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# Contextual control of inhibition with reinforcement: Adaptation and timing mechanisms

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## Abstract

Four experiments with rats studied the effects of switching the context after Pavlovian conditioning. In three conditioned suppression experiments, a large number of conditioning trials created "inhibition with reinforcement" (IWR), in which fear of the conditional stimulus (CS) reached a maximum and then declined despite continued CS – unconditional stimulus pairings. When IWR occurred, a context switch augmented fear of the CS; IWR and augmentation were highly correlated. Neither IWR nor augmentation resulted from inhibition of delay (IOD): In conditioned suppression, IWR and augmentation occurred without IOD (Experiment 3), and in appetitive conditioning (Experiment 4), IOD occurred without IWR or augmentation. IWR may occur in conditioned suppression because the animal adapts to fear of the CS in a context-specific manner. We discuss several implications.

### Keywords

context; fear conditioning; inhibition with reinforcement; inhibition of delay

The present article is concerned with two long-standing issues in the study of Pavlovian learning. The first issue is how contexts, background stimuli that are present whenever conditioning and learning occur, control performance to the conditional stimulus (CS). Although theories of learning and memory often assume that contextual stimuli can control a number of learning, performance, and retrieval processes (e.g., Bouton, 1993; Gallistel & Gibbon, 2000; Miller & Schachtman, 1985; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Wagner, 1981), the context often seems surprisingly unimportant. For example, in the conditioned suppression preparation, in which conditioned fear in rats is indexed by the CS's ability to suppress an operant behavioral baseline maintained by an appetitive reinforcer, a large number of experiments have found that a switch out of the context in which conditioning is conducted causes very little disruption of the conditioned response (e.g., Bouton & King, 1983; Bouton & Swartzentruber, 1986; Grahame, Hallam, Geier & Miller, 1990; Hall & Honey, 1989, 1990; Lovibond, Preston & Mackintosh, 1984; Swartzentruber & Bouton, 1986). In one set of experiments, Kaye and Mackintosh (1990) even found that a switch out of the conditioning context enhanced, rather than decreased, suppression to a CS. Context change can thus have surprising effects on performance in Pavlovian learning.

A second issue is that despite the common assumption that conditioning is a simple monotonic function of CS – unconditional stimulus (US) pairings, conditioned responding often reaches a peak and then declines over trials as the CS and US continue to be paired (e.g., see Kimmel & Burns, 1975, for one review). Such a decline in responding during conditioning, the so-called

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inhibition with reinforcement effect (e.g., Kimmel & Burns, 1975), is surprisingly well documented in the literature. For example, Pavlov (1927) devoted an entire chapter to it (Chapter XIV, pp. 234–259). It has also been widely observed in fear conditioning (e.g., Overmier, Payne, Brackbill, Linder, & Lawry, 1979), and is plainly evident in many experiments using the conditioned suppression preparation (e.g., Ayres, Berger-Gross, Kohler, Mahoney, & Stone, 1979; see also Annau & Kamin, 1961; Kamin, 1961; Kamin & Brimer, 1963; Millenson & Hendry, 1967; Zielinski, 1966). At the present point in time, the cause or causes of inhibition-with-reinforcement (hereafter, IWR) are unclear. It has been variously attributed to habituation to the CS (see Ayres et al., 1979), habituation to the US (Annau & Kamin, 1961; Overmier et al., 1979), or inhibition of delay resulting from the animal learning to time the presentation of the US (Zielinski, 1966). Although inhibition of delay may account for IWR under some conditions (e.g., Zielinski, 1966), its general role is far from certain (e.g., Millenson & Hendry, 1967).

A major point of the present article is that contextual stimuli and the IWR effect are linked. Experiment 1 demonstrates IWR in the conditioned suppression preparation, shows that a context switch at the end of conditioning can augment conditioned responding, and further shows that the strength of IWR and this augmentation effect are highly correlated over individual subjects. Experiment 2 then shows that relatively extended conditioning, and the presence of IWR, predicts the effect of the final context switch: When IWR had developed during conditioning, the context switch enhanced suppression, whereas when IWR had not developed, the context switch did not. The hypothetical "inhibitory" process that causes IWR thus appears to be context-specific. However, Experiments 3 and 4 demonstrate that the inhibitory process is not inhibition of delay, which is neither necessary (Experiment 3) nor sufficient (Experiment 4) for IWR and augmented responding to occur. Ultimately, we suggest that inhibition-with-reinforcement may result from a context-specific mechanism through which the rat learns to adapt to fear of the CS.

## Experiment 1

In the first experiment, rats received repeated pairings of a light-off CS with footshock in one context and similar pairings of a tone CS and footshock in a second context over a series of daily sessions. As in earlier reports (e.g., Ayres et al., 1979; Kamin & Brimer, 1963; Millenson & Hendry, 1967), conditioned suppression first increased as a function of conditioning trials, and then began to decline. This IWR effect occurred with both the light-off and the tone CS. At the end of the experiment, rats were then tested with one of the CSs in both the context in which it had been conditioned and in the alternate context. The design ensured that the two contexts were equally familiar and equally associated with shock and with fear conditioning. Nonetheless, the context switch at the end of the experiment had a strong effect on responding to both CSs: It caused an increase in suppression to both stimuli.

### Method

**Subjects—**The subjects were 16 female Wistar rats obtained from Charles River, St. Constance, Quebec. They were approximately 85–90 days old at the start of the experiment and were individually housed in suspended stainless steel cages in a room maintained on an 18:6-h light:dark cycle. The rats were food deprived to 80% of their free-feeding weight and maintained at this level for the duration of the experiment.

**Apparatus—**The apparatus consisted of two sets of four Skinner boxes housed in separate rooms of the laboratory. The boxes in one set measured 26 × 25 × 19 cm. The front, back, and one side wall were made of aluminum; the remaining side wall and ceiling consisted of clear acrylic plastic. The floor was made of tubular steel bars 16 mm in diameter and spaced 3.2 cm from center to center. The bars were perpendicular to the front wall where the operant manipulanda were located. A 4 × 4-cm food cup was located in the front wall, 1 cm above the floor and 1 cm to the left of a 2.5 × 2.5-cm lever. The lever was centered 5 cm from the right side of the wall and 5 cm above the floor. Rats were placed in these boxes through a door in the right side wall. A dish containing 10 ml of Heinz white vinegar was placed outside of the chamber to provide a distinctive olfactory cue.

The other set of boxes measured 32 × 25 × 21 cm; the front and rear walls, as well as the ceiling, were made of clear acrylic plastic, while the sidewalls were made of brushed aluminum. The floor was made of stainless steel grids, 0.5 cm in diameter and spaced 1.5 cm apart (center-to-center) parallel to the front wall. A recessed 5 × 5 cm food cup was centered on the right wall at about floor level. The lever was positioned to the left of the food cup, approximately 6 cm above the grid floor. A dish containing approximately 1 g of Vicks Vaporub was placed just outside of the chamber to provide a distinctive olfactory cue. Background noise in all boxes was 70 dB. The two types of boxes were counterbalanced throughout the experiment.

In both sets of boxes, illumination was provided by two 7.5-W white incandescent bulbs mounted on the ceilings of the sound attenuation chambers, 25 cm above the grid floor. Turning off these lights provided one of the CSs. The other CS was an 80 dBA 3000-Hz tone delivered through a speaker mounted on the ceiling of the sound attenuation chambers. The duration of each CS was 60 s. The US was a scrambled 0.5-s, 0.6-mA footshock provided by Med Associates (St. Albans, VT) ENV-414 shock sources.

**Procedure—**All sessions were 84 min in duration unless otherwise specified.

**Magazine training:** Each subject first received two 20-min sessions of magazine training in which they received food pellets from the recessed food cups. Magazine training took place in both contexts and the rats received 30–33 pellets on average.

**Baseline training:** The following day, subjects received one 60-min session of lever-press shaping in each context. Food cups and levers were baited prior to training. Rats were rewarded with food pellets for approaching and pressing the lever. After lever pressing began, the rats were rewarded with a food pellet for each of the first 30 responses. They then progressed through leaner schedules of reinforcement until they were performing on a VI-90 schedule. Over each of the next four days, the rats received one 84-min session in each context (i.e., two sessions per day). In these sessions, rats continued to lever press for food reinforcement on a VI-90 schedule.

**Conditioning:** Conditioning began the following day. In this phase, all rats received a conditioning session in each context on each of 16 consecutive days. Each session contained three conditioning trials in which one of the CSs was presented and terminated with the onset of footshock. The light-off CS was consistently used in one context, while the tone was used in the other. The intertrial interval (ITI) was variable with a mean of 26.66 min. The animals were put in the two contexts in a repeating ABBAAB order. The interval between the two daily sessions was approximately 100 min.

**Testing:** On the day following the last day of conditioning, the rats were divided into two groups. One group was tested with the light-off CS and the other was tested with the tone. Each rat received two 51-min sessions that each contained a nonreinforced test of the CS at minutes 24.5 and 49. For each rat, the CS was tested in both the context in which it had been conditioned (Same context) and in the alternative context (Different context), with the order counterbalanced.

