Shock sensitization of startle: learned or unlearned fear?

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Abstract

Following shock, rats exhibit a potentiated startle response to a sudden, loud noise. It has been suggested that this shock sensitization of the startle response can be used as a model preparation for studying unlearned fear. After reviewing the theoretical and empirical bases for this claim, the results of several recent studies that show that the shock sensitization of startle effect is actually mediated by contextually conditioned fear are presented. From this, it is concluded that the shock sensitization of startle procedure is an appropriate model preparation for studying contextual conditioning but is not an appropriate procedure for studying unlearned fear. Several other procedures that have potential as model preparations for studying unlearned fear are discussed briefly. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction.

Anxiety disorders are among the most prevalent psychological disturbance in the industrialized countries, with between 10 and 30% of the population suffering from one at some point in their life. Because of this, there has been a long-standing interest in the experimental examination of the emotional state of fear. The hope is that by gaining a better understanding of this emotion more effective treatment programs for those individuals who suffer from anxiety disorders and phobias will be developed. In this effort, a number of different model preparations have been used for studying the emotional state of fear, but perhaps the most productive model preparation in the analysis of fear at a behavioral, pharmacological, and neural level has been the potentiated startle procedure.

1.1. The startle probe procedure

Presentation of an intense, unexpected stimulus (usually a noise, but in some cases a light flash or tactile stimulus) elicits an unconditioned startle response. This response has been documented in many species [7], and consists of a rapid contraction of the skeletal muscles, especially those around the face and head. In studies with human subjects, the eyeblink is typically taken as the index of the startle response [27,28] while in studies with rats, the whole body jump is usually taken as the index of the startle response [10].

Although the startle response is an unconditioned reaction to sudden, unexpected environmental stimulation, it can be modified by the animal’s emotional state. That is, the startle response to a particular stimulus is enhanced, or potentiated, when the animal is experiencing fear. This fear-potentiation of startle was first experimentally documented by Brown et al. [5]. Specifically, Brown et al. [5] showed that rats exhibited a larger startle reaction to a loud noise when a visual conditioned stimulus (CS) that had been previously paired with a shock unconditioned stimulus (US) was present than when it was absent. This effect has been replicated in numerous laboratories around the world (e.g. [11,26,35]), and the larger magnitude startle response in the presence of an aversive CS is usually attributed to the CS eliciting a central state of fear. This emotional state causes an enhancement in subsequently elicited defensive responses like the startle response.
It is undoubtedly the case that the widespread acceptance of the fear potentiated startle (FPS) procedure is largely the result of the persistent, and innovative, use of this technique by Davis and his colleagues over the past 25 or so years. Indeed this research group has provided the most systematic analysis of the FPS procedure to date, and are responsible for substantially increasing our understanding of the pharmacological and neural mechanisms of fear (for reviews see [8,10,11]). The vast majority of the studies with the FPS procedure, especially those with nonhuman animal subjects, have focused on learned fear. That is, subjects are first given repeated pairings of some neutral stimulus (a light; the CS) with an aversive stimulus (shock; the US). Then, during a subsequent test session, a startle-eliciting stimulus is repeatedly presented. On some test trials, the CS is also presented while on others it is not (i.e. only the startle-eliciting stimulus is presented on these latter trials). As described above, the typical finding is that the startle response is larger on those trials where the CS is present than on those trials where it is absent, and this effect is usually attributed to the CS eliciting a central state of fear that potentiates defensive responses.

2. Shock sensitization of startle

About 10 years ago, Davis and coworkers introduced a new procedure for studying fear potentiation of startle in rats, one that supposedly involves unlearned fear [4,9,20]. They termed this procedure ‘shock sensitization of startle’. Basically, shock sensitization of startle refers to a potentiation of the startle response in rats given a series of shocks compared to rats not given the shocks (this effect has also been demonstrated in humans [19]). In a typical experiment on shock sensitization of startle, rats are placed into the test cages and given several baseline startle trials. That is, their average response to a startle-eliciting stimulus is measured. One group then receives a series of shocks while the other group does not. Immediately following this, the startle response is again measured in all rats. The shocked rats exhibit a potentiated startle response relative to the non-shocked rats on the test trials.

