Long-term retention of fear-potentiated startle following a short training session

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The permanence of aversive memories has been reported to vary when assessed with conditioned emotional response procedures (months) versus avoidance response measures (days). When evaluated with the potentiated startle paradigm, five light-shock pairings at a 2-min intertrial interval produced highly reliable potentiated startle, which was similar in magnitude from 1 to 28 days after training and maximal using a 0.6-mA footshock intensity. These results are consistent with such measures as conditioned emotional response procedures, in which aversive memories have been observed after months following original training. The results obtained with various shock intensities are also discussed in the context of other indices of fear.

Acquisition of fear is generally believed to depend on Pavlovian conditioning processes (W. R. McAllister & D. E. McAllister, 1971). That is, conditioned stimuli (CSs) come to elicit defense reactions only when appropriately paired with noxious unconditioned stimuli (USs). One of the distinguishing characteristics of conditioned fear is that it can be demonstrated in avoidance tasks (Quartermain & Judge, 1983; Quartermain & Jung, 1989), conditioned emotional response (CER) procedures (Brophy & Tremblay, 1971; Gleitman & Holmes, 1967; Leaf & Muller, 1965; Mahoney & Ayres, 1976), conditioned freezing measures (Blanchard & Blanchard, 1969; Fanselow & Bolles, 1979), and the potentiated startle paradigm (Brown, Kalish, & Farber, 1951; Davis, Schlesinger, & Sorenson, 1989) after very few, and often single, CS-US pairings.

One aspect of Pavlovian fear conditioning that has apparently received little experimental analysis is its expression (memory) after various intervals between a small number of CS-US pairings and a retention test (Flaherty, 1985; Gleitman, 1971; Spear, Miller, & Jagielo, 1990). Furthermore, conflicting results in regard to the permanence of aversive memories have been reported when retention was assessed with different performance measures (W. R. McAllister & D. E. McAllister, 1971). For

instance, rats tested in a CER task after a single CS-US pairing demonstrated comparable performance 1 and 29 days after original training (Shurtleff & Ayres, 1981). Four CS-US pairings have been shown to produce comparable CER 24 h and 90 days after training (Gleitman & Holmes, 1967). On the other hand, avoidance measures revealed significant performance decrements 14 days after three CS-US pairings in mice (Quartermain & Judge, 1983; Quartermain & Jung, 1989). Even after as many as 35 CS-US pairings, rats tested on avoidance measures show significantly lower retention performance a few days after original training (D. E. McAllister & W. R. McAllister, 1968; Spear, Hamberg, & Bryan, 1980). Such results support the view that different measures of fear do not always correlate with each other, even though they are assumed to reflect a unitary central state of fear (W. R. McAllister & D. E. McAllister, 1971). Therefore, generalizations about the permanence of aversive memories assessed with different fear measures should not be made without experimental analysis.

One measure of fear routinely employed in our laboratory is the potentiated startle paradigm, in which the amplitude of the acoustic startle reflex is enhanced in the presence of a light CS previously paired with footshocks (Brown et al., 1951; Davis & Astrachan, 1978). Although potentiated startle has been reported as long as 21 days after 20 CS-US pairings in original training (Cassella & Davis, 1985), no study has systematically examined the relative level of potentiated startle at different retention intervals. On the basis of the above considerations, we decided to study the effects of various training-to-testing intervals with the potentiated startle paradigm after rats were conditioned with a relatively small number (five) of CS-US pairings. Also, different footshock intensities were used to assess possible improvements in the magnitude of fear-potentiated startle after five training trials.

This research was supported by National Institute of Neurological Disorders and Stroke Grant NS-18033, Research Scientist Development Award MH-00004 to Michael Davis, National Institute of Mental Health Grants MH-25642 and MH-41298, a grant from the Air Force Office of Scientific Research, and the State of Connecticut. We thank Lee Schlesinger, who tested the rats, and William Falls for his comments on an earlier draft of this manuscript. Correspondence concerning this article should be addressed to Michael Davis, Department of Psychiatry, Yale University School of Medicine, 34 Park Street, New Haven, CT 06508.