**Data Analysis—**Suppression to the CS was indexed in terms of standard suppression ratios of the form $x/(x+y)$, where $x$ represents the number of lever presses made during the 60-s CS and $y$ represents the number of lever presses made during the 60-s period immediately before the CS (the pre-CS period). A ratio of 0 indicates complete suppression of responding during the CS, whereas a ratio of 0.5 indicates no response suppression during the CS. Suppression ratios were analyzed using analyses of variance (ANOVA). Identical analyses were also conducted on pre-CS scores. Pre-CS differences were considered problematic for interpretation of suppression ratios when the analyses uncovered pre-CS effects that were the same as effects detected in the suppression ratios (and could therefore account for them). Throughout, the rejection criterion was $p < 05$.

## Results

**Conditioning—**The results of conditioning with both the light-off CS and the tone CS are summarized in the left portions of the two panels shown in Figure 1. As the figure suggests, conditioning with both CSs reached a maximal point on the 3$^{rd}$ session and then began to decline. A CS x Session ANOVA isolating Sessions 3 through 16 revealed an effect of session, $F(13, 195) = 4.20$; suppression thus decreased over training. There was also a significant effect of CS, $F(1,15) = 4.92$, and a CS x Session interaction, $F(13, 195) = 1.98$, which took the form of a more rapid decline in suppression to the tone. Despite the slightly different pattern with each CS, there was substantially less suppression to either of them on Session 16 than Session 3: for the light-off, $F(1, 15) = 14.08$; for the tone, $F(1,15) = 6.44$. IWR thus developed with both CSs.

A parallel analysis of the pre-CS scores revealed a significant effect of Session, $F(1, 14) = 8.37$, but no other effects approached significance, $Fs<1$. The mean pre-CS scores were 22.26 and 31.40 on the 3$^{rd}$ and 16$^{th}$ sessions, respectively. Although the pattern suggests that the decrease in suppression was correlated with an increase in baseline lever pressing rate, both the test phase of this experiment and the results of subsequent experiments suggest that weaker suppression was not merely an artifact of higher pre-CS rates.

**Testing—**The results of the two test trials in each context are presented in the right-hand parts of the panels of Figure 1. There was more suppression to both CSs when they were tested in the different context, relative to tests in the same context, despite the fact that both contexts had been equally associated with shock and with fear conditioning. (The high first-trial suppression of the tone-tested group in the Same context is consistent with the group's previous tendency to suppress less on the first trial of the session; for example, on the three tone conditioning trials of the last conditioning session, the ratios were 0.36, 0.12, and 0.11.) A Context x Trials x CS x Test Order ANOVA revealed a significant effect of Context, $F(1, 12) = 9.99$. The CS main effect and the CS x Context interaction were not significant, $Fs(1, 12) < 1$. The Trials effect was significant, $F(1, 12) = 5.26$, suggesting extinction over the test trials. There was also a CS x Order interaction, $F(1, 12) = 9.53$, and a CS x Order x Trials x Context interaction was also significant, $F(1,12) = 5.41$. Despite the interactions, there was a clear trend toward more suppression in the different context in all conditions.

A parallel analysis of the pre-CS scores revealed a significant effect of Trials, $F(1, 12) = 4.84$, but no other effects or interactions approached significance, largest $F(1, 12) = 1.97$. The response rates were 30.25 and 29.91 in the same and different context, respectively.

## Discussion

The results of this experiment replicate the inhibition-with-reinforcement effect previously reported in conditioned suppression (e.g., Ayres et al., 1979; Kamin & Brimer, 1963; Millenson & Hendry, 1967). It is noteworthy that the effect was apparent with both the tone and light-off

CSs. Equally important, the context switch at the end of the experiment also caused an increase in suppression to both CSs. The latter effect is consistent with the results by Kaye and Mackintosh (1990), although it is inconsistent with the assumption that context switches decrease conditioned responding (e.g., Millin & Riccio, 2004; O'Reilly & Rudy, 2001).

The augmentation effect is also inconsistent with the common finding that a context switch can cause little change in performance after conditioning (e.g., Bouton & King, 1983; Bouton & Swartzentruber, 1986; Grahame et al., 1990; Hall & Honey, 1989, 1990; Lovibond et al., 1984; Swartzentruber & Bouton, 1986). A unique factor that might have led to the current augmentation effect was the IWR that occurred with the relatively extensive conditioning used here. Thus, whatever process controls IWR might be specific to its context. To further explore the relationship between augmentation and IWR, we examined their statistical correlation. Augmentation and inhibition were first calculated for each subject based on a method used by Bouton and King (1986). For each rat, the size and direction of the context switch effect was determined by subtracting its first-trial suppression ratio during testing in the different context from the first-trial suppression ratio during testing in the original context. The resulting difference score was positive and large when the context switch augmented suppression to the CS. The degree to which IWR was present during testing was calculated by isolating the conditioning trial on which the rat exhibited its lowest suppression ratio and subtracting it from the suppression ratio on the first trial of testing in the same context. When the resulting difference score was positive and high, suppression at the outset of testing was substantially weaker than at its maximum point during conditioning. Calculated this way, the correlation between augmentation and IWR was positive and reliable over the 16 subjects, $r(14) = +.67$. The extent to which suppression to the CS had peaked and then decreased during conditioning thus predicted the extent to which the context switch augmented suppression to the CS.

## Experiment 2

Experiment 1 involved a substantial amount of fear conditioning before testing occurred (there were 16 conditioning sessions, or 48 trials, with each CS). To explore the possible causal relationship between the extent of training and the augmentation effect, Experiment 2 compared the effects of the context switch in groups that first received modest versus extensive conditioning. Rats were trained with a light-off CS and tone CS in different contexts following the procedure of Experiment 1. However, half the rats received 16 sessions of conditioning before testing the light-off CS in the same or the different context (as in Experiment 1), while the other half received only two days of conditioning before the test. As before, there was evidence of IWR with the 16-session procedure; there was no such evidence with the two-session procedure. The question was whether augmentation was likewise unique to the 16-session procedure.

### Method

**Subjects and apparatus—**The subjects were 16 female Wistar rats obtained from the same source and kept under the same conditions as described previously. The apparatus was also the same.

#### Procedure

**Conditioning:** All sessions were 84 min in duration unless otherwise specified. Magazine training, baseline training, and conditioning were each conducted in the manner described previously. The important difference in this experiment was that during the conditioning phase, half the rats received a conditioning session in each context on each day for two consecutive days while the other half received conditioning for sixteen consecutive days.

**Testing:** On the day following the last day of conditioning, each rat was tested with the light-off CS, which was chosen because darkness is especially likely to be perceived as the same stimulus when it is presented in different contexts (e.g., Bouton & Swartzentruber, 1989). As in Experiment 1, testing consisted of two 51-min sessions that each contained a nonreinforced presentation of the CS at minutes 24.5 and 49. The CS was tested in both the context in which it had been conditioned (Same context) and in the alternative context (Different context), with the order counterbalanced.

## Results

**Conditioning—**Suppression during each session of conditioning with the light-off CS is shown for Groups 2 and 16 in the left and right panels of Figure 2, respectively. The conditioning curve of Group 16 was not as smooth as the one observed in the previous experiment (where there were 16, rather than 8, subjects). However, suppression was weaker by the end of conditioning than it was at its maximum point, which was reached on average (and in 5 out of 8 of the rats) during Session 7. Consistent with this impression, suppression was significantly weaker during Session 16 than Session 7, $F$ (1, 7) = 6.06. A parallel analysis of the group's pre-CS scores (mean = 22.46 and 19.67 on Sessions 7 and 16, respectively) revealed no significant difference, $F < 1$.

There was no difference between the two groups on the first two sessions of conditioning: A Group x Session ANOVA revealed more suppression on the second than the first session, $F$ (1, 14) = 29.62, but no effect of Group or a Group x Session interaction, Fs < 1.

**Testing—**The results of the test trials are presented in the right portion of each panel in Figure 2. In the group given 16 sessions of conditioning, there was a substantial increase in suppression when the CS was tested in the different context. In the group given only 2 sessions, there was no such change. A Group x Context x Trial x Test Order ANOVA revealed no significant main effects, highest $F$ (1, 12) = 3.69, but a significant Group x Context interaction, $F$ (1, 12) = 9.81. The interaction suggests the context switch did have a greater impact after 16 days of conditioning than two days of conditioning. Consistent with this conclusion, the difference between suppression in the Same and Different contexts was reliable for the 16-Day group, $F$ (1, 7) = 25.16, but did not approach reliability in the 2-Day group, $F$ (1, 7) < 1. No other interactions were significant, highest $F$ (1, 12) = 3.79.

A parallel analysis of the pre-CS scores revealed a significant effect of trial, $F$ (1, 12) = 8.62; pre-CS rates were higher on the first test trial than the second. However, no other effects were significant, highest $F$ (1, 12) = 3.05. The mean pre-CS response rates for the 16-day and 2-day group in the Same context were 18.30 and 16.06, respectively. The mean pre-CS rates in the different context for the 16- and 2-day group were 19.90 and 22.00, respectively.

The correlation between IWR and the effect of the context switch was calculated following the method described in Experiment 1. It was once again positive and significant, $r$ (14) = +.63. As in Experiment 1, the extent to which an individual rat's suppression had decreased from its maximum during conditioning predicted the size of the augmenting effect of changing the context.

## Discussion

The results of this experiment replicated the augmentation effect observed in Experiment 1 and confirmed that it depends on relatively extensive training; neither augmentation nor an IWR effect was evident after only two sessions of conditioning. The fact that augmentation was correlated with the degree to which suppression decreased during training is again consistent with the idea that the effect of the context switch is to release suppression from whatever "inhibitory" process is responsible for IWR.

