

Reinstatement of Fear to an Extinguished Conditioned Stimulus: Two Roles for Context

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The authors studied the role of context in reinstatement. Freezing was reinstated when the conditioned stimulus (CS) was extinguished in 1 context and rats moved to another context for reexposure to the shock unconditioned stimulus (US) and test. It was also reinstated (rather than renewed) when rats were shocked in the extinction context and moved to another context for test. This reinstatement was CS specific and reduced by nonreinforced exposures to the extinction context. Rats shocked in the context in which a stimulus had been preexposed froze when tested in another context. These findings suggest 2 roles for context in reinstatement: conditioning of the test context (M. E. Bouton, 1993) and mediated conditioning by the extinction context (P. C. Holland, 1990).

The responding that results from learning about an excitatory relation between a conditioned stimulus (CS) and an unconditioned stimulus (US) is reduced if the relation is broken by exposure to the CS in the absence of the US (see Rescorla, 2000, for review). This reduction or extinction of learned responding is relatively specific to the context in which the CS was presented in the absence of the US. For instance, if rats are initially exposed to pairings of a CS and US in one context (A), then moved to a second context (B) in which they receive CS-alone presentations, responding is restored or “renewed” when they are returned to A and tested with the extinguished CS (Bouton & Bolles, 1979a). The renewal of responding to an extinguished CS does not depend on rats being tested in the context in which they had first learned about the CS–US relation. If rats are exposed to CS–US pairings and then to the CS alone in the same context (A), responding is also renewed when the rats are moved to a second context (B) and tested with the extinguished CS (Bouton & Ricker, 1994). These examples of renewal show that breaking the CS–US contingency by subsequent presentations of the CS in the absence of a US does not erase what had been learned about the original contingency (e.g., Rescorla & Wagner, 1972). Rather, extinction imposes a mask on the expression of the original learning (see Rescorla, 1979, for discussion), and this mask is relatively specific to the context in which extinction occurred (see Bouton, 1993, for discussion).

Another technique used to show that the original learning survives extinction is to present the US in the absence of the CS.

Rescorla and Heth (1975) confirmed earlier reports (e.g., Pavlov, 1927) that responding to an extinguished CS was restored or “reinstated” by reexposure to the original US. They also showed that this reinstatement occurred when another CS signaled the reexposed US or when some time (24 hr) elapsed between reexposure to the US and the test for responding to the extinguished CS. These and other studies of reinstatement involved extinction, US reexposure, and test taking place in the same context (e.g., Rescorla & Cunningham, 1977). Therefore, reinstatement, like renewal, could be due to removal of the mask imposed by the context in which the CS had been extinguished. There are various candidates for this mask, but two that have been popular each appeal to the development of contextually controlled inhibition. One of these locates the inhibition between the context and the US, supposing that the extinction-associated context increases the threshold at which the US representation can be activated (e.g., Rescorla, 1979; Rescorla & Cunningham, 1977). The other identifies the mask with the development of occasion-setting properties by the extinction-associated context, supposing that it activates an inhibitory association between the CS and US (e.g., Bouton & Ricker, 1994). Although differing with respect to the locus of context inhibition, these proposals share the view that US reexposure removes the mask imposed on the expression of the original CS–US association by directly conditioning the context. This antagonizes the ability of the context to increase the threshold for activation of the US representation or to activate an inhibitory CS–US association, thereby reinstating responding to the extinguished CS.

An implication of both of these proposals is that reinstatement of responding to an extinguished CS will be influenced by whether animals are reexposed to the US in the extinction context. Specifically, reinstatement should be observed when extinction, US reexposure, and test occur in the same context but not when extinction and test occur in one context and US reexposure in a different context. Bouton and colleagues have provided evidence consistent with this inference. For example, Bouton and Peck (1989; see also Bouton & King, 1983) reported reinstatement of

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responding to an extinguished CS when conditioning, extinction, US reexposure, and test occurred in the same context but not when conditioning, extinction, and test were in one context and US reexposure was in a second context. Similar findings have been reported by Bouton and Bolles (1979b), who arranged CS-US pairings in one context (A), extinguished the CS in a second context (B), and presented the US in A or B. The subsequent test in B revealed reinstatement of responding among rats reexposed to the US in the extinction context (B) but not among those reexposed to the US in the conditioning context (A). Thus, responding to an extinguished CS was reinstated when the US was reexposed in a context associated with both conditioning and extinction or just with extinction, but responding was not reinstated when the US was reexposed in a context just associated with conditioning or in one in which no stimuli had been presented previously.

However, the studies that have just been described observed reinstatement when rats were both reexposed to the US and tested in the extinction context. Therefore, reinstatement could have been due to the test being conducted in the context in which the US had been reexposed rather than to the US being reexposed in the context in which extinction had occurred. Bouton, Rosengard, Achenbach, and Peck (1993) examined these alternatives by exposing rats to pairings of a CS and a food US in Context A and then extinguishing the CS in that context. This was followed by discrimination training that consisted of exposing the rats to two other contexts (counterbalanced) and presenting food in one of them (B) but not in the other (C). The subsequent test revealed more responding when the extinguished CS was tested in B than in C. The increased responding when the rats were tested in B could reflect summation whereby any renewed responding produced by the context shift from A was energized by the conditioned B context (e.g., Wagner & Brandon, 1989). However, there is considerable evidence that a conditioned context acts selectively: It increases responding to an extinguished CS but fails to increase responding to a nonextinguished CS even when care is taken to ensure that the extinguished and nonextinguished CSs provoke comparable levels of responding (see Bouton, 1993, for review). Therefore, some process other than that involved in summation must underlie the impact of contextual conditioning on the levels of responding to an extinguished CS.

Bouton (1993) has developed a memory-based approach to many conditioning phenomena including reinstatement by US presentations. This approach holds that conditioning and extinction experiences are represented as distinct CS-US and CS-no-US memories. Subsequent responding to that CS is determined by which one of these memories is activated. A critical difference between the two types of memories is that activation of the CS-US memory is independent of the context in which conditioning occurred, whereas retrieval of the CS-no-US memory is tied to the context in which extinction took place. These assumptions explain renewal as due to the extinguished CS being tested outside the context that retrieves the CS-no-US memory. Reinstatement is held to occur through slightly different processes. Specifically, context conditioning constitutes part of the "background" against which the original CS-US memory was established. Postextinction context conditioning by US presentations returns the animal to the conditions (of background conditioning) under which the original CS-US memory was formed. Test presentations of the CS in that

conditioned context activate the CS-US memory, leading to a reinstatement of responding.

These conditions of "background conditioning" cannot be identified with the particular context in which the CS-US memory was formed, as reinstatement has been observed when conditioning and extinction occurred in Context A whereas the test was in the recently reinforced B context (Bouton et al., 1993). They could be identified with the responses or the emotional state elicited by context conditioning if it were assumed that these responses or this state served as occasion-setters for subsequent CS-US pairings (see Delamater, 1997, for discussion). However, regardless of the precise nature of background conditioning, the account of reinstatement developed by Bouton emphasizes the role played by the collocation of US reexposure and test rather than by the collocation of extinction and US reexposure: Essentially, it proposes that responding is reinstated when the extinguished CS is tested in a conditioned context.

The findings reported by Bouton et al. (1993) demonstrate that responding is reinstated when the extinguished CS is tested in a context in which the US was reexposed. However, this conclusion does not exclude the possibility that reexposure to the US in the extinction context also plays a role in reinstatement. As discussed previously, US reexposure in the extinction context may provoke reinstatement by removing either the inhibitory (Rescorla, 1979) or occasion-setting (Bouton & Ricker, 1994) properties acquired by the context across the course of extinction. Here, we consider an alternative means by which reexposure to a US in the extinction context could provoke reinstatement. We note that animals learn about the relation between a context and CS across the course of extinction (e.g., Rescorla, 1984) and that these context-CS associations might allow mediated conditioning of the extinguished CS (e.g., Holland, 1981) when the US is reexposed in that context. Thus, according to this proposal, US reexposure in the extinction context produces reinstatement because the CS is reassociated with the US through their common context associate. The present experiments study reinstatement of fear reactions (freezing) in rats reexposed to a shock US. The main objective was to explore this additional possible role of the context associated with both extinction and US reexposure.

Experiment 1

Reinstatement of extinguished responding by reexposure to the original shock US has been studied typically in a conditioned suppression procedure (e.g. Bouton & Bolles, 1979b; Rescorla & Heth, 1975). The aim of Experiment 1 was to show that reexposure to a shock US also reinstates the conditioned freezing that has been extinguished by repeated presentations of the CS in the absence of its associated shock US. The design consisted of a 2×2 factorial in which the first factor was whether rats were exposed to paired (P) or unpaired (U) relations between the CS and US, and the second factor was whether, after nonreinforced presentations of the CS, rats were (R) or were not (N) reexposed to the US. The design used is shown in Table 1.

