Discriminative and nondiscriminative contextual fear conditioning potentiate the acoustic startle response

P. W. FRANKLAND

Cold Spring Harbor Laboratory, Cold Spring Harbor, New York

and

C. L. DOCKSTADER and R. J. McDONALD

University of Toronto, Toronto, Ontario, Canada

The acoustic startle reflex, a short-latency motor response to a loud noise, is modifiable by experience. Here we test whether contextual fear conditioning potentiates startle responses, in addition to two other indices of fear: freezing and defecation. First, we trained rats with zero, one or three 0.6-mA footshocks. Upon reexposure to the same context, startle responses, amount of time freezing, and defecation were increased in the one- and three-shock groups, but not in the zero-shock group, compared with pretraining baseline levels. Second, to test whether these increases in fear responses were context specific, we trained and tested rats in a context discrimination paradigm. Rats were trained to discriminate between two contexts, one in which three footshocks were delivered, the other in which no footshocks were delivered. Startle amplitudes and time spent freezing were increased in the paired as opposed to the unpaired context. These results suggest that the acoustic startle reflex can be modified by a specific memory of an environmental context in which an aversive event has occurred.

The startle reflex is a short-latency motor response displayed by all mammals (Landis & Hunt, 1939). Startle responses are evoked by strong acoustic (e.g., Davis, Gendelman, Tischler, & Gendelman, 1982), tactile (e.g., Taylor, Castro, & Printz, 1991), or vestibular (e.g., Gruner, 1989) stimulation, and they involve the rapid activation of muscles along the length of the body. This rapid activation of the majority of skeletal muscles may serve to protect an animal in the time before a directed response can take place. In particular, the tensing of muscles in the dorsal regions of the body, including the neck and the head, may protect an animal from attack from behind (Yeomans & Frankland, 1996).

Startle amplitudes are affected by experience. For example, startle amplitudes are increased in the presence of a previously neutral stimulus (conditioned stimulus; CS) that has been paired with an aversive event such as the delivery of shock (unconditioned stimulus; US) (*fear-potentiated startle*; e.g., Davis & Astrachan, 1978). In contrast, a CS associated with rewarding events, such as the

delivery of food, attenuates startle (*pleasure-attenuated startle*; Schmid, Koch, & Schnitzler, 1995).

Both fear-potentiated startle and pleasure-attenuated startle are forms of Pavlovian classical conditioning. However, Pavlovian fear conditioning is possible in the absence of a punctate CS. That is, stimuli present in the environment where the shock is delivered can collectively serve as CSs, acquiring the ability to elicit fear. This form of classical fear conditioning has been termed *contextual fear conditioning*, and it has been proposed that an animal forms a unified representation of the cues present in the context and that the association between this complex representation of the environment and the delivery of footshock underpins learning in this paradigm (e.g., Eichenbaum, 1996; Nadel, Willner, & Kurz, 1985; Sutherland & Rudy, 1989).

Previously it has been shown that contextual fear conditioning potentiates acoustic startle responses in much the same way as explicitly paired CSs do (Campeau et al., 1991; McNish, Gewirtz, & Davis, 1997). Similarly, in Experiment 1 below, we show that reexposure to a context where footshocks have been previously presented potentiates startle. In addition, we compare this potentiation of startle with two other indices of conditioned fear: freezing and defecation. In Experiment 2, we tested whether increases in conditioned fear responses are due to generalized increases in "fear" following training, or are specific to the context in which have been delivered. To test for context specificity, we used a context discrimination procedure (McDonald, Koerner, & Sutherland,

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1995), in which rats learned to discriminate between a shock and no-shock context. In the context discrimination procedure, rats spend equal amounts of time in the to-be-discriminated contexts during training. Therefore, this procedure avoids the possible confound of increased exploration (which may compete with conditioned responses such as freezing and/or potentiated startle) when context specificity is tested in a novel context following initial training.

METHOD

Subjects

Experimentally naive male Wistar rats ($n = 48$; Charles River, Montreal) weighing 250–350 g were used in these experiments. They were housed individually on a 12:12 light:dark cycle (lights off at 0900), with food and water freely available. All testing was carried out between 0900 and 1600.