This conclusion is consistent with other research suggesting that contexts are especially likely to control inhibitory processes. Bouton (1984) and Bouton and King (1986) found that conditioning the context (by further associating it with the US after CS conditioning) augmented suppression to a CS only if suppression during testing was depressed from the maximum point it had reached during conditioning (e.g., as it was after extinction). In another set of experiments, Bouton, Ricker, and Frohardt (2003) found that a context switch augmented suppression to the CS depending on the extent to which suppression was likewise depressed from its maximum. Over a series of experiments using a variety of conditioning treatments that often intermixed reinforced and nonreinforced trials, the effect of a context switch on suppression to a CS was found to correlate with the extent to which it was depressed. Because the conditioning procedures used in the current experiments never involved nonreinforcement of the CS, they unambiguously suggest that the same relationship holds for the case of inhibition with reinforcement. They also establish the correlation between IWR and augmentation with individual subjects, rather than groups of subjects. In sum, there is converging evidence to suggest that a context switch augments fear by releasing the CS from processes that otherwise attenuates fear of the CS.

## Experiment 3

As noted earlier, one candidate for the inhibitory process behind IWR is inhibition of delay (e.g., Kimmel & Burns, 1975): Given that the footshock was always presented at the end of a constant-duration CS, a nonmonotonic learning curve might develop if suppression during early periods of the CS were to extinguish as the animal learned to time the late presentation of footshock. Zielinski (1966) proposed inhibition of delay as an explanation of the IWR effect in conditioned suppression. The possibility is worth taking seriously here, because Rosas and Alonso (1997) found that inhibition of delay is attenuated if the context is changed after conditioned suppression training; the attenuation of inhibition caused an increase in suppression to the CS. This means that the acquisition of inhibition of delay over training can potentially account for (1.) the IWR effect, (2.) the enhanced suppression observed after a context switch, and (3.) why the two effects are correlated.

Experiment 3 therefore examined the role of inhibition of delay in producing the IWR and enhanced suppression effects. There were two groups. One group (Group Fixed) received conditioning with a fixed 60-s CS that always ended in footshock. Conditioning trials were continued until a significant IWR effect was obtained. The second group (Group Variable) received the same number of conditioning trials with a 60-s CS, but presentation of the footshock occurred with equal probability at the end of the first, second, or third 20-s interval in the CS. Because the timing of US delivery was not predictable for Group Variable, inhibition of delay was not expected. One question, therefore, was whether Group Variable's treatment would prevent IWR from developing. Another question was whether it would also eliminate the augmentation of suppression to the CS that was expected in Group Fixed when the context was switched at the end of the experiment.

### Method

**Subjects—**The subjects were 16 female Wistar rats obtained from Charles River, Inc., approximately 85–90 days old at the start of experiment. Housing and maintenance were the same as in the preceding experiments.

**Apparatus—**The apparatus consisted of the vinegar-scented boxes used in Experiments 1 and 2 and another set of four boxes housed in a separate room. The latter boxes measured 24

× 22 × 18 cm. The front and back walls were aluminum, and the side wall and ceiling consisted of clear acrylic, with 2-cm wide vertical black stripes spaced 2.5 cm apart. The floor consisted of stainless steel bars 3 mm in diameter and spaced 1.5 cm from center to center. The bars were parallel to the front wall where the operant manipulanda were located. The 4 × 4-cm food cup was recessed in the front wall and was centered 3.5 cm from the right side wall, 1 cm above the floor. A 1-cm-wide lever protruded 4 cm from the front wall into the box and was located 5 cm above the floor and 6 cm to the left of the food cup. Rats were placed in these boxes through a door in the ceiling. A dish containing approximately 1 g of Vicks Vaporub, which was placed outside the Skinner box and below the food cup, provided a distinctive olfactory cue.

As before, in both sets of boxes, illumination was provided by two 7.5-W white incandescent bulbs mounted on the ceilings of the sound attenuation chambers, 25 cm above the floor of the boxes. The footshock US (0.5-s, 0.6 mA) was provided by Grason-Stadler (W. Concord, MA) shock sources and scramblers. Once again, the light-off CS was the target CS. The 3000-Hz tone CS received a comparable treatment throughout in the other context. Both CSs were presented for 60 s.

**Procedure—**Sessions were 84 min in duration unless otherwise specified.

**Baseline training:** Each rat first received 30 min of exposure to Contexts A and B. The food cups were baited with 4 pellets prior to the start of each session. The levers were also baited with crushed food pellets. Shaping and baseline training then proceeded over the next five days following the procedure used in the preceding experiments.

**Conditioning:** Conditioning started the next day. Over the next 14 days, all rats received a conditioning session in Context A and another session in Context B. For both groups, sessions in A and B contained 3 presentations of the 60-s light-off CS or tone CS, respectively, with a variable ITI of 26 min. Each CS presentation was divided into three 20-s time bins. Consistent with the preceding experiments, Group Fixed always received the footshock at the end of bin 3, i.e., at the end of the 60-s CS. Group Variable, in contrast, received the shock at the end of bins 1, 2, or 3 with equal probability. During the three trials of any session, Group Variable received the shock at the end of bins 1, 2, and 3 or 2, 1, and 3, respectively. These sequences were alternated daily, but note that the third trial of each session was always an ordinary delay trial like that received by Group Fixed. For both groups, only the third trial of each session is reported and analyzed, because footshocks given after earlier bins would have unconditional effects that would contaminate measurement of suppression to the CS.

**Testing:** Beginning on the day following the conclusion of the conditioning phase, each group was tested for suppression to the light-off CS in Context A and Context B (order counterbalanced). On each day, each group received one 51-min session during which two nonreinforced trials were presented. The first trial occurred 24.5 min after the beginning of the session; the second trial occurred 24.5 min later.

**Data Analysis:** Suppression ratios were calculated following the usual method. In addition, separate ratios were calculated using responding from each 20-s bin. In this case, counts during the 20-s bins were converted to rates (responses/min) and then entered into the usual formula with number of responses made during that trial's 60-s pre-CS period.

## Results

### Overall suppression to the CS

**Conditioning:** Figure 3 presents overall suppression to the light-off CS on the focal third trial of each of the conditioning sessions. A Group by Session ANOVA revealed a significant effect of Session, $F$ (13,182) = 4.67. There was a significant Group x Session interaction, $F$ (13,182) = 2.33, due in part to differences in the first two days of conditioning between the groups. However, the groups did not differ in their overall suppression across the sessions, Group effect $F$ (1,14) <1.

The groups reached their lowest mean suppression ratios on or prior to Session 4. To test the development of IWR, suppression ratios were analyzed over Sessions 4 – 14. A Group x Session ANOVA confirmed a main effect of Session, $F$ (10,140) = 4.25. The Group effect was not significant, $F$ (1,14) < 1, whereas the Group x Session interaction was, $F$ (10,140) = 2.34. Simple effect analyses nonetheless revealed significant Session effects in each group, Fs (10,70)≥2.18. Both groups thus developed inhibition-with-reinforcement during the conditioning phase.

An identical ANOVA on the corresponding pre-CS scores found no effect of Session, $F$ (10,140) = 1.80. No other effect approached significance, Fs < 1. The mean pre-CS scores were 23.76 for Group Fixed and 22.39 for Group Variable over the phase.

**Testing:** Suppression on the two test trials is shown at right in Figure 3. The data were subjected to a Group x Context x Trial x Order ANOVA. The analysis revealed a significant Context effect, $F$ (1,12) = 11.76. Neither the Group effect, $F$ (1,12) = 1.05, nor the Group x Context interaction, $F$ (1,12)<1, were reliable. Suppression was thus augmented by the context switch in both groups. The order effect was not significant, $F$ (1,12) = 3.81, nor were there any other effects or interactions, the largest $F$ (1,12) = 3.11.

An identical ANOVA on pre-CS scores revealed a nonreliable Context main effect, $F$ (1,12) < 1. There was a significant Trial effect, $F$ (1,12) = 8.43, that interacted with Context, $F$ (1, 12) = 6.94. For reasons that are not clear, pre-CS scores decreased in Context B more than they did in Context A. There was also an Order effect, $F$ (1,12) = 11.77, and a Context x Trial x Group x Order interaction, $F$ (1,12) = 6.16. No other effects were reliable, the largest $F$ (1,12) = 2.74. Although the pattern of pre-CS responding was complex, it did not provide an alternative explanation of the context main effect evident in the suppression ratios. The mean pre-CS scores over trials in Contexts A and B were 30.88 and 28.13 in Group Fixed and 36.38 and 33.25 in Group Variable, respectively.

The correlation between the amount of IWR and the change in suppression caused by the context switch was calculated as in Experiments 1 and 2. Once again, the correlation was positive and significant, $r$ (14) = +.80, suggesting that the amount of IWR that developed over the course of conditioning accounted for 64% of the variance in the augmentation of performance produced by the context switch.

### Suppression over time in the CS

**Conditioning:** Suppression during each 20-s bin of the CS is shown for each group over the conditioning sessions at left in Figure 4. Inhibition of delay did not develop in this experiment; if anything, both groups tended to decrease their suppression, rather than increase it, as time progressed during the CS. A Group x Bin x Session ANOVA confirmed the Group and Session effects reported above. However, the crucial new result was a reliable Bin main effect, $F$ (2, 28) = 9.96; suppression generally decreased over bins. Somewhat surprisingly, the Bin effect did not interact with either Group or Session, the largest $F$ (26,364) < 1. Thus, rats in both groups tended to decrease suppression over time in the CS. The Group x Session x Bin interaction was not significant, F (26,364) = 1.30.