In his initial demonstration of shock sensitization of startle, Davis [9] suggested that this effect was due to unlearned, rather than learned, fear. More specifically, it was suggested that this effect ‘may represent the unconditioned effect of shock that can become associated with a neutral stimulus to support classical fear conditioning’ [9], p. 502. That is, although there is substantial evidence that rats can acquire an association between the training context and shock (e.g. [25,32]), Davis [9] suggested that the immediate potentiation of startle following shock was a consequence of the unconditioned effects of the shock, rather than contextual conditioning. Indeed, Davis and his colleagues stated that: ‘This facilitatory effect is not easily attributed to rapid conditioning to the experimental context in which shocks are presented...’ [20], p. 509. Davis and his colleagues did not claim that contextual associations could not potentiate the startle response (for explicit demonstrations of context potentiated startle see [6,31]), but merely that the immediate potentiation of the startle response following shock was due, at least in part, to the unconditioned effects of the shock. If correct, this suggestion is important because it would mean that the shock sensitization procedure would provide a simple way in which to study unlearned fear. By comparing shock sensitization of startle with the more typical fear potentiation of startle produced by a discrete CS previously paired with shock, it would be possible to directly compare the neural and pharmacological bases of unlearned and learned fear. Such a comparison would be particularly valuable if unlearned fear has more in common with the general state of anxiety than does learned fear.

2.1. Theoretical basis for the suggestion that shock sensitization of startle is due to unlearned fear

A theoretical basis for the claim that shock sensitization of startle is due to unlearned fear can be derived from Wagner and Brandon’s [40] elegant AESOP model of Pavlovian conditioning. The AESOP model is an extension of Wagner’s [39] SOP model of conditioning, and explicitly considers the emotional consequences of a stimulus being represented in memory. In general, according to this theoretical approach, environmental stimuli are represented in memory by nodes. These nodes can be in either an inactive state, or one of two active states (A1 and A2). When a stimulus is physically presented, its node is activated to the A1 state. Over time, this representation decays to the A2 state of activity, and then, finally, into the inactive state. When a stimulus is represented in either the A1 or the A2 state of activity it is capable of eliciting specific behavioral responses and emotional reactions.

According to the AESOP model, the emotional state of fear is a consequence of shock being represented in the A2 state of activity. There are two distinct ways in which the shock node can be activated to the A2 state. First, physical administration of shock would cause the shock node to be activated to the A1 state, and then over time this representation would decay into the A2 state. Second, presentation of a CS that had been previously paired with the shock would result in the shock node being activated directly into the A2 state. That is, a signal for shock causes the shock node to be activated to the A2 state. Clearly, it is the first mechanism Davis and his colleagues had in mind when they
suggested that shock sensitization of startle is due to unlearned fear.

Although AESOP does provide a clear theoretical foundation for the suggestion that shock unconditionally elicits fear, there are other theoretical models of conditioning that suggest that shock does not unconditionally elicit fear. For example, according to the PDR model proposed by Bolles andFanselow [3], shock unconditionally elicits pain, and the emotional state of fear is elicited by stimuli (like CSs or contexts) that predict a painful stimulus. Fear, from the perspective of the PDR model, is a consequence of learning. That is, in order for fear to be elicited, the subject must encounter some stimulus that predicts the potential occurrence of a painful event. Thus, at present there is not a strong theoretical consensus on whether shock unconditionally elicits fear.

2.2. Empirical evidence for the suggestion that shock sensitization of startle is due to unlearned fear

Davis [9] reported the results of one experiment that were taken as evidence that shock sensitization of startle is due to unlearned, rather than learned, fear. In the shock sensitization procedure, the shocks are unsignalled. Therefore, the only learning that could occur in this situation would be between the context and the shock. Many studies have shown that rats are quite adept at learning context-shock associations [25,32]. To examine the potential influence of contextual conditioning on the shock sensitization of startle effect, Davis [9] employed the ‘context-shift’ procedure. Specifically, Davis altered the context between shock administration and test for some rats (i.e. the context change group) while keeping it the same for other rats (i.e. the context same group). If contextual conditioning is responsible for the shock sensitization of startle effect, then rats in the context change condition should exhibit less potentiation than rats in the context same condition. However, Davis found that rats in the context change condition exhibited as much shock sensitization of startle as did rats in the context same condition. From this, he concluded that contextual conditioning could not account for the shock sensitization of startle effect.