Method

Subjects. Sixteen experimentally naive, male, inbred Wistar rats (*Rattus norvegicus*) were used. They weighed between 300 and 350 g and were

Table 1
Summary of Designs for Experiments 1–3

Group	Conditioning	Extinction	Reinstatement	Test
Experiment 1				
PR	A: CS+	A: CS–	A: +	A: CS
PN	A: CS+	A: CS–	A: –	A: CS
UR	A: CS/+	A: CS–	A: +	A: CS
UN	A: CS/+	A: CS–	A: –	A: CS
Experiment 2a				
AA	A: CS+	A: CS–	A: +	A: CS
AB	A: CS+	A: CS–	A: +	B: CS
BA	A: CS+	A: CS–	B: +	A: CS
BB	A: CS+	A: CS–	B: +	B: CS
Experiment 2b				
BB	A: CS+	B: CS–	B: +	B: CS
BC	A: CS+	B: CS–	B: +	C: CS
CB	A: CS+	B: CS–	C: +	B: CS
CC	A: CS+	B: CS–	C: +	C: CS
Experiment 3				
AC	A: CS+	A: CS–	A: +	C: CS
BC	A: CS+	A: CS–	B: +	C: CS
–/C	A: CS+	A: CS–	—	C: CS

Note. A, B, and C refer to three distinct contexts. A clicker was used as the conditioned stimulus (CS). + = presentation of the shock unconditioned stimulus (US); – = absence of shock; P = paired relations between the CS and US; U = unpaired relations between the CS and US; R = rats were exposed to the US; N = rats were not exposed to the US; / = unpaired presentations of the CS and shock; — = nothing happened to the group at this stage.

obtained from the colony of specific pathogen-free rats maintained by the Combined Universities Laboratory Animal Service (Sydney, Australia). They were housed in groups of 8 in plastic boxes (67-cm length $\times$ 40-cm width $\times$ 22-cm height) with food and water continuously available. The boxes were kept in an air-conditioned colony room under natural lighting. All experimental procedures occurred between 7 a.m. and 10 a.m. Each rat was handled 5–10 min each day across 5 days before the start of the experiment. The experimental procedures followed the ethical guidelines established by the American Psychological Association and were approved by the Animal Care and Ethics Committee of the University of New South Wales.

Apparatus. A set of four chambers (20-cm length $\times$ 21-cm width $\times$ 23-cm height) was used. The front and back walls as well as the lids were made of clear plastic, and the sidewalls were made of aluminum. The floor consisted of stainless steel rods, 2 mm in diameter, spaced 13 mm apart (center to center), with a tray containing bedding material below. The chambers were located in separate compartments of a wooden cabinet. The door of each compartment was kept open to permit observation of each rat. Natural lighting illuminated the room.

Unscrambled AC 50-Hz shock could be delivered to the floor of each chamber by a custom-built constant-current shock generator. The current available to each floor could be adjusted using an in-line milliamperemeter. The floor of each chamber was cleaned with a solution of acetic acid (0.5%) on removal of a rat. The CS was a 30-s presentation of a clicker, which consisted of a 78-dB (A: Brüel & Kjaer, Type 2235) 10-Hz spike (rise time $<1.0 \mu\text{s}$ and a decay time of 250 μs) provided by a generator wired to a speaker (160-mm-diameter wideband width) located on the ceiling. The background noise level was 65 dB. The behavior of each rat

was recorded using a camera mounted on the wall facing the open compartment. The camera was connected to a video recorder and monitor located in another room in the laboratory. This room also contained the equipment that controlled CS and shock presentations.

Procedure. The rats were weighed and assigned to four weight-matched groups ($n = 4$). On Days 1 and 2, each rat was exposed to a chamber for 10 min. Shock (0.8 mA, 0.5-s duration) was delivered through the floor 6.5 min after placement in the chamber. For rats in Groups PR and PN, shock onset cooccurred with the offset of a 30-s presentation of the clicker. For rats in Groups UR and UN, the onset of the 30-s CS occurred 30 s after placement in a chamber, and its offset occurred 6 min in advance of shock. On Days 3–10, each rat was placed in a chamber for 10 min. On each of these days, the CS was presented for 30 s on four occasions, 6, 7, 8, and 9 min after the rats were placed in the chamber. On Day 11, rats were exposed to the chambers for 10 min. For rats in Groups PR and UR, shock (0.5 mA, 0.5-s duration) was delivered 5 min after placement in the chamber, but no shock was delivered to rats in Groups PN and UN. The intensity of the shock at reexposure was reduced to avoid substantial levels of freezing to the context on test. On Day 12, rats were tested. The test consisted of exposing the rats to the chambers for 10 min and presenting the CS for 30 s on four occasions, 6, 7, 8, and 9 min after placement in a chamber.

Scoring and statistics. Performance to the CS across extinction and test was videotaped, and the levels of freezing were measured with a time-sampling procedure in which the rat's behavior was scored as *freezing* or *not freezing* every 2 s. Freezing was defined as the absence of all movement, including those of the vibrissae, except those related to breathing (Fanselow, 1980). The percentage of all samples scored as freezing was determined for each rat. Two observers, one of whom was unaware of the rat's treatment condition, scored the videotaped record of each rat. The interrater reliability on the scores in this and the remaining experiments was high, producing correlation coefficients $>.96$ in each experiment. The data presented and subjected to statistical analysis were those scored by the naive observer. Unless otherwise stated, in this and subsequent experiments, contrast testing procedures were used to analyze test data with alpha set at .05 (R. J. Harris, 1994).

Results

There were moderate levels of freezing to the CS on Day 2 by rats in Groups P ($M = 58\%$) but not by those in Groups U ($M = 0\%$). Further, freezing by rats in Groups P was confined to the CS as there was no freezing across the 30-s period prior to its presentation. The levels of freezing to the CS by rats in Groups P declined across Days 3–10 from a mean of 75% (Day 3) to means $<10\%$ (Days 8–10), whereas the levels of freezing to the CS by rats in Groups U were $<10\%$ across each of Days 3–10. There were no differences between the levels of freezing among the rats assigned to Groups PR versus PN nor among those allocated to Group UR versus UN, $F_s < 1.0$.

There was very little freezing in each of the groups (means ranged from 0% to 5%) across the 30-s period prior to the initial CS presentation on test, and none of the differences between the groups were significant, $F_s < 1.0$. The mean levels of freezing averaged across the four test presentations are shown in Figure 1. The statistical analysis confirmed that there were main effects for whether rats were exposed to paired (Groups P) or unpaired (Groups U) presentations of the CS and US, $F(1, 12) = 38.8$, $F_{\text{critical}} = 4.8$, and for whether rats were (Groups R) or were not (Groups N) reexposed to the US, $F(1, 12) = 14.3$. There was also a significant interaction between these factors, $F(1, 12) = 13.1$, which from inspection indicates that the differences between rats

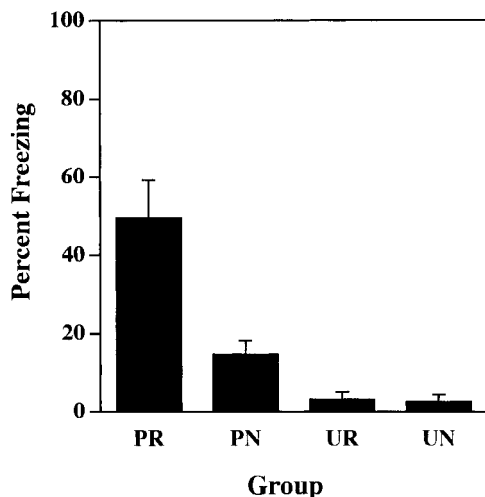


Figure 1. P = paired relations between the conditioned stimulus (CS) and unconditioned stimulus (US); U = unpaired relations between the CS and US; R = rats were exposed to the US; N = rats were not exposed to the US. Mean percentage of freezing to the CS at test in Experiment 1. Rats in Groups PR and PN received CS–US pairings, and those in Groups UR and UN received separate CS and US presentations. After extinction of the CS rats in Groups PR and UR, but not those in Groups PN and UN, were reexposed to the US.

in Groups PR and PN were greater than the differences between rats in Groups UR and UN. Post hoc comparisons using the method described by Scheffé (1959) confirmed that rats in Group PR showed significantly more freezing than did those in Group PN, $F(3, 12) = 27.4$, $F_{critical} = 10.5$, and that there were no significant differences between rats in Groups UR and UN, $F < 1.0$.

Discussion

Experiment 1 confirms well-documented findings: The responding (freezing) generated by exposure to a CS–US pairing was reduced by presentations of the CS in the absence of the US and then reinstated by presentation of the US in the absence of the CS (e.g., Bouton & Bolles, 1979b; Rescorla & Heth, 1975). Reinstatement of freezing was specific to rats exposed to CS–US pairings and reexposed to the US. This indicates that the effect was not a consequence of the interval of time between extinction and test nor of reexposure to the US per se: Rather, reexposure to the US reinstated the learned responding reduced by extinction.

Experiments 2a and 2b

In Experiment 1, responding (freezing) to an extinguished CS was reinstated when extinction, US reexposure, and test all occurred in the same context. Thus, reinstatement could have been due to the rats being reexposed to the US in the context in which testing occurred (thus returning them to the background of conditioning) and/or to the rats being reexposed to the US in the extinction context (thus restoring the CS–US association through mediated conditioning). The present experiments used two-context (Experiment 2a) or three-context (Experiment 2b) arrangements to

study the roles played by reexposure to the US in either the test or the extinction context. In Experiment 2a, rats were conditioned and extinguished in one context (A), reexposed to the US either there or in a second context (B), and, finally, tested either in the extinction or in the second context. The four groups were designated AA, AB, BB, and BA, where the first letter refers to whether US reexposure was in the extinction (A) or the second (B) context and the second letter is whether rats were tested in the A or B context. In Experiment 2b, rats were conditioned in one context (A), extinguished in a second context (B), reexposed to the US either in B or in a third context (C), and finally, tested in either B (Groups BB and CB) or C (Groups CC and BC). The four groups (BB, BC, CC, and CB) were again designated such that the first letter refers to whether US reexposure was in the extinction (B) or the third (C) context, whereas the second letter refers to whether the test was in B or C. The designs used in these experiments are shown in Table 1.