**Testing:** The results of the test trials, now expanded to show responding over time in the CS, are shown at right in Figure 4. The context switch had no impact on the temporal distribution of suppression in the CS. This data set was analyzed by a Group x Context x Bin x Trial x Order ANOVA, which confirmed the effects reported above. The Context by Bin effect did not approach significance, F (2,22) = 1.28; none of the other interactions with bin were significant except for the Group x Bin x Order, F (2, 22) = 3.99, and the Group x Context x Bin x Order, F (2, 22) = 4.98, which seem best attributed to sampling error. No other effects were reliable, Fs < 2.93.

### Discussion

The results of this experiment suggest little role for inhibition of delay in either the IWR or enhanced suppression effects observed here. Acquisition curves were similarly nonmonotonic in groups that received the footshock US consistently at the end of the CS (Group Fixed) or unpredictably at different temporal locations within the CS (Group Variable). Moreover, there was no evidence of inhibition of delay developing in Group Fixed. In fact, the pattern of suppression over time in the CS was the opposite of inhibition of delay: Suppression of lever pressing decreased, rather than increased, as time progressed in the CS. A related pattern has been reported by Rescorla (1968). As Rescorla noted, such results may be consistent with the fact that food pellets scheduled on the VI schedule are increasingly probable over time in the CS if the animal has initially withheld responding. Stronger appetitive motivation later in the CS would presumably reduce fear motivation (Dickinson & Dearing, 1979; Rescorla & Solomon, 1967). Nonetheless, it is clear that inhibition of delay did not develop in this experiment, and that the presence of IWR and the suppression enhancing effect of the context switch did not depend on it.

Of course, inhibition of delay can eventually develop in conditioned suppression, and it would not have been surprising to see it develop here if we had continued the conditioning phase for more sessions or trials (e.g., Rosas & Alonso, 1996; Zielinski, 1966). Moreover, if it had been present, its attenuation with a context switch (Rosas & Alonso, 1997) could no doubt contribute to the enhanced suppression effect. Nevertheless, the results of this experiment clearly indicate that the acquisition of inhibition of delay is not necessary for either the IWR effect or the augmentation of suppression that occurs when the context is changed following conditioning.

## Experiment 4

The purpose of the final experiment was to examine IWR and context switch effects in another conditioning preparation, namely, appetitive conditioning in which the CS is paired with food pellets and responding is indexed by the rat's entries into the foodcup (e.g., Bouton & Nelson, 1998; Bouton & Sunsay, 2001, Kaye & Mackintosh, 1980). The method was of interest because Kirkpatrick and Church (2000) had shown that inhibition of delay is quickly and readily learned in it. Thus, the appetitive conditioning preparation provided another way to examine the potential relationships between inhibition of delay, IWR, and the effects of changing the context on conditional responding.

The experimental design was similar to that of Experiment 3. Two groups received conditioning with a light-off CS in one context and a tone in another context over a series of sessions. Group Fixed received a food-pellet US at the end of every CS, whereas Group Variable received the US unpredictably at various temporal locations within the CS. At the end of the conditioning phase, responding to the light-off CS was tested in both the original and the alternate context. The experiment used methods that have often been employed in this laboratory (Bouton &

Nelson, 1998; Bouton & Sunsay, 2001). Thus, for example, the CSs were 30 s in duration, the US consisted of two 45-mg pellets presented 0.2-s apart, and each of the 60-min conditioning sessions contained 12 conditioning trials. It is worth noting that Kaye and Mackintosh (1990) did not observe enhanced responding with a context switch in an experiment using this preparation.

## Method

**Subjects and Apparatus—**The subjects were 16 female Wistar rats obtained from Charles River, approximately 85–90 days old at the start of experiment. Housing, food deprivation, and maintenance conditions were the same as in the preceding experiments. The apparatus was the same as that used in Experiment 3. Each box contained a 5.08 × 5.08 cm food cup that measured food cup entries by means of an infrared photocell beam positioned approximately 1.2 cm behind the plane of the wall and 1.2 cm above the bottom of the food cup. The CSs were the light-off CS and the tone CS used in the previous experiments presented for 30 s. The light-off stimulus was once again the target CS. The US was always two 45-mg food pellets delivered approximately 0.2 s apart.

**Procedure—**All sessions were 60 min in duration.

**Magazine Training:** The rats were first trained to retrieve food pellets when they were delivered to the food cup in both contexts. In both sessions, the rats received 36–39 pellets delivered over 20 minutes. The interval between two sessions was 25–30 minutes.

**Conditioning:** The rats were randomly assigned to two groups (n = 8) that then received a 60-min session a day in each context. During each of these sessions, the groups received 12 conditioning trials with an average ITI of 4 min. The CS was divided into three 10-s time bins. As in Experiment 3, Group Fixed always received the US at the end of bin 3 (the end of the CS), whereas Group Variable received the US at the end of bins 1, 2, or 3 with equal probabililty from trial to trial. The trials were organized in three-trial blocks in which trials contained the US at the end of bins 1, 2, 3 or 2, 1, 3. As in Experiment 3, only data from the third trials (on which Group Variable received the US at the end of the CS) are reported and analyzed; in this case, consummatory foodcup entries would otherwise inflate the number of responses during subsequent time bins. The conditioning phase was continued for a total of 24 days.

**Testing:** Testing took place on the day that followed the last conditioning session. Each group received one session in either context. The target light-off CS was presented without the US eight times. Half the rats in each group were tested in A first and then in B, while the other half received the reverse order. The sessions were in 39.5 min in duration, and the interval between tests was about 45 min.

**Data Analysis:** The computer recorded the number of food cup photobeam breaks during each 10-s bin within the CS and during the 30-sec interval that immediately preceded it (the pre-CS period). Each trial's data were then converted into "elevation scores" by subtracting the number of responses during the 30-s pre-CS period from the number of responses during the CS. To analyze responding over bins, the number of responses in the 30-s pre-CS period (divided by three) was subtracted from the number of responses made during each 10-s bin in the CS.

## Results

### Overall responding to the CS

**Conditioning:** The results of each session of conditioning with the light-off CS are presented in Figure 5. Conditioned responding was acquired in an orderly fashion; it was also substantially higher in Group Variable than in Group Fixed. The data were subjected to a Group x Session ANOVA. The effects of both Session, F (23,322) = 10.07, and Group, F (1,14) = 22.99, were significant. The Group x Session interaction was also reliable, F (23,322) = 1.64. However, inspection of the learning curves suggested little evidence of an IWR effect in either group. Trend analyses were therefore conducted to characterize the shape of the curves. Both groups exhibited linear, monotonic acquisition curves, Flinear (1, 322) = 5.39. The quadratic functions were not significant, F < 2.69. The results strongly suggest little IWR over the 288 appetitive conditioning trials presented here.

A Group x Session ANOVA was applied to the pre-CS scores. No main effects or interactions were reliable, the largest F (1,14) = 2.99. The mean pre-CS scores were 7.76 and 6.54 for Group Fixed and Variable, respectively.

**Testing:** The results of the test phase are shown at right in Figure 5. Extinction was rapid in both groups. More important, there was no evidence that the context switch had any impact on conditioned responding. A Group x Context x Trial blocks x Order ANOVA revealed a Block effect consistent with extinction, F (3,36) = 11.12. The Group effect was also reliable, F (1,12) = 5.23; Group Variable continued to respond more than group Fixed. However, there was no Context effect, F (1,12) < 1, and neither the Order effect, F (1,12) < 1, or any other interactions were reliable, F (3,36) = 1.86.

An identical ANOVA on pre-CS scores revealed a Block effect, F (3,36) = 5.40, with pre-CS scores decreasing over blocks. There was no effect of Context, F (1,12) = 2.04, Group, F (1,12) = 1.81, Order, F (1,12) < 1, although there were several interactions with Order. The Context x Order interaction, F (1,12) = 30.82, as well as the Group x Context x Order interaction, F (1,12) = 26.03, were significant. The Context by Block by Order interaction was significant as well, F (3,36) = 3.22. The pattern was complex and provided no alternative explanation of the elevation scores. The mean pre-CS scores in the original and different context were 4.53 and 3.39 for Group Fixed and 2.81 and 2.86 for Group Variable.

**Responding over time in the CS—**The distribution of conditioned responses over time in the CS during conditioning is summarized in Figure 6. Rats in Group Fixed began responding primarily in later bins, when the US was most imminent, very early during the phase. A Group x Bin x Session ANOVA on elevation scores confirmed the Group and Session effects described above. In addition, the Bin main effect was significant, F (2,28) = 55.50. The Group x Bin interaction was significant, F (2,28) = 12.71, which is consistent with the fact that the bin effect was especially pronounced in the Fixed group. The pattern developed over sessions: Both the Bin x Session interaction, F (46,644) = 2.66, and the Group x Bin x Session interaction, F (46,644) = 1.61, were significant. The results are clearly consistent with the idea that rats in Group Fixed quickly learned to time the US, although it is worth noting that Group Variable also showed a more modest increase in responding over bins (e.g., analysis of the last three sessions in Group Variable revealed a significant effect of bin, F (2, 14) = 18.47).