Although the results of the experiment by Davis [9] described above are exactly the sort of empirical evidence needed to support the claim that shock sensitization of startle is due to unlearned, rather than learned, fear, there is a potential problem with that experiment. Specifically, it failed to provide independent evidence that the rats detected the change in context. In any experiment where the context change manipulation is employed, a null effect is difficult to interpret without evidence that the subjects detected the change in context. Without such evidence, it is possible that the subjects treated the two contexts as being the same, even though the experimenter made some change(s) in the context. This possibility seems particularly likely in the experiment by Davis because the context change employed in that experiment involved merely turning off the house lights in the test chamber. There were no changes in the auditory, olfactory, or tactile components of the contexts. Thus, the ‘different’ context was in fact the context where shock had been given, only the lights had been turned off. Such a change in context may not be especially salient to rats, given their reliance on olfactory and tactile information in comparison to visual information. Because of this issue, we set out to more thoroughly examine the role of contextual conditioning in the shock sensitization of startle effect.

3. The role of contextual conditioning in the shock sensitization of startle

If shock sensitization of startle is mediated by unlearned fear, then manipulations designed to reduce the amount of contextual conditioning produced by the shock should not alter the magnitude of the sensitization effect. That is, shocked rats should exhibit the sensitization of startle effect whether they learn about the context or not. We explored this issue in the two experiments described below.

3.1. Effects of context change on the shock sensitization of startle

As described above, Davis [9] reported the results of one experiment that examined the effects of a context change on the shock sensitization of startle effect. No effect of context change on the shock sensitization effect was found, but that experiment involved only turning out the house light in the experimental chamber. In the present experiment, we examined the effect of context change on the shock sensitization of startle effect after making a more dramatic change in the context. That is, we shocked rats in either the startle chamber (where testing occurred) or in a completely different chamber that was located in a separate room. This different chamber was much larger than the startle cage, and was housed in a room that had a different auditory background, illumination level, and odor cues than the room where the startle cage was housed (for more details see [33]). Because the rats in both conditions received the same shock, only in different places, they should all exhibit the shock sensitization of startle if it is indeed due to unlearned fear. On the other hand, if shock sensitization of startle is due to learned fear, and the changes in context are detected by the rats, then only those rats tested in the context in which they were shocked should exhibit the sensitization effect.
In this experiment, there were three groups of rats. All groups were placed into the startle cage and given four baseline startle trials. Rats in two of the groups were shocked following the baseline trials while those in a control group were not (i.e. no shock control). Rats in one of the two shocked groups (the shock same group) were shocked in the startle cages (where they would be tested) while rats in the other shocked group (the shock diff group) were shocked in a different context. The same shock was given to both of these latter two groups, and the time between shock and test was the same. Furthermore, the level of handling and the amount of exposure to various contexts were equivalent for all three groups; these groups differed only on whether they were shocked or not and where they received that shock. At test, the startle response to a loud noise was measured for 80 trials in all rats. The average response on these test trials was compared to the rat’s baseline level of startle responding. From the results shown in Fig. 1, it is clear that rats in the Shock same condition exhibited a marked shock sensitization of startle effect. That is, the magnitude of the startle response following the shock was enhanced relative to the baseline level of responding. Further, and most importantly, rats in the shock diff condition responded just like rats in the no shock control group. That is, rats in both of these conditions exhibited a slight, and comparable, increase in startle responding during test that was statistically smaller than that shown by the rats in the shock same group.

The results of this experiment show that the shock sensitization of startle effect is only observed in rats shocked in the test context. Rats given a comparable series of shocks, but in a different context, responded like rats in the no shock control group. These results suggest that the context manipulation made by Davis [9] was not detected by the rats in his experiment. If a sufficiently large change in context is made, rats shocked in a different context respond like rats in a no shock control group. These findings suggest that shock sensitization of startle is mediated by contextual conditioning.

### 3.2. Effects of context pre-exposure on shock sensitization of startle

To continue our examination of the role of contextual conditioning in the shock sensitization of startle effect, we next did an experiment that involved context pre-exposure. That is, some rats were pre-exposed to the context in which they would be shocked and tested while other rats were pre-exposed to an irrelevant context. Exposure to a stimulus before pairing that stimulus with shock has been shown to reduce the level of conditioning to this stimulus, an effect referred to as latent inhibition [23,29]. Such an effect has been found for contextual cues as well as discrete cues. For example, Kiernan and Westbrook [23] reported that conditioned freezing to a shocked context was less in rats given 20 min of exposure to the context on each of 4 days before shock compared with rats that had not been exposed to the context prior to being shocked there. From this, one would predict that if contextual conditioning mediates the shock sensitization of startle effect, then rats pre-exposed to the startle cage, where shock and test subsequently occur, will exhibit less of a sensitization effect than rats not pre-exposed to the startle cage. This prediction was explicitly tested in the experiment described below.