EXPERIMENT 1A

The purpose of this experiment was to provide evidence that an eventual startle enhancement would be produced by associative, as opposed to nonassociative (pseudo-conditioning), learning processes. The parameters used were partly determined from a previous study (Davis et al., 1989).

Method

Subjects

The subjects were 20 experimentally naive male albino Sprague-Dawley rats weighing 300–400 g (Charles River Co.). They were housed in wire cages (17 × 35 × 45 cm) in groups of 5, with water and laboratory chow continuously available, and maintained on a 12:12-h light:dark cycle (lights on at 7:00 a.m.). The rats were acclimated to the colony rooms for 2 to 3 weeks before training began.

Apparatus

Training apparatus. Five identical boxes (30 × 25 × 25 cm), constructed of aluminum sides and tops and clear Plexiglas front and back walls, were located on two shelves within a ventilated, sound-attenuating chamber (2.5 × 2.5 × 2 m; Industrial Acoustic Co.). The floors consisted of stainless steel rods, 4.5 mm in diameter and spaced 19 mm apart. Background noise of 55 dB (SPL) was provided by a white-noise generator. Sound-level measurements were made with a General Radio Model 1551-C sound-level meter (A scale). The visual CS was produced by an 8-W fluorescent light bulb (100 μ sec rise time) located just outside of the back wall of each training box, which was kept entirely dark except when the CS was on. The footshock USs were delivered from five LeHigh Valley constant-current shock generators (SGS-004) located outside the chamber. Current intensity was measured with a 1-k Ω resistor across a differential amplifier of an oscilloscope in series with a 100-k Ω resistor connected between adjacent floor bars in each of the boxes. Current was defined as the root mean square voltage across a 1-k Ω resistor ($\text{mA} = 0.707 \times 0.5 \times \text{peak-to-peak voltage}$).

Testing apparatus. The boxes used to measure the amplitude of startle responses were five separate stabilimeter devices, as described previously by Cassella and Davis (1986). Briefly, each stabilimeter consisted of a 8 × 15 × 15 cm Plexiglas and wire mesh cage suspended within a 25 × 20 × 20 cm heavy steel frame. Within this frame, the cage was compressed between four springs above and a 5 × 5 cm rubber cylinder below, with an accelerometer (M. B. Electronics Type 302) located between the bottom of the cage and the top of the rubber cylinder. Cage movement resulted in displacement of the accelerometer, the output of which was amplified (M. B. Electronics Model N504) and fed to a PDP-11 computer. Startle amplitude was defined as the maximum accelerometer voltage that occurred during the first 200 msec after the startle stimulus was delivered and was proportional to the amplitude of the rat's startle response. The stabilimeters were housed in a chamber (Industrial Acoustic Co.) similar to the one containing the training chambers. The startle stimuli were delivered by high-frequency speakers (Radio Shack Supertweeter) located 10 cm from each stabilimeter. The stimuli were 50-msec bursts of white noise, having a rise-decay time of 5 msec. The intensities used could be varied. Background noise, provided by a white-noise generator, was 55 dB (SPL).

Procedure

Matching. On the first 2 days, the animals were placed in the stabilimeter cages and, 5 min later, presented with 30 noise bursts at a 30-sec interstimulus interval (ISI). Intensities of 90, 95, and 105 dB were used with 10 noise bursts at each intensity. Noise bursts

were presented in a balanced, irregular order, with the restriction that each of the three intensities had to occur in every three trial blocks. The mean amplitude startle across the 30 noise bursts on the last matching day was used to assign the animals into groups of 5 rats each with similar means before training began.

Training. On the day after the last matching session, the animals were placed in the training cages and, 15 min later, paired animals ($n = 10$) received five CS-US presentations, using a 3.7-sec light CS coterminating with a 0.5-sec, 0.6-mA footshock US. The intertrial interval was 2 min. The rats were removed from the cages 5 min after the last CS-US presentation and returned to the colony room. Unpaired animals ($n = 10$) were treated similarly, except that the CS preceded the US by 1 min.