**Testing:** Responding over bins during the test trials is presented at the right of Figure 6. A Group x Context x Trials x Bin x Order ANOVA confirmed the effects and interactions described earlier. The Bin effect was significant throughout testing, F (2,24) = 6.99. Consistent with the conditioning phase, this effect interacted with Group, F (2,24) = 9.69. The bin effect diminished over the test (extinction) trials, as evidenced by a Bin x Trial Block interaction, F (14,168) = 7.22. The Group x Bin x Trials interaction was significant as well, F (14,168) = 1.88. The Context effect was not significant, F (1,12) = 3.12. There was no Order effect, F (1,12) = 1.05, however the Context x Bin x Order interaction was significant, F (2,24) = 3.35. The Context x Bin x Trials x Order interaction was not significant, F (14,168) = 1.68.

### Discussion

The results of this experiment contrast with the results of the preceding conditioned suppression experiments. First, in contrast to the analogous group in Experiment 3, rats in Group Fixed quickly showed a temporal anticipation of the US (see also Kirkpatrick & Church, 2000). (The more modest inhibition of delay evident in Group Variable presumably resulted from the fact that no US was ever presented before the $10^{th}$ second in the CS.) Second, in further contrast to Experiment 3, there was little evidence of IWR in either the Fixed or the Variable group. It is worth noting that we have not typically observed nonmonotonic conditioning curves in our many experiments with this conditioning preparation. Thus, although the details of the conditioned suppression and appetitive methods differ in many ways, IWR is more characteristic of conditioned suppression than appetitive conditioning in our laboratory.

Third, and equally important, there was no effect of the context switch on conditioned responding. The lack of such an effect is also consistent with our own previous work in appetitive conditioning (e.g., Bouton & Peck, 1989; Bouton & Sunsay, 2001; Brooks & Bouton, 1994), and that of Kaye and Mackintosh (1990), who replicated the methods used in conditioned suppression experiments that had yielded enhanced conditioned responding with a context switch. The fact that there was neither IWR nor enhanced responding with a context switch here continues to be consistent with the idea that the two effects are linked. But the results of the present experiment also further dissociate the two phenomena from inhibition of delay. Although inhibition of delay was evident here, it was not connected with IWR or an augmentation of responding after the final context switch. Taken together, the results of Experiments 3 and 4 thus suggest that inhibition of delay is neither necessary (Experiment 3) nor sufficient (Experiment 4) to produce these effects.

## General Discussion

The present results further document an inhibition-with-reinforcement (IWR) effect in the conditioned suppression preparation. More important, they also suggest that the strength of IWR predicts the effect of a subsequent context switch: If IWR is present, a context switch increases suppression to the CS. The pattern thus suggests that IWR might depend in part on the acquisition of a context-dependent process that reduces suppression to the CS.

Consistent with this view, the augmenting effect of the context switch was consistently correlated with the extent to which IWR had developed in individual subjects. To further examine this point, Figure 7 plots augmentation for each rat in Experiments 1 – 3 as a function of the strength of the rat's IWR (both defined as explained in Experiment 1). As the figure makes clear, over all three conditioned suppression experiments, the effect of the context switch was strongly correlated with the extent to which suppression to the CS was "inhibited" after training, $\underline{r}$ (46) = +.71. Thus, when fear of the CS decreased over the course of conditioning, augmentation occurred, and the degree of that decrease accounted for 50.4% of the variance in the effect of the context switch. One potential complication is that the amount of augmentation produced by the context switch was also correlated with the level of suppression shown in the original context of training at the outset of testing, $\underline{r}$ (46) = +.44. Rats exhibiting IWR also tended to exhibit weaker suppression, and it is possible that weaker suppression is more sensitive to the augmentation effect. However, when the level of suppression exhibited in the same context was controlled by means of partial correlation, the relationship between IWR and augmentation was still substantial and reliable, partial $\underline{r}$ (45) = +.62. Thus, reduced suppression, and not merely position on the suppression ratio scale in the Same context, predicts the strength of the suppression-augmenting effect of changing the context.

The correlation between IWR and enhanced suppression following the context switch has implications for understanding of the role of context in conditioning. As noted earlier, it is

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reminiscent of related results that have been obtained in this laboratory (Bouton & King, 1986). In several conditioned suppression experiments using a number of different continuous- and partial-reinforcement procedures, Bouton and King (1986) examined the effects of further contextual conditioning created by additional exposure to the US after a conditioning treatment. When suppression to the CS had been extinguished, contextual conditioning “reinstated” extinguished suppression to the CS. In contrast, when suppression to the CS was not under the influence of extinction, contextual conditioning had little impact on suppression to the CS. Several conditioning procedures yielded results that were in between these extremes. Ultimately, the best predictor of the effect of contextual conditioning on a group’s CS performance was not the conditioning procedure per se, but the extent to which average suppression to the CS was otherwise “depressed” at the start of testing. Indeed, the degree of depression and the size of the context effect were calculated using the methods we followed here (Figure 7). The present results thus converge on the earlier findings. The effects of either conditioning the context (Bouton & King, 1986) or switching the context (present results) depend on the extent to which CS performance is depressed or inhibited compared to an earlier point in training. Either manipulation partially restores a depressed level of conditioned suppression.

The key to understanding the present results thus depends on understanding the process that causes the IWR effect. The possibility that the effects of a context switch might depend on some kind of inhibition or adaptation process was previously suggested by Hall, Honey, and their collaborators (Hall & Honey, 1990; see also Hall & Mondragón, 1998). Hall and Honey (1990) were the first to suggest that context switches might have two opposing effects. The first, anticipated by views supposing that contexts act as retrieval cues or occasion setters, is that conditioned responding would be reduced by a change of context. This sort of mechanism is consistent with the loss of conditioned suppression they observed after a single conditioning trial (Hall & Honey, 1990). However, with extended CS-US pairings, some additional process may come into play to help the organism adapt to the CS, the US, or even the fear CR (see below). Some such adaptation process is presumably responsible for the IWR effect that has often been observed in conditioned suppression (e.g., Ayres et al., 1979; Schachtman, Channell, & Hall, 1987; Vigorito & Ayres, 1987) and is further documented here. For present purposes, the important thing is that this process is also potentially disrupted by a context switch. The net result of any context switch, therefore, will depend on the balance of these two factors. As initially noted by Hall and Honey (1990) and further developed by Hall and Mondragón (1998), failures to observe an effect of switching the context (e.g., Bouton & King, 1983) may result from the simultaneous loss of both types of processes, which could cancel one another.

Experiments 3 and 4 considered the possibility that the loss of suppression that occurs over training is due to the development of inhibition of delay (e.g., Zielinski, 1966). That is, early parts of the CS may come to evoke less suppression than later parts of the CS if the animal learns to anticipate the US in time. Inhibition of delay often develops gradually over trials in the conditioned suppression method (e.g., Rosas & Alonso, 1996; but see Schachtman et al., 1987), and it may thus account for the decline in conditioned suppression we observed over training. But more important, inhibition of delay can be attenuated with a context switch (Rosas & Alonso, 1997), potentially causing the increase in overall conditioned suppression we also observed here.

The results of Experiments 3 and 4, however, suggest that inhibition of delay does not produce the effects of interest. In Experiment 3, there was evidence of equivalent IWR and enhanced suppression in a group that had the US at the end of the CS (where inhibition of delay was expected) and a group that had the US with equal probability earlier in the CS. Moreover, there was no evidence of inhibition of delay developing over the number of conditioning trials used there. In Experiment 4, the development of inhibition of delay in appetitive conditioning did not yield either IWR or increased responding with a context switch. It is also worth noting that in their experiments demonstrating enhanced conditioned suppression with a context switch, Kaye and Mackintosh (1990, Experiment 3) presented evidence suggesting that the temporal pattern of responding within the CS, which was otherwise consistent with the presence of inhibition of delay, did not change when the context was switched and therefore did not account for their augmentation effect. That result was mainly seen as arguing against a role for dishabituation of any habituated unconditioned suppression to the CS. But like the results of Experiments 3 and 4, it also argues against an account emphasizing the loss of inhibition of delay, although the results will need to be reconciled with those of Rosas and Alonso (1997).

Another candidate for the adaptation process is suggested by Wagner's SOP model (e.g., 1981). According to SOP, repeated exposure to the CS during either CS-US or CS-no US trials would allow the animal to associate the CS with the context. As a consequence, the context alone would prime a memory representation of the CS into a secondarily active state ("A2"). Putting the CS into this state might reduce its ability to evoke a CR. A new context would not put the CS into A2, and would therefore allow an increase in the strength of the CR. Consistent with this possibility, Honey, Hall, and Bonardi (1993) have shown that presenting an appetitive CS outside of the "context" provided by a stimulus in the presence of which it was paired with food can sometimes invigorate conditioned responding (see also Hall & Mondragón, 1998). Also consistent with this possibility, orienting responses evoked by a stimulus, which would also be reduced by priming the CS into A2, are lower when the stimulus is accompanied by a reliable rather than an unreliable predictor (Honey & Good, 2000; Honey, Good, & Manser, 1998). Although the related literature on the role of context in habituation contains a mixture of results (see Hall, 1991, or Bouton, 1993, for reviews), relatively recent evidence suggests that a change of context can increase non-learned responding to an habituated stimulus under some conditions (Jordan, Strasser, & McHale, 2000). If we assume that the ability of a CS to evoke a CR is correlated with its ability to evoke an orienting response, the implication is that a context switch can liberate the CR under some conditions.