Startle Apparatus

Amplitudes of startle reactions were determined by using a stabilimeter that was housed in a sound-attenuated chamber ($46 \times 41 \times 41$ cm interior dimensions). The stabilimeter consisted of a Plexiglas cage with wire mesh walls on the long side, compressed between four springs on the top and bottom within a heavy steel frame. The cage measured $8 \times 8 \times 15$ cm, which was sufficiently large to allow the rat to move and to orient itself in one of two directions at any given time. Movements of the rat were recorded by an accelerometer (Endevco 2217E) embedded in a rubber bung and placed between the bottom of the cage and the base of the heavy steel frame. The output of the accelerometer was filtered at 2 Hz, amplified 10 times, integrated by a Endevco Signal Conditioner (Model 2775A), and then displayed on a storage oscilloscope (Hitachi VC-6025A). Startle amplitudes were defined as the peak-to-peak voltage recorded by the accelerometer within 100 msec of the delivery of the startle-eliciting noise.

Acoustic stimuli were produced by a Pacer 8- Ω speaker placed within the sound-insulated chamber at a distance of 10 cm from the long side of the cage. Acoustic stimuli were 4-msec 119-dB noise bursts (measured by a Brüel and Kjær modular Precision Sound Level Meter, Model 2231). Background white-noise levels were maintained at 75 dB throughout testing.

Shock Delivery

The unconditioned stimuli were 0.6-mA footshocks, 1.5 sec in duration. They were delivered to the cage floor bars by a Grason-Stadler constant-current generator with an Elektra grid scrambler. Shock current (in milliamperes) was measured as the voltage drop across a 1-k Ω resistor in series with a 100-k Ω resistor connected between electrified floor bars.

Procedure for Experiment 1: Contextual Fear Conditioning and Startle

Pretraining baseline. Rats ($n = 24$) were placed in the startle apparatus on each of 2 consecutive days. During these sessions, following an initial period of 2 min when no stimuli were presented, rats were presented with 40 startle-eliciting noise bursts at 30-sec intertrial intervals (ITIs). Startle amplitudes, time spent freezing, and boli were measured for the entire 20 min test session. An animal was determined to be freezing when it refrained from all movements of the body and vibrissae aside from respiratory movement (Fanselow, 1990). Freezing was monitored continuously through the test period. Following the completion of the session, boli were removed from the cage and weighed.

Training. On the day following the completion of pretraining baseline testing, each rat was placed back into the startle apparatus for 5 min. During this period, rats were presented with zero ($n = 8$), one ($n = 8$), or three ($n = 8$) 1.5-sec, 0.6-mA footshocks delivered via the cage floor bars. For the one footshock group, the footshock was delivered after 2 min. For the three-footshock group, footshocks were delivered after 2, 3, and 4 minutes.

Testing. Posttraining testing consisted of two startle test sessions identical to those described above for pretraining. Again, startle, freezing, and boli were measured.

Procedures for Experiment 2: Discriminative Contextual Fear Conditioning

To test whether the increase in startle, freezing, and boli measures in Experiment 1 were specific to the chamber in which rats were shocked, we trained a second set of rats ($n = 24$) in a context discrimination procedure (McDonald et al., 1995). In addition, a second startle apparatus that was housed in an identical sound-attenuated chamber was used in this experiment. The apparatus to deliver startle stimuli and footshocks and to record startle amplitudes was identical to that in the first startle apparatus. However, the second startle apparatus (Context B) differed from the first startle apparatus (Context A) in the following ways: (1) It was located in a different room; (2) the room was darker; (3) background noise in the room was provided by a radio; (4) the startle chamber was rotated 90° with respect to the sound-attenuated box in Context A; and (5) an almond odor cue was present within the sound-attenuated box. The procedures and counterbalancing for Experiment 2 are summarized in Table 1.