On the basis of previous findings (e.g., Bouton & Bolles, 1979b), we hypothesized that rats moved out of the extinction context for US reexposure would exhibit reinstatement when tested in that context (i.e., Group BB in Experiment 2a and Group CC in Experiment 2b) but not when they are returned to the extinction context for test (Group BA in Experiment 2a and Group CB in Experiment 2b). Further, on the basis of the findings observed in Experiment 1, we thought reexposure to the US in the extinction context would produce reinstatement when rats were tested there (Group AA in Experiment 2a and Group BB in Experiment 2b). However, the additional question of interest was whether rats reexposed to the US in the extinction context would also exhibit reinstatement when moved out of that context for test (Group AB in Experiment 2a and Group BC in Experiment 2b). Such an outcome would be expected if (a) reexposure to the US in the extinction context mediated conditioning of the CS and (b) mediated conditioning (like direct conditioning) was expressed in performance independently of the context in which it had occurred.

Method

Subjects and apparatus. Thirty-two experimentally naive rats (300–350 g) of the same stock and sex and from the same source were used in each experiment. They were kept under the conditions described previously for Experiment 1. Two contexts were used in Experiment 2a. One consisted of four chambers, each of which measured 30-cm length $\times$ 30-cm width $\times$ 27-cm height. Their sidewalls and ceiling were made of aluminum, and their back and front walls were made of clear plastic. The sidewalls and ceiling were painted white, and the outside back wall was covered with white cardboard. The floor consisted of stainless steel rods, 2 mm in diameter, spaced 10 mm apart (center to center). The four chambers were placed in separate compartments of a wooden cabinet. The second context used in Experiment 2a consisted of four chambers that were identical to those just described except that the sidewalls and ceiling were painted black, and the outside back wall was covered with black cardboard. Each of these black chambers was located adjacent to one of the white chambers such that two chambers (one from each set) were located in one of the compartments of the wooden cabinet. The bedding below each of the chambers in one set was sprayed with 1 ml of diluted eucalyptus oil (0.25%), whereas the bedding below each chamber of the other was sprayed with 1 ml of diluted banana essence (1%) to provide distinctive odors. The chambers were located in a room illuminated by a white fluorescent tube located on the ceiling. The third context used in Experiment 2b was that described in Experiment 1. Unscrambled AC 50-Hz

shock could be delivered to each floor in each of the three contexts by the constant-current shock generator described previously for Experiment 1. The stimulus used as the CS was the clicker described previously for Experiment 1. It was provided by identical generators wired to identical speakers located on the ceiling of each room. The background noise level was 65 dB in each room. The behavior of each rat was recorded using a camera mounted on the wall facing the open compartments in each of the rooms. Each camera was connected to a video recorder and monitor located in another room in the laboratory. This room also contained the equipment that controlled CS and shock presentations.

Procedure. The rats were assigned to four weight-matched groups ($n = 8$) in each experiment. In Experiment 2a, on each of Days 1 and 2, rats were exposed to a CS–shock pairing in either the black or white chambers (counterbalanced in each of the groups) in the manner described in Experiment 1. Then, on each of Days 3–8, all rats were exposed to one context in the morning (between 7 a.m. and 10 a.m.) and to the other in the afternoon (between 4 p.m. and 7 p.m.). Each exposure was 10 min, and the order in which rats were exposed to each context was irregular. Each exposure to the context in which the rats had received the CS–shock pairings involved four CS-alone presentations in the manner described previously for Experiment 1, whereas no stimuli were presented in the other context. On Day 9, all rats received a single shock (0.5 mA, 0.5-s duration) 5 min after placement in a context. For rats in two of the groups, shock was delivered in the context in which conditioning and extinction had occurred (A), whereas for those in the remaining groups, shock was presented in the other context (B). On Day 10, rats were tested in the manner described previously for Experiment 1. Half of the rats that had been reexposed to shock in the extinction context were tested there (Group AA), whereas the other half were tested in the second context (Group AB). Likewise, half of the rats that had been reexposed to shock in the nonextinguished second context were tested there (Group BB), whereas the other half were tested back in the extinction context (Group BA).

In Experiment 2b, on each of Days 1 and 2, rats received a CS–shock pairing in the context (A) used in Experiment 1 and according to the procedure described for that experiment. Then, on each of Days 3–8, all rats received alternating exposures to two further contexts (the black and white chambers used in Experiment 2a). The CS was presented without shock (extinction) in one of these contexts (B) according to the schedule described in Experiment 1. No stimuli were presented in the other context (C). The particular set of chambers constituting the B and C contexts was counterbalanced within each of the groups. The daily 10-min exposures to each of these contexts occurred between 7 a.m. and 10 a.m. and 4 p.m. and 7 p.m. During either the morning session or the afternoon session (counterbalanced) of Days 9 and 10, rats in Groups BB and BC were shocked in Context B (the extinction context) but were not shocked in Context C, whereas rats in Groups CC and CB were shocked in Context C but not shocked in Context B. Shock (0.5 mA, 0.5-s duration) occurred 5 min after placement in a context, and the rats remained there for a further 5 min. The duration of exposure to the nonshocked context on each of these days was 10 min. On Day 11, rats in Groups BB and CB were tested in B, and those in Groups BC and CC were tested in C. The test was conducted in the manner described in Experiment 1.

Results

In Experiment 2a, there was substantial freezing by rats in all four groups in the second conditioning trial ($M = 70\%$). Freezing was confined to the CS as the levels of freezing across the 30-s period prior to its presentation were low ($M = 12\%$). Freezing declined across the extinction sessions (Days 3–8) from a mean level of 85% on Day 3 to $<10\%$ (Days 7–8). There were no significant differences between the levels of freezing across these days neither in terms of the particular sets of chambers used as the

conditioning–extinction context nor among the four groups, $F_s < 1.0$.

There were low levels of freezing ($M = 10\%$) across the 30-s period prior to the initial CS presentation on test, and none of the differences between the groups were significant, $F_s(1, 28) < 2.6$, $F_{\text{critical}} = 4.3$. The mean levels of freezing averaged across the four CS presentations during test are shown in the left panel of Figure 2. The statistical analysis revealed significant main effects for whether rats were exposed to shock in the conditioning–extinction context (A) or the other context (B), $F(1, 28) = 4.9$, $F_{\text{critical}} = 4.3$, and whether the test occurred in A versus B, $F(1, 28) = 6.3$. There was a significant interaction between these factors, $F(1, 28) = 5.9$. From inspection of the figure, this interaction confirms that the differences in freezing between rats in Groups AA and AB were less than those between rats in Groups BB and BA. Post hoc comparisons (Scheffé, 1959) confirmed that rats in Group BB showed significantly more freezing than did those in Group BA, $F(3, 28) = 11.8$, $F_{\text{critical}} = 9.2$, and that rats in Groups AA and AB did not differ from each other, $F < 1.0$.

In Experiment 2b, there was substantial freezing on the second conditioning trial ($M = 51\%$). Freezing was confined to the CS because the levels of freezing across the immediately preceding 30-s period were low ($M = 2\%$). Freezing declined across extinction sessions from a mean of 88% (Day 3) to $<10\%$ (Day 8). There were no significant differences among the groups across Days 3–8, $F_s < 1.0$. The levels of freezing across the 30-s period prior to the initial presentation of the CS on test were low ($M = 10\%$), and there were no differences among the groups, $F_s < 1.0$. The mean levels of freezing averaged across the four CS presentations during test are shown in the right panel of Figure 2. The statistical analysis of these data revealed significant main effects for whether rats were reexposed to shock in the extinction context (B) or in the third context (C), $F(1, 28) = 5.5$, $F_{\text{critical}} = 4.3$, and whether they were tested in B versus C, $F(1, 28) = 9.7$. There was a significant interaction between these factors, $F(1, 28) = 6.6$, which from inspection shows that the differences between rats in Groups BB

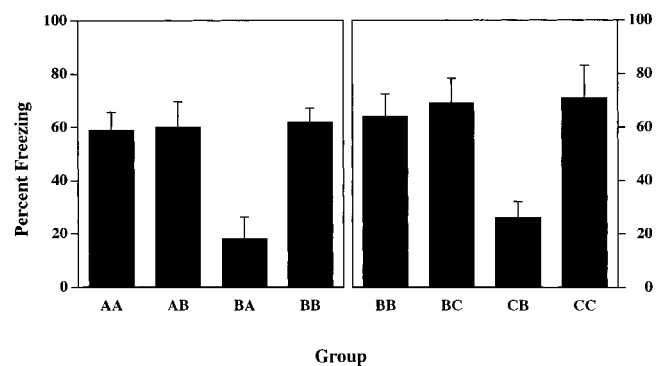


Figure 2. Mean percentage of freezing to the conditioned stimulus (CS) at test in Experiments 2a (left panel) and 2b (right panel). In Experiment 2a, rats were conditioned and extinguished to a CS in Context A, reexposed to the US either in A or in a second context, B, and tested in A (Groups AA and BA) or in B (Groups BB and AB). In Experiment 2b, rats were conditioned in Context A, extinguished to a CS in a second context, B, reexposed to the US in either B or a third context, C, and tested either in B (Groups BB and CB) or in C (Groups CC and BC).

and BC were less than those between Groups CC and CB. Post hoc comparisons (Scheffé, 1959) confirmed that rats in Group CC froze more than did those in Group CB, $F(3, 28) = 16.1$, $F_{\text{critical}} = 9.2$, and that rats in Groups BB and BC did not differ, $F < 1.0$.