One problem for this analysis, however, is the fact that the 288 context-CS pairings during conditioning in the appetitive conditioning experiment (Experiment 4) did not yield augmented responding when the context was changed. In contrast, the groups that showed augmentation in the conditioned suppression experiments received only 42–48 conditioning trials. Thus, the adaptation process correlated with augmentation is not a simple function of the number of CS presentations. Kaye and Mackintosh (1990) likewise found no evidence of an augmentation effect in experiments on appetitive conditioning. And it is worth emphasizing that there was no evidence in Experiment 4 of a nonmonotonicity in the conditioning curve to suggest an adaptation process analogous to the one observed in conditioned suppression. Hall and Honey (1990) emphasized this point in their discussion of possible differences in the manner in which context switches influence responding to appetitive and aversive CSs. The present findings may thus begin to suggest some differences between appetitive and aversive conditioning.

Yet another candidate for a mechanism behind the IWR phenomenon is a process like the one proposed in opponent-process theory (Solomon & Corbit, 1974; see Overmier et al., 1979). According to that view, presentation of the shock US may engage a process that grows nonassociatively as a function of US exposures (Solomon & Corbit, 1974) or associatively as a function of CS-US pairings (Schull, 1979) and serves to oppose the emotional impact of the US. For example, one possibility is the conditioned release of endorphins (endogenous opiates), which would minimally reduce the painfulness of shocks on late conditioning trials (e.g., Young & Fanselow, 1992). However, administration of naloxone, an opiate antagonist, does not appear to eliminate the adaptation effect that can occur over trials within sessions of conditioned suppression training (Vigorito & Ayres, 1987). And perhaps more important, the present experiments demonstrated that the context switch augmented the rat's reaction to the CS-- not reaction to the US, which was not presented during testing. Note that even the conditioned opponent process envisioned by Schull (1979) is supposed to modulate the organism's reaction to the US, rather than the CS. Thus, even if the conditioned opponent process were context-specific, there are no grounds for expecting its loss to enhance the conditioned response to the CS, as we observed here.

The present experiments thus link inhibition-with-reinforcement to a CS-related process that influences the CR. One possibility is the SOP mechanism, discussed critically above, in which the context-CS association reduces the CR by priming the CS node in A2. Alternatively, the rat may learn to adapt to its fear of the CS over the course of repeated CS-US pairings. For example, as we noted earlier, the presence of the VI reinforcement schedule in the conditioned suppression method introduces a contingency in which a food reinforcer is increasingly imminent as time without responding in the CS goes by. With repeated exposure to CS-US pairings, the animal might thus be occasionally reinforced for responding in later portions of the CS (Experiment 3). Such response-reinforcer pairings would increase instrumental responding in the presence of fear. The fact that the resulting adaptation was attenuated when the CS was tested in a different context (that had itself been associated with fear conditioning with a different CS) suggests that there is considerable stimulus-specificity to the process.

In summary, the current results confirm an IWR effect in the conditioned suppression preparation, suggest that it does not depend on inhibition of delay, and importantly suggest that it is due to some other context-specific process that may involve adaptation to fear. Previous failures to observe any effect of switching the context after conditioning may have reflected the simultaneous loss of both excitation and adaptation, which might cancel each other out (e.g., Hall & Mondragón, 1998). The findings may be relevant to understanding human anxiety disorders. In panic disorder, a person may undergo a series of panic attacks that can cause the conditioning of fear to various exteroceptive and interoceptive cues (e.g., Bouton, Mineka, & Barlow, 2001). One example of an interoceptive cue that might be associated with panic is a pounding heart. The present results suggest that a person might learn to adapt to fear over trials as the pounding heart and panic are repeatedly paired in the context of the home. But if he/she were to encounter the CS (the pounding heart) in another context, augmented fear would result. Augmented fear outside the conditioning context might motivate the person to stay at home—and thus provide a mechanism for agoraphobia. The context-specificity of fear adaptation, perhaps coupled with the context-specificity of fear extinction (e.g., Bouton, 2002), may conceivably contribute to the persistence of many anxiety disorders.

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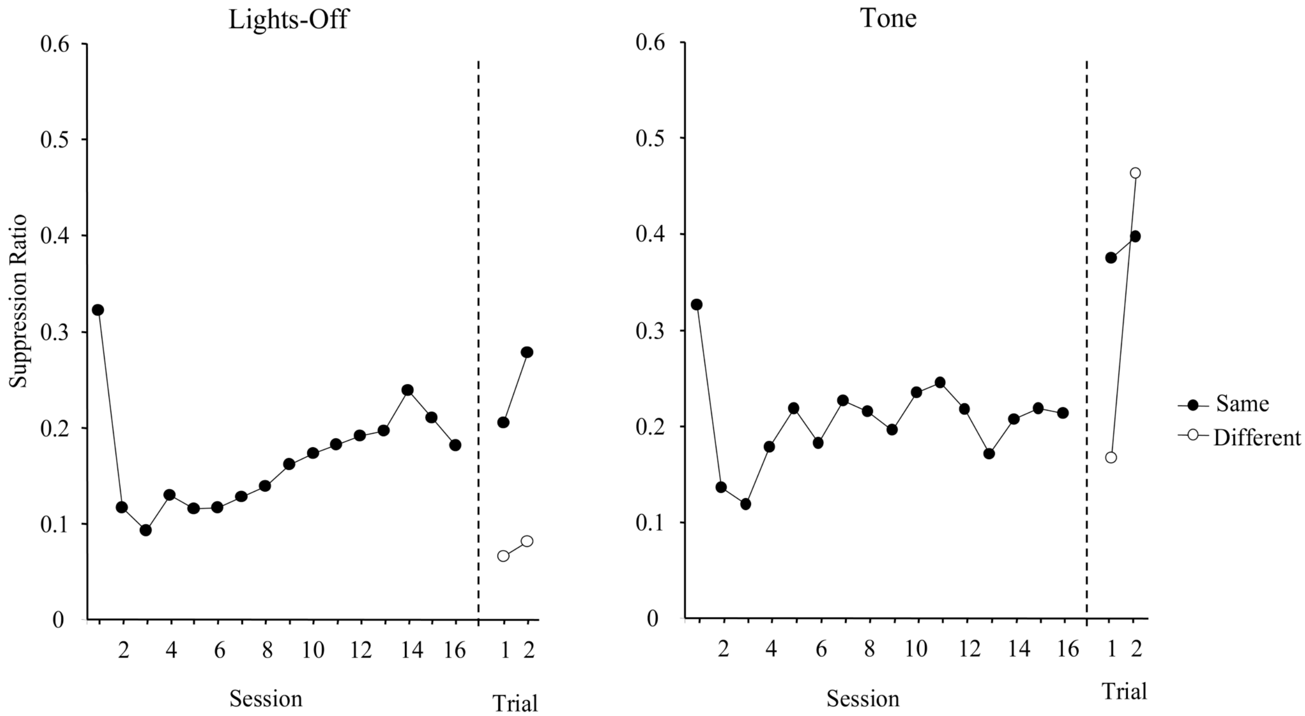


**Figure 1.**

Mean suppression to the light-off (left) and tone (right) CSs during Experiment 1. In each panel, the conditioning phase is shown at left and testing is shown at right.

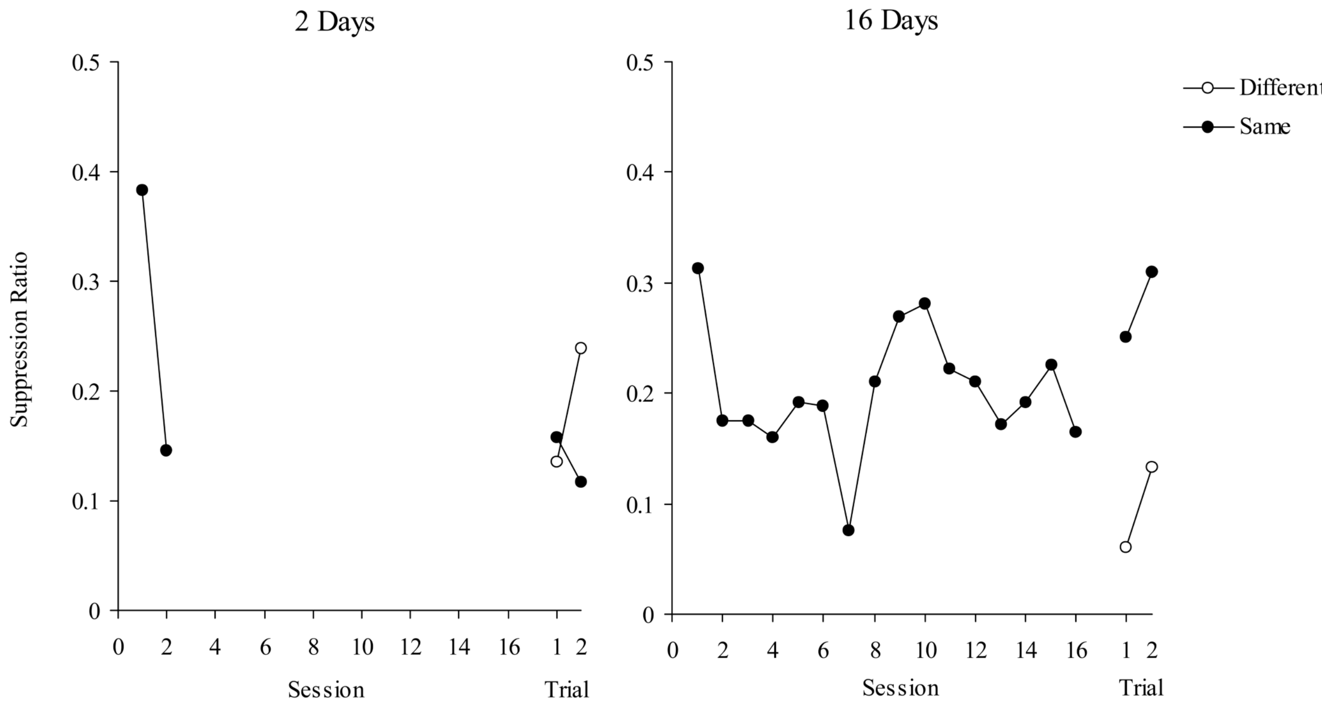


**Figure 2.**
Mean suppression to the CS during the conditioning and testing phases of Experiment 2. In each panel, the conditioning phase is shown at left and testing is shown at right.