Testing. Three days after training, all of the animals were returned to the testing cages and presented with a total of 70 100-dB noise bursts at a 30-sec intertrial interval; 10 initial bursts, followed by 10 noise bursts at each of three different light-noise intervals (800, 1,600, and 3,200 msec), intermixed with 30 additional noise bursts. Noise bursts were presented in a balanced, irregular order, with the restriction that each of the four trial types had to occur in every six-trial block (one of each light-noise trial type [three] and three noise-alone trials). Different light-noise intervals were used during testing because previous data have shown that animals trained with a small number of CS-US pairings often show maximum potentiation at test intervals that differ from the training interval (Davis et al., 1989).

Results and Discussion

An analysis of variance (ANOVA) was performed on the mean difference scores for each test interval (800, 1,600, and 3,200 msec). These scores were computed by subtracting the mean startle amplitude on the noise-alone trials from that on the light-noise trials for each rat. There were no significant effects of test interval; therefore, the three light-noise intervals were averaged for further analyses and data presentation [$F(2,36) = 0.50$]. This result is consistent with the results obtained by Davis et al. (1989), in which five training trials at a 3,200-msec CS-US delay interval produced comparable potentiated startle at 800- and 3,200-msec light-noise test intervals (a 1,600-msec interval was not used in the latter study). Figure 1 shows the mean amplitude startle response of the noise-alone and light-noise trials averaged across the testing session and the difference scores for the paired and unpaired groups. An ANOVA was conducted using trial type (noise-alone and light-noise) as a within-subjects factor and group (paired and unpaired) as a between-subjects variable. Five CS-US pairings produced significant fear potentiation in the paired group, as revealed by a significant group $\times$ trial type interaction [$F(1,18) = 22.24, p < .001$]. Subsequent dependent t tests on the mean noise-alone and light-noise trials for each group confirmed a reliable potentiation in the paired group only [$t(9) = 4.35, p < .01$].

Significant fear-potentiated startle was revealed only in the paired animals using an intertrial interval of 2 min during the training phase. This result is consistent with an earlier report in which five trials at an average intertrial interval of 4 min produced reliable potentiated startle (Davis et al., 1989).

Figure 1. Mean amplitude startle on the noise-alone and light-noise test trials and difference scores ($\pm SEM$) of rats exposed to five paired or unpaired lights and shocks.

EXPERIMENT 1B

Demonstration of the associative nature of fear potentiation in Experiment 1A allowed the determination of fear potentiation at different retention intervals.

Method

Subjects

Sixty experimentally naive rats were used.

Procedure

The matching, training, and testing procedures, as well as the apparatus, were identical to those used in Experiment 1A. However, different groups of animals ($n = 10$, in each group) were trained with paired presentations of the light and a 0.6-mA footshock, but were tested at intervals of 1, 3, 7, 10, 14, or 28 days after training.

Results and Discussion

An ANOVA revealed that the mean difference scores were not reliably different at the three light-noise intervals [$F(2,108) = 0.55$]. Therefore, averages collapsed over the three intervals were used for the following data presentation and analyses. Figure 2 presents the potentiated startle obtained at different retention intervals. This figure shows that fear-potentiated startle was present at each training-to-test interval. This impression was confirmed by a two-way ANOVA on trial type and group (different retention intervals), which found a significant effect of trial type, reflecting fear-potentiated startle across the groups [$F(1,54) = 86.63$, $p < .001$]. Importantly, however, there was no significant group $\times$ trial type inter-

action [$F(5,54) = 0.47$]. Paired t tests found significant potentiated startle at each retention interval [$t(9) = 3.68$, 4.63, 6.04, 3.26, 5.66, 2.45, for 1-, 3-, 7-, 10-, 14-, and 28-day training-to-testing intervals, respectively; all p s $< .05$]. These results suggest that retention of aversive memories is unchanged over a 1-month period with the parameters used, as measured with the potentiated startle paradigm.