Discussion

These experiments confirmed that reexposure to shock in the conditioning–extinction context (Group AA in Experiment 2a) or just in the extinction context (Group BB in Experiment 2b) reinstates freezing when rats were tested with the extinguished CS in that context. They have also replicated previous findings reported by Bouton and colleagues (Bouton & Bolles, 1979b; Bouton & King, 1983; Bouton & Peck, 1989) regarding the conditions for reinstatement. Specifically, exposure to shock outside the extinction context provoked reinstatement when rats were tested with the extinguished CS in that context (Group BB in Experiment 2a and Group CC in Experiment 2b). This pattern of results is part of the evidence used by Bouton (1993) to argue that US presentations reinstate responding to an extinguished CS by conditioning the context in which the test is performed. According to this argument, reinstatement occurred among rats tested in the context in which the US was reexposed because the conditioned context returned the animals to the background under which the CS–US association was originally formed. This background is not the physical context in which this association was formed (e.g., in Experiment 2b, the CS–US pairings were in Context A and the CS was tested in Context B or C), but it may be the emotional state or the reactions generated by the conditioning of that context. In any case, this argument implies that reinstatement will not be observed when the test is performed in a nonconditioned context. Consistent with this implication and with previous findings by Bouton and colleagues, rats that were moved out of the extinction context, shocked in a different context, and then returned to the extinction context for test exhibited low levels of freezing (Group BA in Experiment 2a and Group CB in Experiment 2b).

However, the present experiments also found that rats shocked in the conditioning–extinction context (Group AB in Experiment 2a) or in a context just associated with extinction (Group BC in Experiment 2b) and moved out of that context for testing showed levels of freezing to the extinguished CS just as substantial as those by rats tested in a conditioned context. This finding suggests another role for context in addition to that identified by Bouton et al. (1993). In particular, it is consistent with the proposal concerning mediated conditioning. This holds that reexposure to the US in the extinction context mediated conditioning of the CS that was expressed in freezing when the rats were moved out of that context for testing.

Experiment 3

Rather than reflecting mediated conditioning, the substantial levels of freezing exhibited by rats shocked in the extinction context and tested in another context could have been due to renewal. That is, the shift from the extinction context per se was the critical factor in the restoration of freezing when these rats were tested with the extinguished CS. Experiment 3 studied the consequence for reinstatement when rats were shocked either in an extinction context or a second context and then tested with the

extinguished CS in a third context. The design involved exposing rats to a CS–US pairing in one context (A) and then extinguishing the CS in that context. Across the days when the CS was extinguished, rats were additionally exposed to a second context (B). Then rats were either shocked in A or B and tested for freezing to the extinguished CS in a third context, C. To determine the impact of shock per se on the levels of freezing when the extinguished CS was tested in C, we included an additional group of rats that were treated identically to the groups described previously (i.e., they received CS–shock pairings in A followed by extinction in A and exposures to B) but did not receive a reinstating shock (i.e., they were simply exposed to A or B but in the absence of shock) prior to the test in C. The design used in this experiment is shown in Table 1.

Method

Subjects and apparatus. Twenty-four experimentally naive rats (300–400 g) of the same stock and sex and from the same source were used. They were kept under the same conditions described previously for Experiment 1. The contexts used for conditioning–extinction and US presentation were the black and white chambers (designated as A and B) described in Experiments 2a and 2b. The test context (C) was that described in Experiment 1. The equipment was that described previously for Experiment 1.

Procedure. The rats were weighed and assigned to three weight-matched groups ($n = 8$). On each of Days 1 and 2, the rats were exposed to a CS–shock pairing in either the black or the white chambers in the manner described in Experiment 1. Then, on each of Days 3–10, rats received four CS-alone presentations in that chamber while receiving exposures to the other context. The CS was presented in the manner described in Experiment 1. The chambers were counterbalanced in each group, with that used for conditioning–extinction designated A and the other B. The daily 10-min exposures to each of these contexts alternated in an irregular manner across morning (7 a.m. to 10 a.m.) and afternoon (4 p.m. to 7 p.m.). On the morning session of Day 11, rats in two of the groups were shocked 5 min after placement in one of the contexts and were kept there for a further 5 min. The shock (0.5 mA, 0.5-s duration) occurred in A for rats in Group AC and in B for those in Group BC. Half of the rats in Group –C received a 10-min exposure to the A context, whereas the remainder were exposed to the B context but shock was not presented in either context. On the afternoon session of Day 11, all rats received a 10-min exposure to Context C. This was done to familiarize the rats with the test context and to minimize generalization from the shocked context. On Day 12, all rats were tested in C in the manner described previously for Experiment 2a.

Results

There was substantial freezing by rats on the second conditioning trial ($M = 65\%$). This was confined to the CS because the levels of freezing across the 30-s period prior to its presentation were low ($M = 1\%$). Freezing declined across the extinction sessions from a mean of 85% (Day 3) to $<10\%$ (Day 10), and there were no significant differences between the levels of freezing among the groups across these days, $F_s < 1.0$. The levels of freezing across the 30-s period prior to the initial CS presentation on the test in C were low ($M = 4\%$). The mean levels of freezing averaged across the four CS presentations during test are shown in Figure 3. An overall analysis of variance confirmed that there were significant differences among the groups, $F(2, 21) = 36.8$, $F_{\text{critical}} = 3.07$. Post hoc tests (Scheffé, 1959) confirmed that rats in Group AC exhibited significantly more freezing than did rats in either

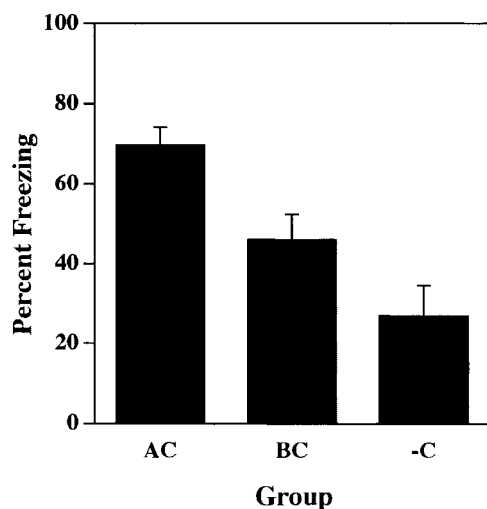


Figure 3. Mean percentage of freezing to a conditioned stimulus (CS) at test in Experiment 3. Rats were conditioned and extinguished to a CS in Context A, reexposed to the US in either A (Group AC) or a second context, B (Group BC), or not reexposed to the US (Group -C), and tested in a common context, C.

Group BC, $F(2, 21) = 7.3$, $F_{\text{critical}} = 6.14$, or Group -C, $F(2, 21) = 24.5$. Rats in Group BC also froze more than did rats in Group -C, but these differences did not reach conventional (and conservative) levels of significance, $F(2, 21) = 5.0$.

Discussion

Experiment 3 has shown that reexposure to shock in an extinction context provoked substantial levels of freezing when rats were moved out of that context and tested with the extinguished CS (Group AC). These levels of freezing were greater than those exhibited by rats simply moved out of the extinction context for testing (Group -C). Thus, the effects of reexposure to shock in the extinction context (e.g., Experiments 2a and 2b) were not simply due to renewal. Further, reexposure to shock in the extinction context reinstated freezing to the extinguished CS more than did reexposure to shock in a nonextinguished context. Therefore, the reinstatement of responding observed here was a relatively specific consequence of reexposure to shock in the extinction context. This outcome is just that expected on the basis of mediated conditioning.

Experiment 4

According to an analysis in terms of mediated conditioning, the reinstatement exhibited by rats in Group AC was due to (a) the context-CS association formed across extinction, (b) the context-shock association formed at reexposure, and (c) the test presentation of that particular CS. However, the design used in Experiment 3 did not assess whether the reinstatement exhibited by these rats was specific to the CS whose context associate was shocked. That is, it leaves open the possibility that reexposure to shock in an extinction context reinstates responding to any extinguished CS, not just the particular CS extinguished in that context. Experiment 4 examined these alternatives. The design was similar to one

used previously in this laboratory to study context-specificity of extinction (J. A. Harris, Jones, Bailey, & Westbrook, 2000, Experiment 1). Rats were trained with pairings of CS1 with shock and CS2 with shock in Context A. CS1 was then extinguished in Context B and CS2 was extinguished in Context C (counterbalanced). Finally, rats were shocked in one of these contexts (e.g., B) but not in the other (C) before being tested for freezing to each of the extinguished CSs in a fourth, neutral context (D). All rats were thus reexposed to shock in an extinction context. Therefore, the question of interest is whether rats reexposed to shock in one of the extinction contexts (e.g., B) subsequently exhibit more freezing to the CS associate of that context (CS1) than to the CS associate (CS2) of the other (nonshocked) context (C) when each CS is tested in a common context (D). The designs used in this and the remaining experiments are shown in Tables 2 and 3.

Method

Subjects and apparatus. Twenty-four experimentally naive rats (280–340 g) of the same stock and sex and from the same source were used. They were kept under the same conditions described previously for Experiment 1. The context used for conditioning (A) was that described in Experiment 1, whereas the black and white chambers described in Experiments 2a and 2b were those used for extinction (B and C). The context used for test (D) consisted of four chambers located in the third room in the laboratory. Each of these chambers measured 33-cm height $\times$ 31-cm length $\times$ 26-cm width. The sidewalls and ceiling were made of aluminum, and the back and front walls were made of clear plastic. The floor consisted of stainless steel rods, 5 mm in diameter, spaced 10 mm apart, center to center, with a tray containing bedding material below. The chambers were located in separate compartments of a wooden cabinet. The door of each compartment was kept open to permit observation of the rat. Concentrated rose oil (Cara-Mia, Sydney, Australia) was used to provide a distinctive odor. The oil (1 ml) was sprayed over the bedding material before each session. A red fluorescent light located in the ceiling illuminated the room, and the background noise level was 65 dB. One of the CSs was the clicker used previously [for Experiment 1], whereas the other CS was a 75 dB white noise (A: Brüel & Kjaer, Type 2235). The equipment for delivering each of the CSs and the shock US and for recording each rat's behavior was identical to that described previously for Experiment 1.