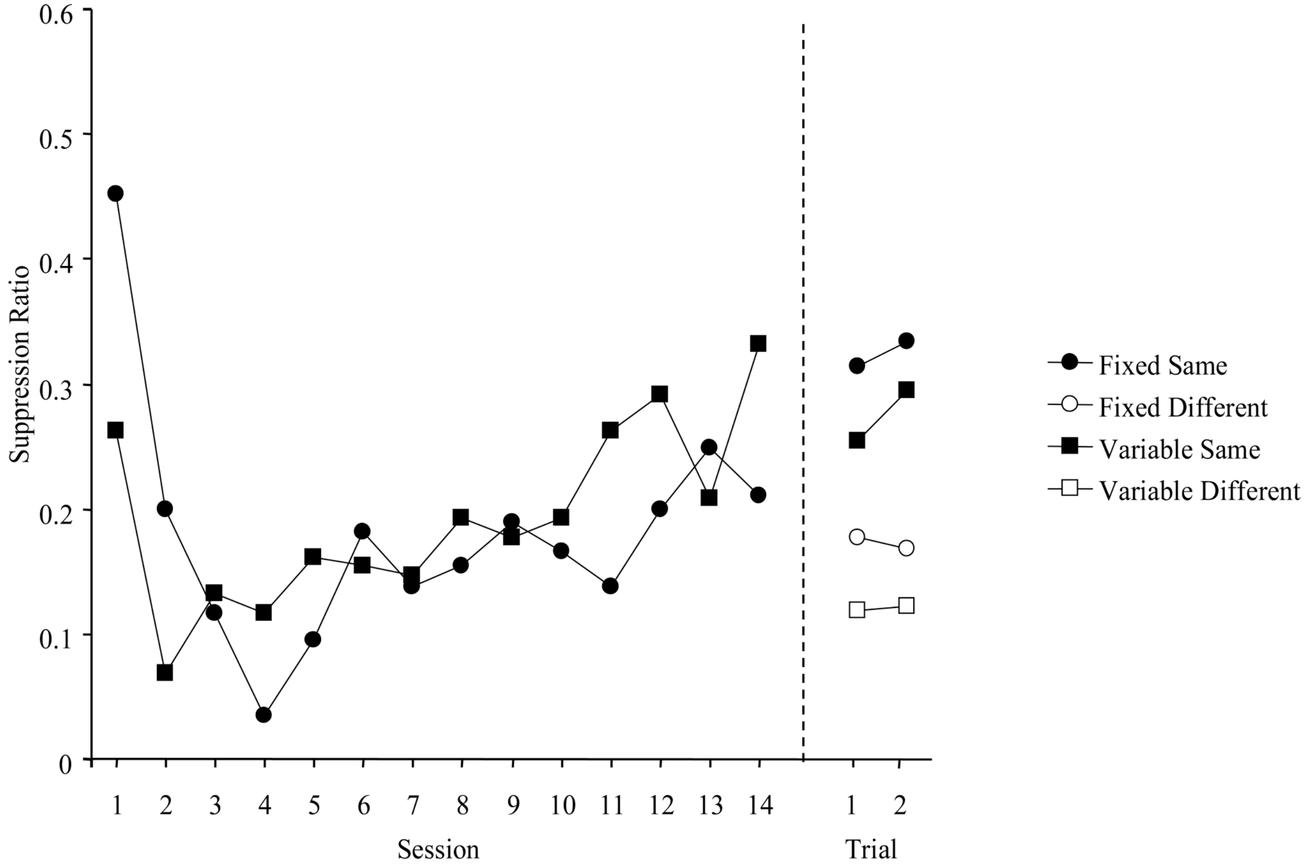


**Figure 3.**
Mean overall suppression to the CS during conditioning and testing in Experiment 3.

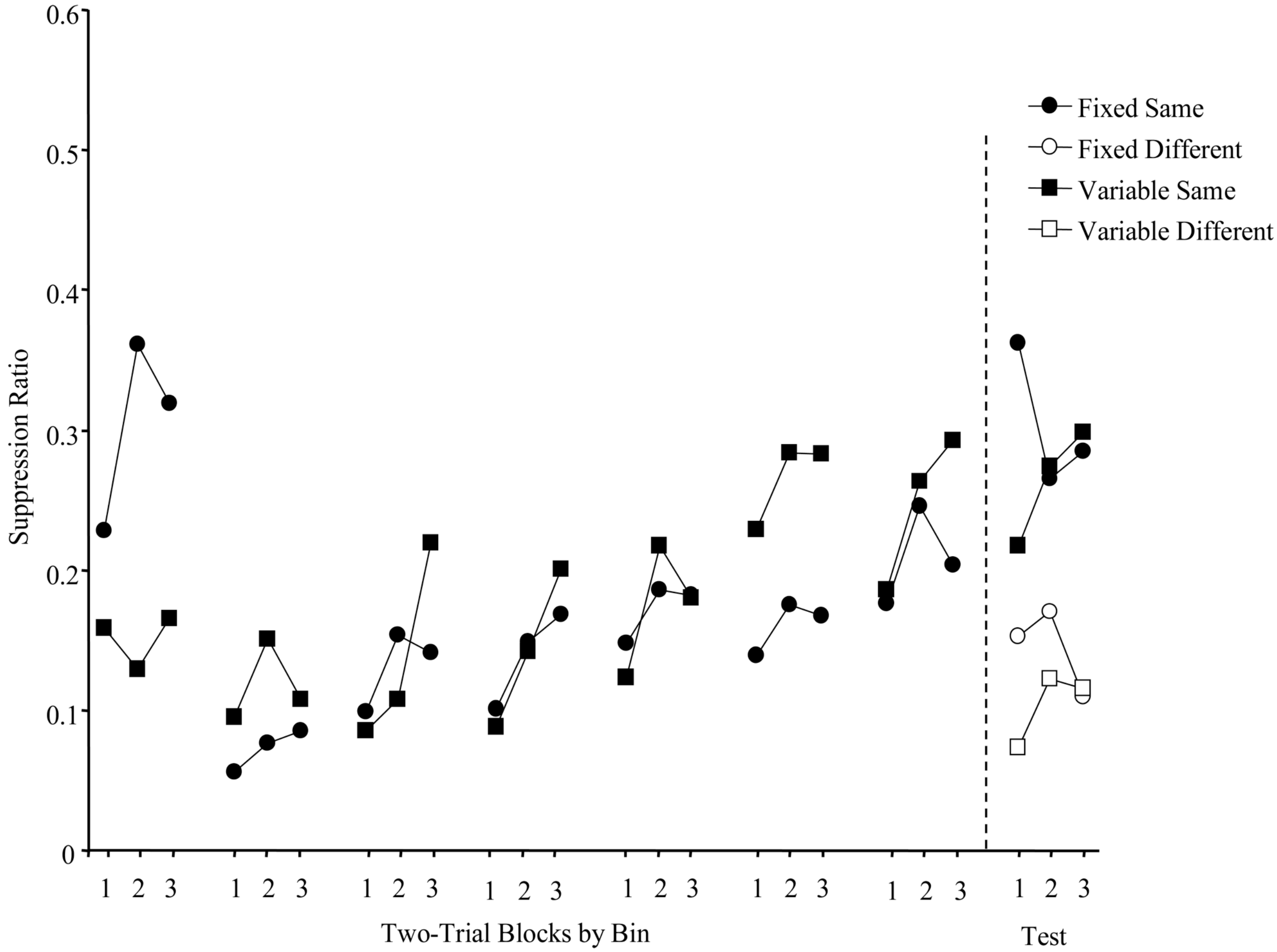


**Figure 4.**
Mean suppression to the CS during 20-s bins of the 60-s CS during conditioning and testing in Experiment 3. The conditioning data are shown over two-trial (two-session) blocks.