EXPERIMENT 2

The magnitude of potentiation in Experiment 1B was similar at all retention intervals. However, the absolute magnitude of potentiation was lower than that routinely obtained with a greater number of CS-US pairings (Davis & Astrachan, 1978; Davis et al., 1989). In Experiment 2, different footshock intensities were used in an attempt to improve the magnitude of potentiated startle. Both lower and higher shock intensities were employed, because a nonmonotonic relation previously has been demonstrated between shock intensity and magnitude of potentiated startle with more CS-US pairings (Davis & Astrachan, 1978; Leaton & Borszcz, 1985).

Method

Subjects

Sixty experimentally naive rats were used.

Procedure

The matching, training, and testing procedures, as well as the apparatus, were identical to those used in Experiment 1A. Five different groups of animals received either five presentations of the light alone ($n = 10$) or paired presentations of the light and footshock using shock intensities of either 0.4, 0.6, 1.0, or 1.2 mA ($n = 10$, in each group). The animals were tested 7 days after training. Two additional groups of animals ($n = 5$, in each group) trained with shock intensities of either 0.4 or 1.0 mA were given 5 consecutive days of exposure to the testing context (30 min/day) prior to testing.

Results and Discussion

No reliable effect of the three different light-noise intervals was found [$F(2,90) = 0.76$]. Subsequent analyses and data presentation were therefore performed on the average of the three light-noise intervals. The effect of varying the shock intensity is shown in Figure 3. The two-way ANOVA on trial type and group (different shock intensities) found a reliable group difference in startle amplitude [$F(4,45) = 3.52$, $p < .05$]. The pattern of startle amplitudes seen in Figure 3 suggest that startle amplitude was nonmonotonically related to shock intensity. To evaluate this, the matching score for each rat was subtracted from the mean startle amplitude on the initial 10 noise bursts. The mean change scores ($\pm SEM$) were -7.9 (8.5), 23.3 (7.2), 38.2 (13.9), 48.4 (15.0), and 34.7 (7.7), for the 0.0-, 0.4-, 0.6-, 1.0-, and 1.2-mA groups, respectively. These change scores were significantly different across groups [$F(4,45) = 3.91$, $p < .01$] and

Figure 2. Mean amplitude startle on the noise-alone and light-noise test trials and difference scores ($\pm$ SEM) of rats exposed to five light-shock pairings tested at various retention intervals.

were related both linearly [$F(1,45) = 10.15, p < .01$] and quadratically [$F(1,45) = 5.32, p < .05$] to the shock intensity used in training. The initial two-way ANOVA further revealed a reliable group $\times$ trial type interaction, indicating different levels of potentiated startle across groups [$F(4,45) = 2.81, p < .05$]. The results presented in Figure 3 suggest that the magnitude of potentiated startle was also nonmonotonically related to the shock intensity used in training and a quadratic trend on the difference scores was statistically reliable [$F(1,45) = 8.92, p < .01$], provided the light-alone group was used in the analysis. Furthermore, t tests on each group found that only the 0.6- and 1.0-mA shock groups showed signifi-

cant potentiated startle [$t(9) = 3.51$ and 4.67 , respectively; $ps < .01$].

The enhancement of the startle reflex during the initial 10 noise bursts was linearly and quadratically related to the training shock intensity, suggesting that some cues common to both the training and the testing apparatus may gain excitatory strength and be responsible for the observed modification of startle. To test this hypothesis, two additional groups were trained and then tested following 5 consecutive days of exposure to the test context, which is a procedure known to reduce the excitatory value of contextual cues (Bouton & Bolles, 1979; Bouton & King, 1983). The data of the extinguished animals were com-

Figure 3. Mean amplitude startle on the noise-alone and light-noise test trials and difference scores ($\pm$ SEM) of rats exposed to five lights only or to five light-shock pairings at various shock intensity.