Procedure. The rats were weighed and assigned to two weight-matched groups ($n = 12$). On Day 1, rats were exposed to Context A for 10 min during which they received separate presentations of the clicker and of the noise. Each CS lasted for 30 s and terminated in a 0.8-mA $\times$ 0.5-s shock. The first CS (clicker for half the rats in each group and noise for the remainder) was presented 3 min into the session, whereas the second CS was presented 6 min into the session. On each of Days 2–7, all rats received 10-min exposures to the B and C contexts (counterbalanced across the black and white chambers). Half of the rats received the clicker in B and the noise in C, whereas the remainder received the clicker in C and the noise in B. On each of these exposures, the relevant CS was presented on four occasions in the manner described previously for Experiment 1. The presentation of the clicker and the white noise during extinction was counterbalanced between the morning and afternoon sessions. On the morning of Day 8, all rats were shocked. Half of the rats were shocked in the context (B or C) in which the clicker had been extinguished (Group Clicker: Cxt+/Noise: Cxt-), whereas the remainder were shocked in the context (B or C) in which the noise had been extinguished (Group Noise: Cxt+/Clicker: Cxt-). (Cxt+ refers to context with shock, and Cxt- refers to context without shock.) Shock (0.5 mA, 0.5-s duration) was delivered 5 min into the 10-min exposure to the relevant context. On the afternoon of Day 8, all rats received a 10-min nonshocked exposure to the other context (that is, if the morning session had entailed a shocked exposure to the

Table 2
Summary of Designs for Experiments 4 and 5

Experiment 4	Conditioning A: CS1+ and CS2+	Extinction B: CS1– C: CS2–	Reinstatement B: + C: –	Test D: CS1 and CS2	
Experiment 5	Conditioning A: CS1+ and CS2+	Extinction B: CS1– C: CS2–	Reinstatement B: + C: +	Reexposure B: –	Test D: CS1 or CS2

Note. A, B, C, and D refer to four distinct contexts. For conditioned stimuli (CS), a clicker (CS1) and white noise (CS2) were used, counterbalanced. + = presentation of the shock unconditioned stimulus; – = absence of shock.

clicker-associated context, the afternoon exposure was to the context in which the noise had been extinguished and vice versa). On Day 9, rats were tested in Context D both in the morning and the afternoon. The duration of each test exposure to D was 10 min, and each test consisted of four presentations of one of the CSs. Half of the rats in each group were first tested with the clicker and then with the noise, whereas the remainder received the reverse order. Each test was identical in terms of duration of CS and interval between CS presentations to that described in Experiment 1.

Results

The levels of freezing by rats to each of the CSs declined across extinction sessions (Days 2–7) from means of 95% to the noise and 90% to the clicker (Day 2) to means of <10% to the noise and to the clicker (Day 7). There were no significant differences between the levels of freezing to the noise versus the clicker nor between the two groups across Days 2–7, $F_s < 1.0$. There were low levels of freezing ($M = 5\%$) in the 30-s period prior to the first CS presentation in the initial test in Context D and some freezing ($M = 15\%$) in the 30-s period prior to the first CS presentation in the second test. However, there were no significant between-groups differences in the pre-CS levels of freezing, $F < 1.0$. The mean levels of freezing to the clicker and noise by rats shocked in the clicker-associated context (Group Clicker: Cxt+/Noise: Cxt–) and by those shocked in the noise-associated context (Group Noise: Cxt+/Clicker: Cxt–) are shown in Figure 4. There appeared to be more freezing by rats shocked in the noise-associated context than by those shocked in the clicker-associated context, but rats in both groups froze more to the CS whose context had been shocked than to the CS whose context had not been shocked. The statistical analysis confirmed that overall rats shocked in the noise-associated context froze more than did rats shocked in the clicker-associated context, $F(1, 22) = 6.2$, $F_{critical} = 4.2$. There were no

significant differences between freezing overall to the noise versus to the clicker, $F < 1.0$. Importantly, there was a significant interaction between these factors, $F(1, 22) = 28.5$, such that rats froze more to the CS (clicker or noise) whose context had been shocked than they did to the CS (noise or clicker) whose context had not been shocked.

Discussion

Experiment 4 has provided evidence that reexposure to a US reinstates extinguished responding in a CS-specific manner. Rats shocked in the context in which a particular CS was extinguished subsequently froze more when tested with that CS than they did to another CS whose extinction-associated context had not been shocked. Further, each rat was shocked in a context in which extinction had occurred. Therefore, the difference between the test performances to each CS cannot be due to reexposure to shock in an extinction context (such as may have been the case in Experi-

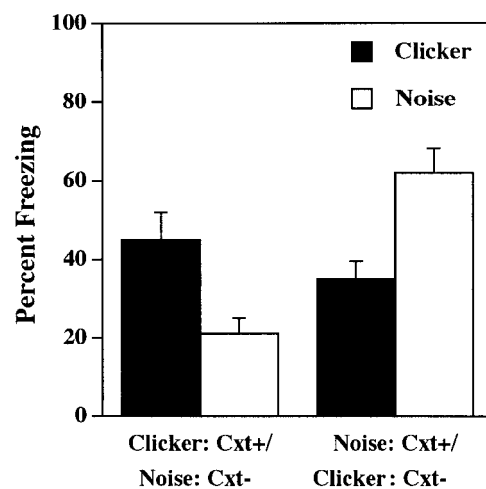


Figure 4. Mean percentage of freezing to a noise and clicker at test in Experiment 4. Rats in Group Clicker: Cxt+/Noise: Cxt– were reexposed to the unconditioned stimulus (US) in the context in which the clicker had been extinguished, and those in Group Noise: Cxt+/Clicker: Cxt– were reexposed to the US in the context in which the noise had been extinguished. All rats were tested in a common context with the clicker and noise on separate tests. Cxt+ = context with shock; Cxt– = context without shock.

Table 3
Summary of Design for Experiment 6

Preexposure	Shock	Test
A: CS1– B: CS2–	A: + B: –	C: CS1 and CS2

Note. A, B, and C refer to three distinct contexts. For conditioned stimuli (CS), a clicker (CS1) and white noise (CS2) were used, counterbalanced. + = presentation of the shock unconditioned stimulus; – = absence of shock.

ment 3 in which reexposure to the US occurred in either an extinction or a nonextinguished context).

Experiment 5

The results of Experiment 4 are consistent with the proposal that the reinstatement observed when rats were tested with the CS associate of the shocked context was due to mediated conditioning. The aim of Experiment 5 was to determine whether reinstated responding can then be reduced through mediated extinction. The design used in Experiment 4 involved shocking rats in a context in which a particular CS had been extinguished and not shocking them in a second context in which another CS had been extinguished. Experiment 5 used the same procedure as in Experiment 4 but shocked rats in both of the extinction contexts. Then rats were exposed to one of these contexts but in the absence of shock. Thus, rats were exposed to pairings of CS1–shock and CS2–shock in Context A. Each rat then received nonreinforced exposures to CS1 in B and to CS2 in C (counterbalanced). Subsequently, rats were shocked in both the B and the C contexts and then repeatedly exposed to one of these contexts without shock before being tested in Context D for freezing to either CS1 or CS2. The design used in this experiment is shown in Table 2. Given that shock in both of the extinction contexts reinstates freezing to both CSs, the question of interest is whether subsequent exposures to one of these contexts in the absence of shock reduces the levels of freezing to its CS associate.

Method

Subjects and apparatus. Thirty-two experimentally naive rats (310–350 g) of the same stock and sex and from the same source were used. They were kept under the same conditions described previously for Experiment 1. The various contexts, the two CSs, and the US were those described in Experiment 4.

Procedure. The rats were weighed and assigned to four weight-matched groups ($n = 8$). On Day 1, rats were exposed to Context A for 10 min during which they received a clicker–shock and a noise–shock pairing in the manner described in Experiment 4. Then, on each of Days 2–7, all rats received twice daily (morning and afternoon) 10-min exposures to the B and C contexts counterbalanced with respect to whether the clicker was extinguished in B and the noise in C or vice versa. The presentation of the clicker and the white noise across these days was counterbalanced between morning and afternoon sessions. On the morning of Day 8, half of the rats were shocked in the context in which the clicker had been extinguished, whereas the remainder were shocked in the context in which the noise had been extinguished. Then on the afternoon of Day 8, rats shocked in the clicker-associated context were now shocked in the noise-associated context, whereas the rats shocked in the noise-associated context were now shocked in the clicker-associated context. On each of these sessions, shock (0.5 mA, 0.5-s duration) was delivered 5 min into the 10-min exposure to the relevant context. On Days 9–10, rats received twice daily 10-min exposures to one of these contexts, half of the rats being exposed to the clicker-associated context and the remainder to the noise-associated context. On the morning of Day 11, all rats received a 10-min familiarizing exposure to Context D, and on the afternoon of that day, all rats received a single test in D. Half of the rats that had received postshock nonreinforced exposures to the clicker-associated context (Group Clicker: Cxt+ –/Noise: Cxt+) were tested with the clicker, and the remainder were tested with noise, whereas half of the rats given postshock nonreinforced exposures to the noise-associated context (Group Noise: Cxt+ –/Clicker: Cxt+) were tested with the noise, and the remainder were tested with the

clicker. The duration of test exposure to D was 10 min, and the test consisted of four presentations of one of the CSs in the manner described in Experiment 1. A between-subjects test was used here to ensure the robustness of the effects obtained with the within-subject test in Experiment 4.