Pretraining baseline. During pretraining, rats were tested for startle in Box A and in Box B. On the morning of the 1st day, rats were placed in Box A (or B) and were presented with 20 noise bursts at 30-sec ITIs. In the afternoon, rats were placed in Box B (or A) and presented with 20 noise bursts at 30-sec ITIs. These pretraining test sessions were repeated on Day 2. Startle amplitudes were recorded and freezing was monitored throughout the 20-min test session; and at the completion of training, boli were weighed. These measures were only taken in Box A.

Training. On Days 3 and 4, each rat was placed back in Startle Box A in the morning, and then in Box B in the afternoon (or vice versa) for 5 min each in a counterbalanced order. During this period, rats were presented with three 1.5-sec, 0.6-mA footshocks delivered via the cage floor bars. Half of the rats received shocks in Box A (Group A; $n = 12$); the other half, in Box B (Group B; $n = 12$).

Table 1
Design and Counterbalancing for Context Discrimination (Experiment 2)

		Baseline				Training				Test Day 5
		Day 1		Day 2		Day 3		Day 4		
Group	<i>n</i>	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	
1	6	A	B	B	A	A−	B+	B+	A−	A
2	6	B	A	A	B	A−	B+	B+	A−	A
3	6	A	B	B	A	B−	A+	A+	B−	A
4	6	B	A	A	B	B−	A+	A+	B−	A

Note—Rats received pretraining testing in Contexts A and B on Days 1 and 2. On Days 3 and 4, half of the rats received three footshocks in Context A (A+), and none in Context B (B-). The other half of the rats received three footshocks in Context B (B+), and none in Context A (A-). Both groups of rats were subsequently tested in Context A on Day 5.

Posttraining testing. One day following training, rats were placed back into Box A and tested for startle. In this session, 20 startle-eliciting stimuli were presented at 30-sec ITIs. Startle amplitudes were recorded, and freezing and boli were also measured.

Data Analysis

The effect of training on startle amplitudes, time spent freezing, and defecation was assessed in Experiment 1 using analysis of variance (ANOVA). Because startle amplitudes decline across sessions (long-term habituation; see, e.g., Jordan, 1989) the mean startle amplitudes in the second pretraining session were compared with the mean startle amplitudes in the first posttraining session. Similarly, pretraining data from the second test session were compared with data from the first posttraining test session for freezing and defecation. Planned comparisons were carried out to compare pre- and posttraining levels of startle, freezing, and defecation in the zero-, one-, and three-shock groups. In addition, to assess whether increases in startle, time spent freezing, and defecation were correlated within rats, a correlation analysis was carried out to compare difference scores (posttraining – pretraining) for each of the three measures.

In Experiment 2, the effect of group (shocks in Context A vs. shocks in Context B) on pre- versus posttraining startle amplitudes, time spent freezing, and defecation was assessed with ANOVAs. Specifically, mean startle amplitudes in Box A (20 trials) in the second pretraining session were compared with those in the posttraining session (20 trials) in Box A. Similarly, time spent freezing and defecation in the second pretraining session in Box A were compared to those in the posttraining session in Box A.

RESULTS

Experiment 1

Reexposure to the apparatus where rats had received footshock increased startle amplitudes, time spent freezing, and defecation. For each of these three measures, reliable increases were observed following training with one or three, but not zero, footshocks (Figure 1). The effects of fear conditioning on startle, freezing, and defecation were assessed with mixed ANOVAs, with group (three levels: zero, one, or three shocks) as a between-subjects variable and test (two levels: pre- and posttraining) as a within-subjects variable.

For startle, there was a main effect of test [$F(1,21) = 13.62, p < .01$], showing that training affected startle amplitudes. Importantly, there was a significant interaction between group and test [$F(2,21) = 3.55, p < .05$], indicating that there were different levels of potentiation of startle following training in the three groups. Planned comparisons showed that startle amplitudes were significantly increased following training in the one- ($p < .05$) and three- ($p < .01$), but not the zero- ($p = .99$), shock groups.

For freezing, there was a main effect of test [$F(1,21) = 12.22, p < .01$], showing that training affected time spent freezing. There was a significant interaction between group and test [$F(2,21) = 4.35, p < .05$], indicating that there were different levels of conditioned freezing following training in the three groups. Planned comparisons showed that time spent freezing was significantly increased following training in the one- ($p < .05$) and

three- ($p < .001$), but not the zero- ($p = .86$), shock groups.