Figure 4. Mean amplitude startle on the noise-alone and light-noise test trials and difference scores ($\pm$ SEM) of rats given five light-shock pairings with either 0.4- or 1.0-mA shock intensity and exposed or not exposed to the testing context for 5 days prior to testing. Note that the groups not exposed to the testing context are the same as those presented in Figure 3 at the corresponding training shock intensities, for comparison with the context-exposed animals.

pared with those of animals with a similar training history but not reintroduced to the test context prior to testing (see Figure 4). A two-way ANOVA on the difference scores with training shock intensity (0.4 vs. 1.0 mA) as a between-subjects variable and context manipulation (exposure vs. no exposure) as another between-subjects variable found no significant effect of shock intensity [$F(1,26) = 0.01$], context manipulation [$F(1,26) = 2.27$], or shock intensity $\times$ context manipulation interaction [$F(1,26) = 0.76$]. To better assess contextual effects, an additional two-way ANOVA on the change score means obtained by subtracting each animal's matching score from its mean startle amplitude during the initial 10 noise bursts was performed, with the same variables used in the analysis of the difference scores. The mean change scores ($\pm$ SEM) were 23.3 (7.2), 21.2 (10.1), 48.4 (15.0), and 56.2 (21.3), for the 0.4-mA not-exposed group, the 0.4-mA exposed group, the 1.0-mA not-exposed group, and the 1.0-mA exposed group, respectively. This analysis revealed a significant effect of shock intensity [$F(1,26) = 4.36$, $p < .05$] but, importantly, no reliable context manipulation effect [$F(1,26) = 0.04$] or shock intensity $\times$ context manipulation interaction [$F(1,26) = 0.12$]. These results indicate that the exposure manipulation prior to testing did not affect either the magnitude of potentiated startle or the enhancement of baseline startle produced by the prior shock experience in the training context.

GENERAL DISCUSSION

Fear-potentiated startle was reliably produced when five pairings of a light and footshock were presented at 2-min intervals. No potentiation was found with unpaired presentations of light and footshock (Experiment 1A) or following exposure to lights alone (Experiment 2), consistent with previous data using a larger number of light-footshock pairings and with the suggestion that the effect is associative. The magnitude of potentiated startle was comparable at all the retention intervals tested from 1 to 28 days. In general, potentiated startle was best using a 0.6-mA footshock. Increasing or reducing the footshock intensity during training did not increase the magnitude of startle potentiation. Instead, there was an overall nonmonotonic increase in startle amplitude, as revealed by the differences on the light-noise versus noise-alone trials as a function of shock intensity. In addition, the mean startle amplitude on the initial 10 noise bursts also showed a nonmonotonic relationship to shock intensity. Interestingly, however, this effect was not generally observed in studies using many more training trials (e.g., Davis & Astrachan, 1978; Leaton & Borszcz, 1985).

The nonmonotonic increase in startle amplitude may reflect a general sensitizing effect of footshocks or the development of fear to contextual cues common to the training and testing situations. If conditioning to the train-

ing contextual cues generalizes to the testing contextual cues, then procedures known to extinguish such conditioning should, at least, have attenuated startle enhancement. Five days of exposure to the testing context following training with 0.4- or 1.0-mA shock intensities did not significantly reduce the increase in startle amplitude on the 10 initial noise bursts. It should be noted that these initial startle stimuli are the best estimate of fear to contextual cues because, at the beginning of testing, no CSs have yet been presented. The lack of effect observed is surprising because it has repeatedly been demonstrated that 5 days of context exposure (extinction) significantly reduce the sensitizing effect of initial acoustic startle stimuli in naive rats (Borszcz, Cranney, & Leaton, 1989) or the excitatory value of contextual cues after conditioning with footshocks (Bouton & Bolles, 1979; Bouton & King, 1983; see also Lovibond, Preston, & Mackintosh, 1984). It is possible that more than 5 days of exposure or extinction of the *training* context would have produced a different outcome. Therefore, it is still not clear whether the nonmonotonic startle amplitude increase in relation to shock intensity results from fear to situational cues or a more general nonassociative sensitization effect.