Results

There was very little freezing in the 30-s periods ($M = 5\%$) prior to the initial presentations of the noise or clicker in Contexts B and C but considerable freezing to each of these CSs (noise $M = 90\%$; clicker $M = 88\%$) across their initial extinction sessions on Day 2. Freezing declined across extinction sessions and was $<10\%$ to each CS on Day 7. There were no significant differences between the levels of freezing elicited by the noise or clicker in either the black or white chambers across extinction, $F < 1.0$. There was no freezing in the 30-s period prior to the initial CS presentation on the test in Context D. The mean levels of freezing averaged across the four CS presentations by rats in each of the groups are shown in Figure 5. The statistical analysis confirmed that there were no significant differences between the levels of freezing to the noise versus the clicker, $F(1, 28) = 2.5$, $F_{\text{critical}} = 4.2$, nor between the levels of freezing of rats for which the noise context was shocked and extinguished versus rats for which the clicker context was shocked and then extinguished, $F < 1.0$. However, there was a significant interaction between these factors, $F(1, 28) = 12.5$, confirming that the rats froze less to the CS whose associated context had been shocked and then extinguished than to the CS whose associated context had been shocked but not extinguished.

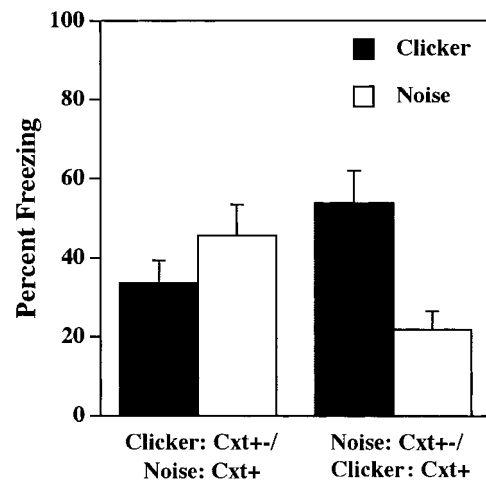


Figure 5. Mean percentage of freezing to a noise and clicker at test in Experiment 5. Rats in both groups were reexposed to the unconditioned stimulus in the context in which a clicker conditioned stimulus (CS) had been extinguished and in the context in which a noise CS had been extinguished. Then rats in Group Clicker: Cxt+ –/Noise: Cxt+ received nonreinforced exposures to the clicker-associated context, whereas those in Group Noise: Cxt+ –/Clicker: Cxt+ received nonreinforced exposures to the noise-associated context. Rats from each group were tested in a common context once with either the clicker or the noise CS. Cxt+ = context with shock; Cxt+ – = context with shock and then without shock.

Discussion

Experiment 5 has provided evidence that the CS specificity of reinstatement by US reexposure is modified by the subsequent treatment afforded the context in which the CS had been extinguished and the US reexposed. Rats shocked in each of the contexts in which a particular CS had been extinguished exhibited reinstatement to each CS when tested in the common D context. However, the level of this reinstatement was reduced by postshock exposures to the context in which the CS had been extinguished. Thus, the degree to which an extinguished CS re-elicits freezing appears to be controlled by the current value of its extinction-associated context: If this context has been conditioned, freezing is reinstated in a CS-specific manner when tested in a neutral context; if the extinction-associated context has been conditioned and then extinguished, freezing to the CS is reduced when tested in a neutral context.

Experiment 6

The reinstatement of responding to an extinguished CS whose context associate was shocked could be due to that context serving to link together two separate associations. The first is the context–CS association formed across extinction and the second is the context–US association formed across US reexposure. This linking could take place at the time of US reexposure whereby the association formed across extinction results in the context activating the CS representation concomitantly with receipt of the US (e.g., Holland, 1990). Alternatively, these separate associations could be linked together at test when presentation of the extinguished CS activates the representation of its context associate that had been subjected to US reexposure (e.g., Hall, 1996). In either case, evidence for such an association should be observed among rats exposed to a stimulus in a particular context, then shocked in that context and tested with that stimulus elsewhere.

The intention of Experiment 6 was to provide a direct assessment of the role played by context in bridging context–stimulus and context–US associations. The design consisted in exposing rats to two contexts, A and B, in each of which a stimulus was presented (clicker or noise). Rats were then shocked in one of these contexts (A) but not the other (B). On test, rats were placed in a third context (C) and tested for performance to the clicker and noise. The design used in Experiment 6 is shown in Table 3. The question of interest is whether the test in the third context, C, reveals more freezing to the CS whose context associate had been shocked than to the CS whose context associate had not been shocked.

Method

Subjects and apparatus. Sixteen experimentally naive rats (300–350 g) of the same stock and sex and from the same source were used. The contexts used for stimulus preexposure and shock presentations were the black and white chambers described in Experiments 2a and 2b, whereas the test context was located in another room in the laboratory and was that used for testing in Experiment 4. The equipment for delivering the CSs and US and for recording each rat's behavior was that described previously for Experiment 1.

Procedure. The rats were weighed and assigned to two weight-matched groups ($n = 8$). The parameters selected for preexposure were

based on previous studies that had provided evidence for context–stimulus associations in a latent inhibition procedure (Westbrook, Jones, Bailey, & Harris, 2000, Experiment 2). On each of 6 days, rats were exposed for 20 min to one context in the morning and for 20 min to the second context in the afternoon. Rats received eight 30-s presentations to one CS in Context A and eight 30-s exposures to the other CS in Context B. For rats in one group (Clicker: Cxt+/Noise: Cxt–), the clicker was presented in A and the noise in B, whereas for rats in the other group (Noise: Cxt+/Clicker: Cxt–), these presentations were reversed such that the noise was presented in A and the clicker was presented in B. The interval between CS exposures in each context was 2 min. The groups were counterbalanced for the physical context in which the rats received each stimulus and the time of day (morning or afternoon) at which rats were exposed to each context was alternated across days. On the morning of Day 7, rats were placed in Context A and shocked (0.8-mA, 0.8-s duration) 5 min later, then were kept in that context for a further 5 min. On the afternoon of Day 7, rats were exposed to Context C for 10 min. This was done to familiarize them with the test context and minimize generalization from the shocked context. On Day 8, rats were exposed to Context C for 10 min in the morning and 10 min in the afternoon. Rats were tested for performance to each CS as described in Experiment 1. The type of CS presentation, clicker or noise, was counterbalanced across these morning (Test 1) and afternoon (Test 2) sessions.

Results

The levels of freezing across the 30-s period prior to initial presentation of the CS on each of the test occasions were low (Test 1 $M = 11\%$; Test 2 $M = 24\%$). The mean levels of freezing averaged across the four CS presentations during test are shown in Figure 6. The statistical analysis confirmed what is clear from inspection of this figure. There was no overall difference among rats shocked in the noise-associated context versus those shocked in the clicker-associated context, $F(1, 14) < 1.0$, $F_{critical} = 4.6$, nor an overall difference between freezing to the noise versus the clicker, $F < 1.0$. However, there was a significant interaction

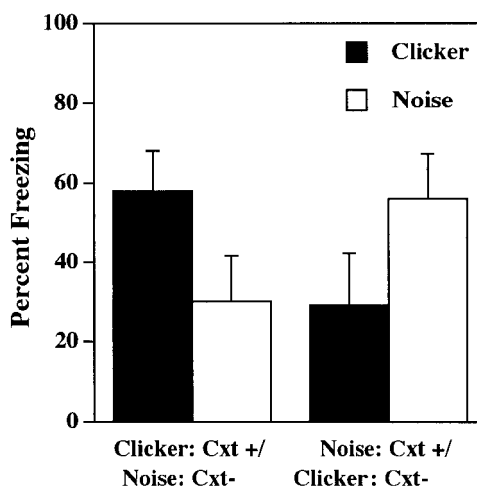


Figure 6. Mean percentage of freezing to a noise or clicker at test in Experiment 6. Rats in both groups were exposed to a noise in one context and to a clicker in another, then exposed to the unconditioned stimulus in either the clicker-associated (Group Clicker: Cxt+/Noise: Cxt–) or the noise-associated (Group Noise: Cxt+/Clicker: Cxt–) context. All rats were tested in a third context with clicker and noise on separate tests. Cxt+ = context with shock; Cxt– = context without shock.

between these factors such that rats froze more to the stimulus (clicker or noise) whose context associate had been shocked than to the stimulus (noise or clicker) whose context associate had not been shocked, $F(1, 14) = 11.3$. Thus, rats shocked in a context subsequently exhibited more freezing to the stimulus associate of that context than to a stimulus whose context associate had not been shocked.

Discussion

Experiment 6 has provided evidence that the associations formed between a context and a CS and then between a context and shock imbue that CS with the capacity to elicit fear reactions (freezing) when presented in a neutral context. The procedures used to establish these associations are those embedded within the paradigm that reinstates freezing to an extinguished CS. Accordingly, the reinstatement of extinguished responding that results from US reexposure in the extinction context could be due to the role played by that context in reassociating the CS with the US.

General Discussion

This series of experiments confirms that fear reactions (freezing) to an extinguished CS are reinstated by reexposure to a shock US in the absence of further CS-US pairings. In Experiment 1, rats exposed to CS-US pairings and reexposed to the US after extinction (Group PR) exhibited substantial levels of freezing when tested with the extinguished CS. These levels of freezing were greater than those shown by rats exposed to the CS-US pairings but not reexposed to the US (Group PN) or by rats not exposed to CS-US pairings but reexposed to the US (Group UR). Therefore, freezing to the extinguished CS was contingent on the initial CS-US pairings and postextinction presentations of the US. These findings show that some or all of the original CS-US association survived extinction. This conclusion implies that some process other than loss of the CS-US association produced the reductions in freezing across extinction. It also implies that the removal of this process unmasked the original CS-US association, thereby reinstating freezing to the extinguished CS. What mask is imposed on the expression of the CS-US association and how is it removed by reexposure to the US?