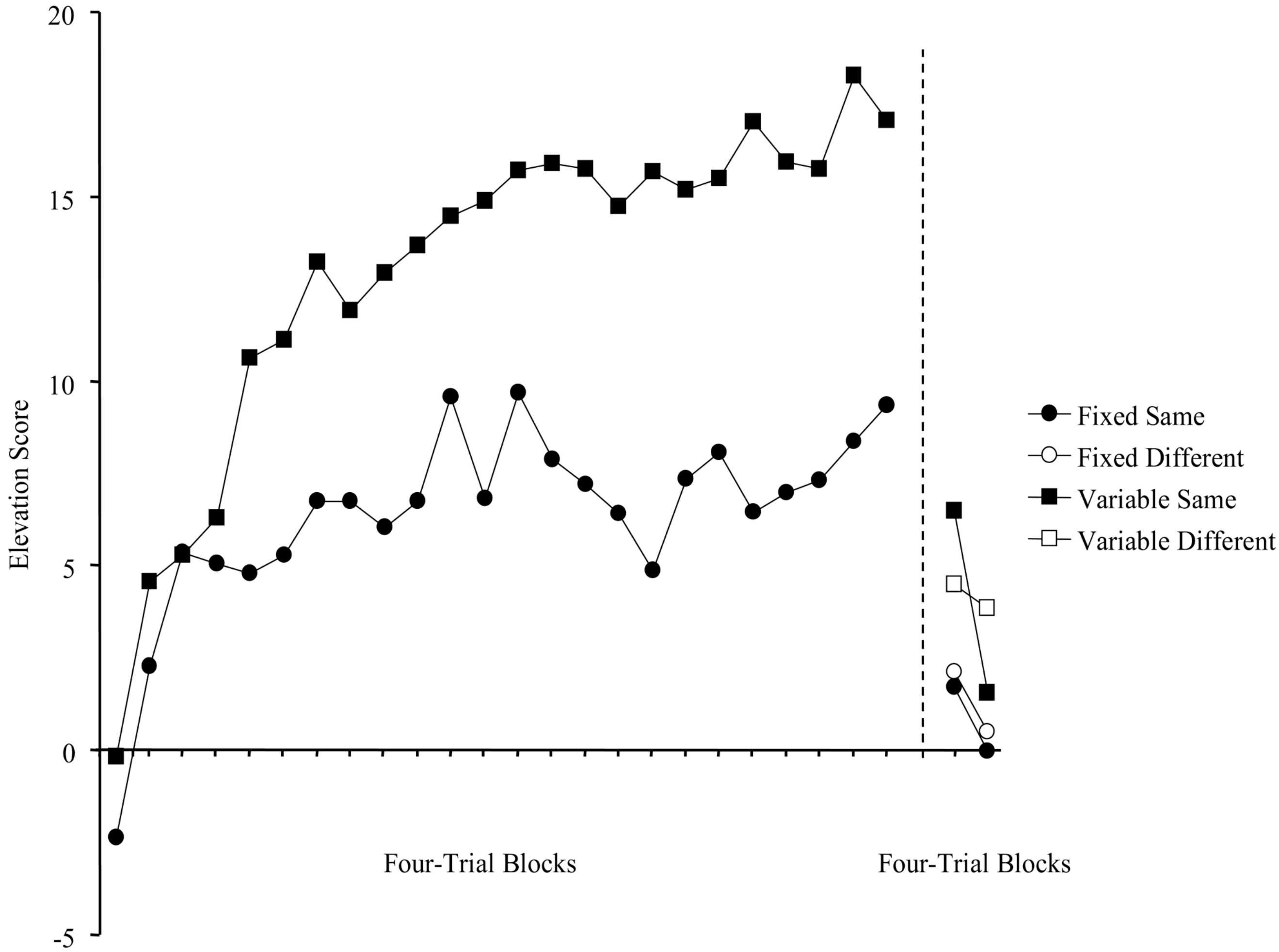


**Figure 5.**
Mean elevation scores during conditioning and testing in Experiment 4.

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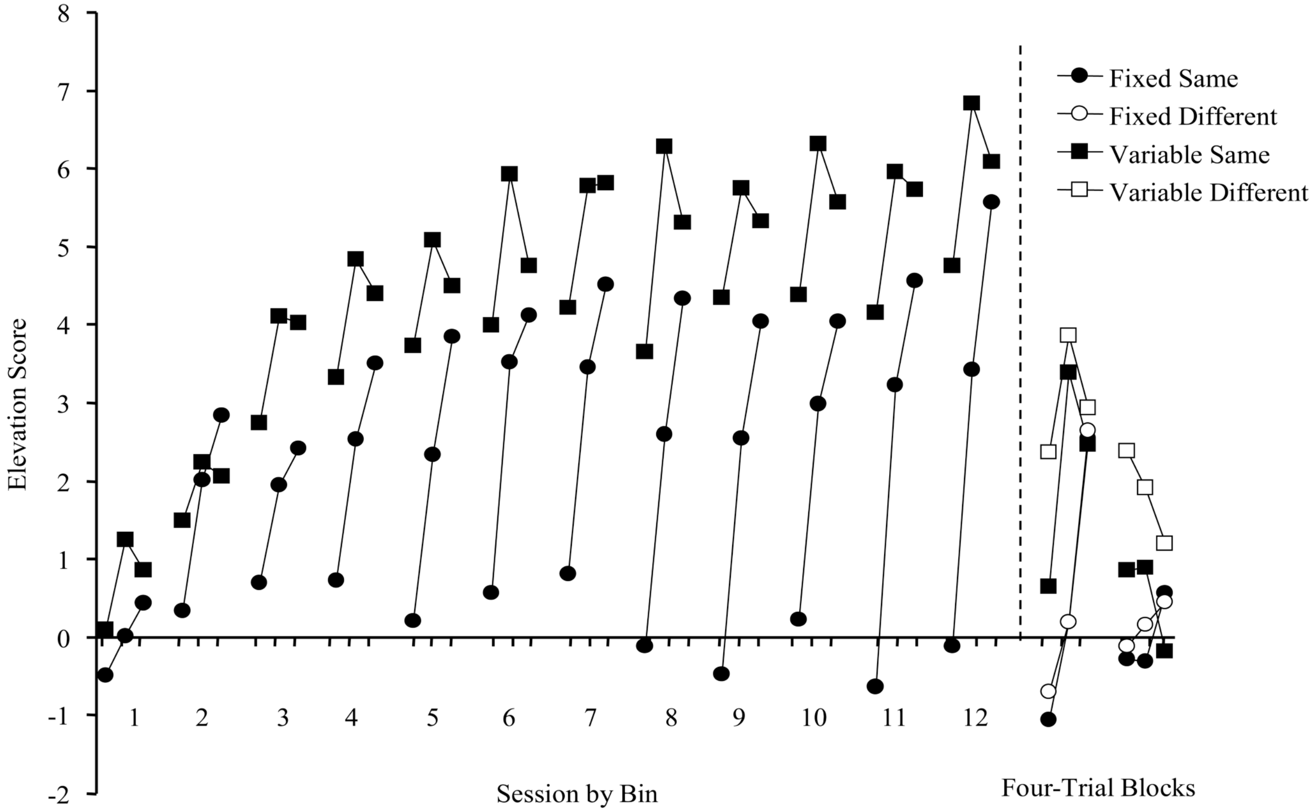


**Figure 6.**
Mean elevation scores during 10-s bins of the 30-s CS during conditioning and testing in Experiment 4. Conditioning data are shown over two-session blocks.

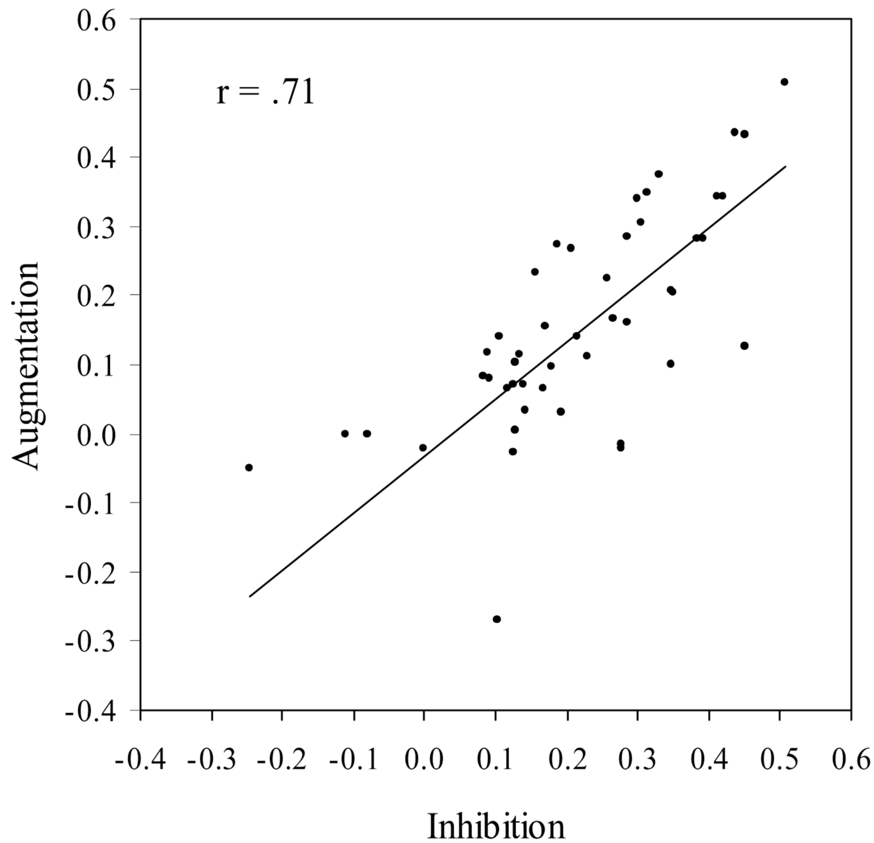


**Figure 7.**
Size of the effect of changing the context during testing (y axis) as a function of the degree to which suppression to the CS was inhibited at the outset of testing (x axis). Each point represents a subject tested in Experiments 1 – 3.