In addition to causing a change in baseline startle amplitude, there was some evidence for a nonmonotonic relationship between the absolute magnitude of potentiated startle and the intensity of shock used in training. These results cannot simply be accounted for by a general increase in startle amplitude because, at the highest shock intensity (1.2 mA), startle was lower than it was in groups trained with 0.6 and 1.0 mA. Moreover, in studies using many more training trials, elevation of startle amplitude in the absence of the CS is generally not observed (Davis & Astrachan, 1978; Leaton & Borszcz, 1985). Together, these results indicate that, at moderate shock intensities, increasing the number of training trials may elevate the absolute magnitude of potentiated startle by reducing the amplitude of the startle reflex in the absence of the CS (e.g., Davis & Astrachan, 1978; Leaton & Borszcz, 1985; see also Davis et al., 1989). These observations are reminiscent of one of the predictions of the Rescorla and Wagner (1972) theory of Pavlovian conditioning, in which the excitatory value of contextual cues is assumed to decrease (relative to that of explicit CSs) when the number of training trials increases. However, with higher shock intensities, a relatively low magnitude of potentiated startle prevails when five or 20–30 training trials are employed (Davis & Astrachan, 1978; Leaton & Borszcz, 1985). This outcome is not expected from the Rescorla and Wagner model of conditioning. Moreover, this effect is not restricted to the potentiated startle paradigm; freezing has also been reported to be nonmonotonically related to shock intensity with three (see Fanselow, 1984, Experiment 3) or 30 training trials (Leaton & Borszcz, 1985; see also the results of Sigmundi, Bouton, & Bolles, 1980, with a light CS). Additional studies have reported nonmonotonic relationships between shock intensity and

shuttlebox avoidance (Levine, 1966; Moyer & Korn, 1964).

The above observations do not readily distinguish between the interpretation that startle and some other measures are nonmonotonically related to fear or the alternative interpretation that fear is nonmonotonically related to shock intensity. However, studies assessing conditioned fear with the CER and other studies using escape and avoidance measures have usually found monotonic relationships between the number of training trials or shock intensity and the measure of fear (Annau & Kamin, 1961; Brophy & Tremblay, 1971; Estes & Skinner, 1941; Goldstein, 1960; Kamin & Brimer, 1963; W. R. McAllister & D. E. McAllister, 1962). It therefore appears that potentiated startle is nonmonotonically related to *fear* per se. Additional data may support the interpretation that startle is nonmonotonically related to fear. For instance, Davis and Astrachan (1978) observed that animals trained with high shock intensity show higher potentiated startle in the course of extinction, relative to animals trained with moderate shock intensity (however, see Leaton & Borszcz, 1985). In addition, animals trained with high shock intensity and treated with a mild stressor shortly before testing show high levels of startle potentiation, relative to animals not stressed before the potentiated startle test (Melia, Liang, Miserendino, & Davis, 1989). These observations suggest that animals trained with high shock intensities can exhibit high levels of fear, but their test performance is normally inhibited, thereby masking the excitatory effects of CSs. These observations, taken collectively, may imply that an additional and qualitatively different conditioning process that inhibits the expression of some behavioral indices of fear may be engaged by high training shock intensities. The relationship between this inhibitory mechanism and other inhibitory processes documented in the learning literature is not known (e.g., Pavlov, 1928; see also Rescorla, 1985; Wagner & Rescorla, 1972). In view of the above results, it might be informative to reexamine some of the response systems used to assess fear conditioning in relation to the effects produced by both shock intensity and the amount of training.

Finally, the magnitude of potentiated startle was essentially identical at all the training-to-testing intervals ranging from 1 to 28 days. These results are consistent with previous studies using a CER task, in which four CS-US pairings were sufficient to produce reliable CER 24 h and 90 days after training (Gleitman & Holmes, 1967) and in which a single CS-US pairing produced reliable CER 29 days after training (Shurtleff & Ayres, 1981). However, the present results contrast with some literature using avoidance measures as an index of fear conditioning, in which animals show poor performance after only a few days (D. E. McAllister & W. R. McAllister, 1968; Quartermain & Judge, 1983; Quartermain & Jung, 1988; Spear et al., 1980). The relative permanence of potentiated startle in the present study may indicate rela-

tively strong conditioned fear generated with relatively few training trials. These results also suggest that potentiated startle is more similar to CER tasks than it is to avoidance measures of fear, when used as an index of aversive memories produced with moderate shock intensities.

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