Rescorla (1979) argued that the mask imposed by extinction on the expression of the CS-US association consisted in the development of an inhibitory context-US association. The development of this association maintained the CS-US association (Rescorla & Wagner, 1972) by increasing the threshold of US activation (Konorski, 1948). Reexposure to the US reset this threshold by counterconditioning the inhibitory context, thus enabling expression of the CS-US association. A critical prediction of this argument is that reinstatement should be relatively specific to the case in which extinction and US reexposure occur in the same context. However, Experiments 2a and 2b confirmed previous reports (e.g., Bouton et al., 1993) that reinstatement is observed when extinction is in one context but US reexposure and test are in another. Further, the present experiments have demonstrated that US reexposure acts selectively, reinstating freezing to the CS extinguished in that context but not to a CS extinguished in some other context. For instance, in Experiment 4, rats extinguished to CS1 in Context B and to CS2 in Context C and then shocked in B froze more to

CS1 than to CS2 when tested in a neutral Context D. According to the argument developed by Rescorla (1979), reexposure to shock in B should have antagonized the inhibitory context-US association. This would have freed the expression of the CS1-US association in that context but would not have imbued CS1 with the capacity to elicit more freezing than did CS2 when tested in the neutral context. These findings suggest that rats additionally learn about the relation between the context and the CS across extinction, and that this learning plays some role in reinstatement.

Bouton (e.g., 1993) argued that the information acquired about a CS across conditioning and extinction is represented in separate memories with contrasting content (a CS-US and a CS-no-US memory) and different conditions of activation (a context-independent CS-US memory and a context-specific CS-no-US memory). Performance to an extinguished CS thus depends on which of its contrasting associates (US vs. no-US) is activated. Context conditioning by US reexposure favors activation of the CS-US memory by restoring the background under which the CS-US memory rather than the CS-no-US memory was established. Thus, rats froze when tested with an extinguished CS in the context in which they had been reexposed to the US because that context elicited fear (Experiments 1, 2a, and 2b). This memory-based approach assumes that postextinction responding to a CS is determined by the similarity between the test and extinction contexts: the less similar, the more responding will be renewed to the extinguished CS. This assumption can be used to explain the findings observed in Experiment 3. When reexposed to the US in the extinction context and moved out of that context for testing in a third context, rats in Group AC froze more than did those reexposed to shock in a second context, Group BC, or rats not reexposed to the US, Group -C. That is, renewal was greatest among rats reexposed to the US in the extinction context. Because the contexts used as A and B were counterbalanced, the differences between the test levels of freezing of rats in Groups AC and BC cannot be due to generalization of context conditioned fear. However, they could be explained in terms of the extent to which the extinction or CS-No-US memory generalized from A to C. Reexposure to shock in A would have effectively antagonized the ability of that context to retrieve the CS-No-US memory. This would have reduced the extent that extinction could generalize to C, thus producing substantial freezing on test among rats in Group AC. Reexposure to shock in B would have conditioned fear that resulted in some generalization to A, thereby producing a partial reduction in the ability of A to retrieve the extinction memory. The partial reduction of the control by A over the extinction memory would have translated into a partial recovery of responding on the test in C among rats in Group BC compared with the low levels of freezing resulting from generalization of the extinction memory among nonshocked rats in Group -C.

Similar arguments can be made for the results observed in Experiment 4, in which rats were trained with CS1-shock and CS2-shock in A and then extinguished to CS1 in B and to CS2 in C. Reexposure to shock in B produced more freezing to CS1 than to CS2 when each was tested in a fourth context, D. Because the contexts used as B and C were counterbalanced, these differences on test cannot be due to differential generalization of excitation. But they can be explained by the argument that responding to each of the extinguished CSs in D was influenced by generalization from B, which cannot retrieve the CS1-no-US memory, and C,

which can retrieve the CS2–no-US memory. Effectively, freezing is greater to CS1 than to CS2 because there is less generalization of inhibitory control from the context associate of CS1 (B) than from the context associate of CS2 (C). Experiment 5 used a similar design to that just described for Experiment 4 but shocked rats in both of the extinction contexts (B and C) and then exposed them to one of these contexts (B) without shock. The final test in D revealed that rats froze less to CS1, whose context associate (B) had been subjected to postshock nonreinforced exposures, than to CS2, whose context associate had not received that postshock treatment. Here the description that has been offered in terms of variations in context-controlled generalization of the extinction memory appears to fail (unless it is further assumed that post-US exposures to B reinstated its control over the CS1–no-US memory), as each of the extinction contexts were shocked. Therefore, each context would have lost its ability to retrieve its specific CS–no-US memory, and responding should have been equivalent when each of the extinguished CSs was tested in D—but that did not occur.

An alternative explanation of the findings observed in Experiments 4 and 5 can be derived from proposals by Holland (1990) concerning so-called mediated conditioning. These proposals originated in demonstrations that performance to a US is influenced by manipulations involving the CS (e.g., Holland, 1981; Holland & Forbes, 1982; Ward-Robinson & Hall, 1996). For instance, rats learned that one outcome (O1: a particular food) was signaled by CS1, and a second outcome (O2: another food) was signaled by CS2. Then, CS1 was presented and rats were made sick by injection of lithium chloride (LiCl). A subsequent test performed elsewhere revealed that rats selected O2 rather than O1 whose signal (CS1) had been poisoned, indicating that an absent event can be imbued with associative value (mediated acquisition). A variant of this design involved training rats with CS1 as a signal for O1 and with CS2 as a signal for O2. Then aversions were separately established to O1 and O2. Subsequently, rats were exposed to one of the CSs (e.g., CS1) in the absence of any outcome and, finally, tested for their choice between O1 and O2. This test revealed that rats selected the outcome (O1) whose associate (CS1) had been presented without consequences, indicating that the existing associative value of an absent event can be reduced (mediated extinction).

Holland (1990) interpreted these findings to mean that the associative value of an absent event can be changed and proposed rules for this change that can be described in terms of a modified version of the sometimes opponent process model (SOP; Wagner, 1981; Wagner & Brandon, 1989). Specifically, Holland (1990) proposed that an excitatory association can be formed from an event representation in an A2 state of activity to the representation of an event in an A1 state of activity and that inhibitory associations can be formed between event representations simultaneously excited to an A2 state of activity (see Dwyer, Mackintosh, & Boakes, 1998). Thus, according to this modified version of SOP, the presentation of a signal (CS1) for an outcome (O1) excited the representation of O1 to an A2 state of activation when the LiCl-induced illness was excited to an A1 state of activation. The consequence of the conjoint activation of the O1 representation in A2 and that of illness in A1 was the formation of an excitatory association from O1 to illness, leading to subsequent rejection of that O1 on test. Further, the presentation of a signal (CS1) whose

outcome (O1) had been devalued by illness resulted in the conjoint excitation of the representations of both O1 and illness to an A2 state of activation. The consequence of these representations being conjointly excited to an A2 state of activity was that inhibitory associations were formed between them, leading to a reduction in the aversion to the outcome whose CS associate had been presented without any consequences, that is, to the selection on test of O1 rather than to the still devalued O2.

The designs used in Experiments 4 and 5 of the present series were modeled on those just described. Their results can be explained in the same way. Specifically, associations were formed between each context and its associated CS across extinction (i.e., a B–CS1 association and a C–CS2 association). Then the context retrieval of the relevant CS representation to an A2 state of activity (e.g., CS1 by B) concomitantly with the shock exciting its representation to an A1 state of activity strengthened the CS1–shock association. This reassociation of CS1 with shock reinstated freezing when CS1 was tested in a neutral context relative to the freezing elicited by CS2 (Experiment 4). Reexposure to shock in each of the extinction contexts would have served to reassociate each CS with shock. However, subsequent exposure to one of these contexts (B) in the absence of either of its associates (CS1 and shock) should have resulted in the formation of inhibitory associations between these associates. One implication of this reasoning is that the inhibitory association from CS1 to shock would result in less freezing when CS1 was tested in D relative to that elicited by CS2. Just these results were obtained (Experiment 5).

According to this mediated conditioning explanation, reinstatement is due to the context serving to renew the link between its CS and US associates and this linkage occurs when the context is conditioned by US reexposure. An alternative explanation also appeals to the linking of the CS with the US but holds that this occurs at the time of test (Hall, 1996). This “associative chaining” explanation argues that bidirectional associations were formed between each context and its CS across extinction (e.g., B–CS1 and C–CS2) and that reexposure to shock in one of these contexts resulted in an excitatory context–shock association (e.g., B–shock). Test presentations of each CS in neutral context, D, produced different levels of freezing because CS1 activated the representation of its fear-eliciting context associate, B (Experiment 4). Reexposure to shock in either of the extinction contexts would have reinstated freezing to each of their CS associates when tested in D. However, reexposure to one of these contexts in the absence of shock (e.g., B) reduced its ability to elicit fear with the result that test presentation of its CS associate (CS1) in context D provoked less freezing than did that exhibited to CS2 whose context associate was still associated with shock (Experiment 5).

These explanations of reinstatement in terms of mediated conditioning or associative chaining differ from each other with respect to when the extinguished CS is linked to the US by the common context. However, both explanations imply that fear reactions will be established to a stimulus by shocking its context associate. In fact, there is considerable evidence that learned responses can be established to a stimulus as a consequence of the relations arranged between its associate and a US. This evidence is provided by techniques used to demonstrate the existence of within-event learning. Further, exactly those alternatives of mediated conditioning and associative chaining have been offered as explanations of the processes involved (see Rescorla & Cunning-

ham, 1978, for discussion). Experiment 6 provides additional support for the establishment of such learned responses. The design used was similar to that of Experiment 4 except that the initial pairings of CS1–shock and CS2–shock were omitted. Thus, rats were simply exposed to one stimulus (e.g., a noise) in one context and to a second stimulus (a clicker) in another context (counterbalanced). Then rats were exposed to shock in one of these contexts and tested for freezing to each stimulus in a third context. The test revealed that rats froze more to the stimulus (e.g., noise) whose context associate had been shocked than to the other stimulus (e.g., clicker) whose context associate had not been shocked.