For defecation, there was a main effect of group [$F(2,21) = 7.46, p < .01$], reflecting different levels of defecation across groups. There was a significant main effect of test [$F(2,21) = 42.95, p < .001$] showing that training affected defecation across groups. There was a significant interaction between group and test [$F(2,21) = 10.74, p < .001$], indicating that there were different levels of defecation following training in the three groups. Planned comparisons showed that time spent freezing was significantly increased following training in the one- ($p < .001$) and three- ($p < .001$), but not the zero- ($p = .88$), shock groups.

For each rat, increases in startle amplitudes, time spent freezing, and defecation following training were moderately correlated. Comparing difference scores for post- versus pretraining levels for each of the three measures gave the following correlations: startle–freezing, $r = +.48$ ($p < .05$); startle–defecation, $r = +.64$ ($p < .05$); freezing–defecation, $r = +.38$ ($p = .07$).

During startle testing (either pre- or posttraining) it is possible that the startle-eliciting noise burst could act as a US. That is, the startle-eliciting noise burst is a potentially aversive stimulus that could become associated with the experimental environment (Kiernan & Cranney, 1992; Leaton & Borszcz, 1985). If such contextual conditioning were to occur, one might expect (1) increases in startle amplitudes, time spent freezing, and defecation in the control group (zero shocks) during posttraining testing; and (2) increases in startle amplitudes across trials within the initial pretraining baseline startle testing. First, the analyses above indicate that startle amplitudes, freezing, and defecation were not significantly increased in the posttraining test session in comparison with the pretraining test session in the control group. Second, startle amplitudes did not increase within the pretraining baseline session in any of the three groups (zero, one, or three shocks) (Table 2). Although there was no effect of trial block on startle amplitudes in the zero [$F(3,21) = 1.18, p > .05$] or the three- [$F(3,21) = 0.98, p > .05$] shock group, startle amplitudes significantly declined across blocks in the one-shock group [$F(3,21) = 3.73, p < .05$].

Experiment 2

During training, Group A received three footshocks in Context A and no footshocks in Context B on each of 2 consecutive days. Group B received three footshocks in Context B and no footshocks in Context A on each of 2 consecutive days. Both groups were tested in Context A 1 day following the completion of training, and startle, time spent freezing, and defecation were measured (Figure 2). Startle and time spent freezing were increased in rats tested in the same context in which they received footshocks (Group A). In contrast, startle and time spent freezing in Context A were not significantly different from pretraining baselines for rats that received foot-

A **B** **C**

Figure 1. The effect of training with zero, one, or three shocks. Posttraining (solid bars) versus pretraining (open bars) levels of (A) startle, (B) time spent freezing, and (C) defecation are shown. Planned comparisons showed that startle amplitudes, time spent freezing, and defecation were significantly increased following training with 1 or 3 footshocks but not zero footshocks. * $p < .05$. ** $p < .01$. *** $p < .001$. n.s.d., no significant difference.

Table 2
Within Session Habituation of Startle Responses for
Pretraining Baseline Data

Block (10 Startle- Eliciting Stimuli)	Group		
	Zero Shock	One Shock	Three Shocks
1	0.58 ± 0.07	0.51 ± 0.06	0.52 ± 0.06
2	0.48 ± 0.06	0.44 ± 0.04	0.46 ± 0.06
3	0.50 ± 0.08	0.43 ± 0.04	0.43 ± 0.05
4	0.50 ± 0.09	0.40 ± 0.05	0.45 ± 0.06

Note—Rats were presented with a total of 40 startle-eliciting noise bursts. The mean startle amplitudes are broken down into blocks of 10 trials for each group (zero, one, and three shocks).

shocks in Context B (Group B). The effects of training context (Context A vs. Context B) on startle, freezing, and defecation tested posttraining in Context A were assessed with mixed ANOVAs with group (two levels: Group A vs. Group B) as a between-subjects variable and test (two levels: pre- and posttraining) as a within-subjects variable.

