (Ctx 1)	US Intensity (mA)	Phase 2 (Ctx 1)	Test X (Ctx 2)
0.8 mA-Elemental-20 min	20 X-US	0.8	20 min	CR
1.8 mA-Elemental-20 min	20 X-US	1.8	20 min	Cr
0.8 mA-Compound-20 min	20 AX-US	0.8	20 min	cr
1.8 mA-Compound-20 min	20 AX-US	1.8	20 min	CR
0.8 mA-Elemental-480 min	20 X-US	0.8	480 min	CR
1.8 mA-Elemental-480 min	20 X-US	1.8	480 min	CR

Note: CS X was a 30-s click train. CS A was a 30-s tone. The US was a 0.5-s footshock, the intensity of which was a function of group assignment. Ctx = context. CR indicates strong expected conditioned responding, Cr indicates moderate expected conditioned responding, cr indicates weak expected conditioned responding based on SOCR simulations.