These findings with a sensory preconditioning-like procedure (Experiment 6) demonstrate the existence of the processes (either mediated conditioning or associative chaining) taken to be causal for the CS-specific reinstatement of responding when rats were reexposed to the US in an extinction context and moved out of that context for testing (Experiments 2–5). However, there are problems in invoking either of these processes to explain reinstatement when rats were both reexposed to the US and tested in the extinction context (e.g., Experiment 1). According to associative chaining, this reinstatement is due to the rats forming a CS–context association across extinction and a context–US association across reexposure. Test presentations of the CS provoke freezing because they activate the US representation via the common context associate. But that context would have activated the US representation in advance of the test presentations of the CS. Thus, the associative chaining explanation implies that test presentations of the CS are irrelevant to the reinstatement found when rats are both reexposed and tested in the extinction context. Presumably, this reinstatement is to be identified with the freezing provoked by the context–US association. But this cannot be correct: In Experiment 1, relatively low levels of freezing were elicited by the test context in comparison with the substantial levels elicited by test presentations of the CS. In other words, reinstatement was specific to the CS, a fact that seems to be denied by the associative chaining explanation.

According to mediated conditioning, the reinstatement observed in Experiment 1 was due to the formation of context–CS associations across extinction and of CS–US associations at reexposure via the common context. It will be recalled that this reinstatement was specific to rats initially exposed to CS–US pairings and reexposed to the US after CS-alone presentations (Group PR). This reinstatement may be contrasted with the negligible levels of freezing exhibited on test by rats reexposed to the US after CS-alone presentations but initially exposed to unpaired relations between the CS and US (Group UR). The negligible levels of freezing by rats in Group UR may also be contrasted with the substantial levels of freezing elicited on test by a CS whose context associate had been shocked (Experiment 6). Taken together, these several findings suggest that the initial exposures to unpaired CS–US relations interfered with the subsequent development of (mediated) CS–US associations. Assuming that such exposures did not attenuate the formation of context–CS associations, one locus of the interference is at the level of associative formation between the context-activated CS representation and the reexposed US. A possible mechanism for this associative interference is the learned inhibition that could have developed to the CS as a result of its repeated (nonreinforced) presentations against an excitatory conditioned context (Rescorla & Wagner, 1972).

This interpretation of the test performance of rats in Group UR in Experiment 1 holds that (mediated) excitatory conditioning was impaired because the target CS had developed an inhibitory association with the reexposed US. If correct, this means that the variables controlling changes in the associative value of an absent event may be those regulating the value of one that is present. In both cases, the ability of a retrieved and a presented CS to enter into an excitatory association with a US is impaired if that CS has already acquired inhibitory properties, but this may not be generally correct. For instance, the parameters selected for CS preexposure in Experiment 6 were those that produced evidence for context specificity of latent inhibition when that CS was subsequently paired with a shock US (Westbrook et al., 2000). Nevertheless, these parameters resulted in evidence for mediated conditioning when shock was delivered in the CS-associated context. Here, the variables controlling changes in the value of the absent event appeared to differ from those regulating the value of one that was present. In the case of mediated conditioning, the retrieved CS representation entered into a strong association with the reexposed US via the common context; in the case of latent inhibition, the presented CS is commonly assumed to fail to enter into an association with that US via the common context (see Westbrook et al., 2000, for discussion).

In sum, the results of the present series of experiments suggest that context plays two roles in reinstating responding to an extinguished CS. These roles can be distinguished according to where extinction, US reexposure, and test occur. If extinction is in one context but US reexposure and test are in another, freezing is reinstated because the fear elicited by the conditioned context retrieves a CS–US memory; if extinction and US reexposure are in the same context but test is in another, freezing is reinstated in a CS-specific manner because the CS and US are linked by their common context associate. Finally, it may be worth noting that this explanation of reinstatement in terms of mediated conditioning questions the usefulness of US reexposure as a technique for illuminating the mask imposed on the expression of the original CS–US association. According to this explanation, reexposure to the US in the extinction context reinstated freezing to the extinguished CS because of new learned fear rather than the unmasking of old fear.

References

- Bouton, M. E. (1993). Context, time, and memory retrieval in the interference paradigms of Pavlovian learning. *Psychological Bulletin*, 114, 80–99.
- Bouton, M. E., & Bolles, R. C. (1979a). Contextual control of the extinction of conditioned fear. *Learning & Motivation*, 10, 445–466.
- Bouton, M. E., & Bolles, R. C. (1979b). Role of conditioned contextual stimuli in reinstatement of extinguished fear. *Journal of Experimental Psychology: Animal Behavior Processes*, 5, 368–378.
- Bouton, M. E., & King, D. A. (1983). Contextual control of the extinction of conditioned fear: Tests for the associative value of the context. *Journal of Experimental Psychology: Animal Behavior Processes*, 9, 248–265.
- Bouton, M. E., & Peck, C. A. (1989). Context effects on conditioning, extinction, and reinstatement in an appetitive conditioning preparation. *Animal Learning & Behavior*, 17, 188–198.
- Bouton, M. E., & Ricker, S. T. (1994). Renewal of extinguished responding in a second context. *Animal Learning & Behavior*, 22, 317–324.

- Bouton, M. E., Rosengard, C., Achenbach, G. G., & Peck, C. A. (1993). Effects of contextual conditioning and unconditioned stimulus presentation on performance in appetitive conditioning. *Quarterly Journal of Experimental Psychology: Comparative and Physiological Psychology*, 46(B), 63–95.
- Delamater, A. R. (1997). Selective reinstatement of stimulus–outcome associations. *Animal Learning & Behavior*, 25, 400–412.
- Dwyer, D. M., Mackintosh, N. J., & Boakes, R. A. (1998). Simultaneous activation of the representations of absent cues results in the formation of an excitatory association between them. *Journal of Experimental Psychology: Animal Behavior Processes*, 24, 163–171.
- Fanselow, M. S. (1980). Conditioned and unconditional components of post-shock freezing. *Pavlovian Journal of Biological Sciences*, 15, 177–182.
- Hall, G. (1996). Learning about associatively activated stimulus representations: Implications for acquired equivalence and perceptual learning. *Animal Learning & Behavior*, 24, 233–255.
- Harris, J. A., Jones, M. L., Bailey, G. K., & Westbrook, R. F. (2000). Contextual control over conditioned responding in an extinction paradigm. *Journal of Experimental Psychology: Animal Behavior Processes*, 26, 174–185.
- Harris, R. J. (1994). *ANOVA: An analysis of variance primer*. Itasca, IL: Peacock.
- Holland, P. C. (1981). Acquisition of representation-mediated conditioned food aversions. *Learning and Motivation*, 12, 1–18.
- Holland, P. C. (1990). Event representation in Pavlovian conditioning: Image and action. *Cognition*, 37, 105–131.
- Holland, P. C., & Forbes, D. T. (1982). Representation-mediated extinction of conditioned flavor aversions. *Learning and Motivation*, 13, 454–471.
- Konorski, J. (1948). *Conditioned reflexes and neuron organization*. New York: Cambridge University Press.
- Pavlov, I. P. (1927). *Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex*. London: Oxford University Press.
- Rescorla, R. A. (1979). Conditioned inhibition and extinction. In A. Dickinson & R. A. Boakes (Eds.), *Mechanisms of learning and motivation: A memorial volume to Jerzy Konorski* (pp. 83–110). Hillsdale, NJ: Erlbaum.
- Rescorla, R. A. (1984). Associations between Pavlovian CSs and context. *Journal of Experimental Psychology: Animal Behavior Processes*, 10, 195–204.
- Rescorla, R. A. (2000). Experimental extinction. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 119–154). Mahwah, NJ: Erlbaum.
- Rescorla, R. A., & Cunningham, C. L. (1977). The erasure of reinstated fear. *Animal Learning & Behavior*, 5, 386–394.
- Rescorla, R. A., & Cunningham, C. L. (1978). Within-compound flavor associations. *Journal of Experimental Psychology: Animal Behavior Processes*, 4, 267–275.
- Rescorla, R. A., & Heth, C. D. (1975). Reinstatement of fear to an extinguished conditioned stimulus. *Journal of Experimental Psychology: Animal Behavior Processes*, 1, 88–96.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning: II. Current research and theory* (pp. 64–99). New York: Appleton-Century-Crofts.
- Scheffé, H. (1959). *The analysis of variance*. New York: Wiley.
- Wagner, A. R. (1981). SOP: A model of automatic memory processing in animal behavior. In R. R. Miller & N. E. Spear (Eds.), *Memory mechanisms in animal behavior* (pp. 5–47). Hillsdale, NJ: Erlbaum.
- Wagner, A. R., & Brandon, S. E. (1989). Evolution of a structured connectionist model of Pavlovian conditioning (AESOP). In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Pavlovian conditioning and the status of traditional learning theory* (pp. 149–189). Hillsdale, NJ: Erlbaum.
- Ward-Robinson, J., & Hall, G. (1996). Backward sensory preconditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 22, 395–404.
- Westbrook, R. F., Jones, M., Bailey, G., & Harris, J. (2000). Contextual control over conditioned responding in a latent inhibition paradigm. *Journal of Experimental Psychology: Animal Behavior Processes*, 26, 157–173.

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