For startle, there was a main effect of test [$F(1,22) = 5.06, p < .05$], indicating that training affected startle amplitudes. There was also a significant interaction between group and test [$F(1,22) = 6.58, p < .05$], indicating that there were differences in startle responsivity in Context A between Group A and Group B. Planned comparisons showed that startle amplitudes in Context A were significantly increased in Group A ($p < .01$), but not in Group B ($p = .83$). There was no significant main effect of group [$F(1,22) = 1.72, p > .05$].

For freezing, there was a main effect of group [$F(1,22) = 22.38, p < .001$], reflecting different overall levels of freezing in Groups A and B. There was a main effect of test [$F(1,22) = 38.87, p < .001$], showing that training affected time spent freezing. In addition, there was a significant interaction between group and test [$F(1,22) = 20.58, p < .001$], indicating differences in posttraining freezing in Context A between Group A and Group B. Planned comparisons showed that time spent freezing in Context A was significantly increased in Group A ($p < .001$), but not in Group B ($p = .24$).

For defecation, there was a main effect of group [$F(1,22) = 5.23, p < .05$], reflecting different overall levels of freezing in Groups A and B. There was a main effect of test [$F(1,22) = 51.93, p < .001$], showing that training affected defecation. In addition, there was a significant interaction between group and test [$F(1,22) = 7.87, p < .05$], indicating differences in posttraining defecation in Context A between Groups A and B. Planned comparisons showed that defecation in Context A was significantly increased in both Group A ($p < .001$) and Group B ($p < .01$).

DISCUSSION

These results show that contextual fear conditioning potentiates acoustic startle responses. In Experiment 1,

we showed that startle amplitudes are significantly increased when rats are reexposed to a context in which they have previously received footshocks, as previously reported (Campeau et al., 1991; McNish et al., 1997). In Experiment 2, we showed that this potentiation of startle is not due to generalization, since startle amplitudes increased only when rats were reexposed to the context in which footshocks were delivered, and not when they were reexposed to a context in which no footshocks were delivered. A similar pattern of results was observed with two other behavioral indices of fear: freezing and defecation.

Presently, there is much interest and controversy in the neural systems underpinning learning in contextual as opposed to cued fear conditioning (e.g., Cho, Friedman, & Silva, in press; Frankland, Cestari, Filipkowski, McDonald, & Silva, 1998; Good & Honey, 1997; Kim & Fanselow, 1992; Maren, Aharonov, & Fanselow, 1997; Maren, Anagnostaras, & Fanselow, 1998; Maren & Fanselow, 1997; McNish, Gewirtz, & Davis, 1997, 1998; Phillips & LeDoux, 1992, 1994; Selden, Everitt, Jarrard, & Robbins, 1991; Sutherland & McDonald, 1990). An advantage of the startle reflex is that it is a graded, rather than an all-or-none (e.g., freezing), response. It may thus prove to be a valuable tool in determining the relative contributions of different memory systems to cued and contextual conditioning, because it allows for quantitative, rather than qualitative, measurement of conditioned responding.

In Experiment 1, reexposure to the training apparatus resulted in increases in the mean time spent freezing following training with either one or three footshocks. These data are consistent with previous reports which have shown that contextual fear conditioning with one training trial (e.g., Fanselow, 1990) or more (e.g., Kim, Rison, & Fanselow, 1993) increases freezing rates in rats. Consistent with previous reports (Campeau et al., 1991; McNish et al., 1997), we have shown that acoustic startle responses are also potentiated by contextual fear conditioning. Therefore both cues explicitly paired with USs and static contextual cues present in the chamber serve as conditioned stimuli and result in an enhancement of startle responsivity. Critically, startle amplitudes were not increased posttraining for the control group (zero shocks), indicating that increases in startle responsivity in the one- and three-shock groups cannot be attributed to dishabituation of startle responses.

These results show that training with a single footshock is sufficient to produce reliable potentiation of startle. The levels of startle potentiation following contextual fear conditioning in the present study (27% and 37% following training with one and three footshocks, respectively) were generally lower than those in two other similar studies (~45%–65%; Campeau et al., 1991; McNish et al., 1997). Since more intensive training protocols were used in these studies (fifty 0.6-mA footshocks: Campeau et al., 1991; ten 0.6-mA footshocks:

Figure 2. Contextual discrimination paradigm. Pre- and posttraining levels of (A) startle, (B) time spent freezing, and (C) defecation in Context A are shown for Groups A and B. Group A received footshocks in Context A, and none in Context B during training. Group B received footshocks in Context B, and none in Context A during training. Planned comparisons showed that posttraining levels of startle and time spent freezing in Context A were significantly increased following training for Group A, but not B, indicating that increases in these measures were specific to the training context. Defecation, however, increased post-training in both Groups A and Group B. $**p < .01$. $***p < .001$. n.s.d., no significant difference.

McNish et al., 1997), it seems likely that training with three or less shocks results in submaximal levels of potentiated startle.

In Experiment 2, we showed that increases in startle and freezing are not due to a generalized increase in fear following training; rather, they are specific to the shock context. Both groups of rats were trained in Contexts A and B. Group A received footshocks in Context A and none in Context B, whereas Group B received footshocks in Context B, and none in Context A. Group A, but not B, showed increases in startle amplitudes and freezing in Context A in the posttraining test. Defecation was increased in both groups posttraining. These data suggest that rats are able to discriminate between a context paired with shock and a context not paired with shock. An alternative interpretation, however, of the context discrimination data is that the animals might not be discriminating between contexts, but simply showing context salience effects. This interpretation is possible since testing in the paired and unpaired contexts at the terminal test was not fully counterbalanced. According to this view, any difference in conditioned fear between the groups shocked in the two contexts might be due to weaker context conditioning in Context B because it was somehow less salient. Yet although possible, this interpretation of the context discrimination results is unlikely, because various experiments done with similar chambers and fully counterbalanced designs (during training and testing) have shown discriminative fear conditioning to context with no indication of context salience effects (Antoniadis & McDonald, in press; Ferbinteanu, Holsinger, & McDonald, in press; Frankland et al., 1998; McDonald et al., 1995).

This context discrimination procedure is advantageous over other procedures in testing for context specificity because it controls for novelty effects. In other studies, context specificity is usually tested by comparing conditioned responding in both the training chamber and a novel chamber following conditioning (e.g., McNish et al., 1997). Because rats tend to explore novel environments, however, attenuation of conditioned responding may be due to increased exploratory activity in the novel chamber. In the present study, we avoided this confound because the rats spent equal amounts of time in the two contexts that they had to discriminate. The key difference between the experiences in the two contexts was that rats received footshocks in one and not the other. These data show that increases in freezing and potentiated startle were specific to the chamber, and not due to nonspecific aspects of the experimental protocol (e.g., transport to testing room) or testing environments (e.g., startle apparatus, sound-attenuated chamber). Rather, specific features or cues within the chamber or the testing room were either collectively or individually important. These results replicate those of a recent study by McDonald et al. (1995). Using multiple behavioral mea-

sures (freezing, conditioned place preference, locomotion) they found that rats discriminated between a context in which footshocks were delivered and another in which footshocks were not.

In conclusion, these data show that three different indices of fear (startle amplitude, time spent freezing, defecation) are increased in rats when they are reexposed to a context previously paired with shock. Increases in each of these measures are consistent with the idea that conditioned fear stimuli evoke a broad range of highly correlated behavioral and autonomic responses associated with "fear" (Davis, 1992; LeDoux, 1993). The context discrimination experiment further showed that these correlated increases in fear responses are specific to the training context (while controlling for effects of novelty), and not due to some generalized increase in fear. Taken together, these data support the idea that startle amplitudes are sensitive to situation or circumstance. That is, just as cues explicitly paired with rewarding stimuli (Schmid et al., 1995) or aversive stimuli (Davis, Schlesinger, & Sorenson, 1989) affect the startle responsivity, the places or contexts in which these cues occur also exert control over startle responsivity.

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