We tested four groups of rats in this experiment. Rats in two groups were placed in the startle cage for 20 min on each of 4 successive days. No shocks or startle-eliciting stimuli were presented during these four pre-exposure sessions. Rats in two additional groups were placed in plastic white buckets for 20 min on each of these 4 days (for more details see [33]). Following this, all rats were placed in the startle cages and given four baseline startle trials. Half of the rats in each pre-exposure condition were then given a series of shocks (i.e. groups shock-no pre and shock-pre) while the remaining rats in each condition were not shocked (i.e. groups no shock-no pre and no shock-pre). All rats then received a series of test trials where an acoustic startle stimulus was presented. The average response on these test trials was compared to the rat’s baseline startle response in order to determine the degree of shock sensitization. The results are shown in Fig. 2. A pronounced shock sensitization effect was observed in
3.2.1. Other empirical evidence that shock sensitization of startle is mediated by learned, rather than unlearned, fear

The two experiments described above explicitly tested the idea that the shock sensitization of startle effect is mediated by contextual conditioning. The results of both experiments show that the sensitization effect is not a result of unlearned fear. The results of other studies provide suggestive evidence in support of this conclusion. For example, Kiernan et al. [24] examined shock sensitization of startle in rats shocked either immediately after they had been placed in the startle cage or after a 60-s delay. The rats shocked 60 s after being placed in the startle cage exhibited a marked sensitization of the startle response, but the rats shocked immediately after being placed in the startle cage failed to exhibit the shock sensitization effect. Importantly, rats given a shock immediately after being placed in a novel context also fail to freeze when returned to that context, an effect referred to as the immediate shock freezing deficit [15]. Fanselow [14] suggested that rats given an immediate shock fail to acquire fear of the context because they do not have sufficient time to form a representation of the context to associate with the shock (however, see [1]).

One interpretation of the results reported by Kiernan et al. [24] is that rats given a shock immediately after being placed in the startle cage fail to exhibit sensitization of the startle response because these rats fail to acquire fear of the context. However, as Kiernan et al. noted, it is also possible to interpret these findings as being due to the immediate shock not being processed as fully as the delayed shock. In other words, the immediate shock may not be as effective as the delayed shock in activating the shock node into the A1 state. Thus, the A2 representation of the shock node, which is responsible for the state of fear, would also be less for the rats in the immediate shock condition. This would result in less sensitization of the startle response in the immediate shock rats. Although this is a possible interpretation for the results reported by Kiernan et al., it does not account for the results reported by Richardson and Elsayed [33] that are described above. That is, in both the context change and the latent inhibition experiment, shock was given after a 3-min delay for all rats.

Another recent study that provides suggestive evidence that shock sensitization of startle is mediated by learned, rather than unlearned, fear comes from Davis’ laboratory. Specifically, McNish and Davis [30] reported several experiments that examined olfactory bulbectomy as a possible model preparation for studying depression. In some of these experiments, McNish and Davis used the shock sensitization of startle procedure. Of importance to the present argument was the finding that both sham-operated and unoperated control rats in that study failed to exhibit shock sensitization of startle even though the experimental procedures were those used by Davis [9] to first document the shock sensitization effect. In discussing this, McNish and Davis [30] noted that there was one critical difference in their procedure compared to those used by Davis [9]. Specifically, the rats in the study by Davis were naive with respect to the startle cage while those used by McNish and Davis had been repeatedly exposed to that cage (to measure baseline startle responding over several days) prior to being tested for shock sensitization of startle. This procedure could, as McNish and Davis [30] pointed out, have latentely inhibited the context conditioning normally produced by the shock. The experiment by Richardson and Elsayed [33] on latent inhibition and shock sensitization described above provides explicit support for this suggestion.

Finally, several studies have examined the neural bases of the shock sensitization of startle effect. It has been shown that lesions of the central nucleus of the amygdala [20] or of the central gray [16] block the shock sensitization of startle effect. Lesions of these structures, however, also block conditioned freezing to a context [25]. Therefore, these lesion studies suggest that the neural bases of the shock sensitization of

![Figure 2](image_url)
startle effect may be the same as that for contextual conditioning.

4. The ontogeny of the shock sensitization of startle effect

It has been reported that preweanling rats exhibit less contextual fear than older rats [37], and therefore, one might predict that preweanling rats would exhibit a smaller shock sensitization of startle effect than older rats. It is important, however, to distinguish between short- and long-term contextual fear in the developing rat. That is, although preweanling rats appear to be deficient in comparison to older rats in terms of long-term contextual fear, they do not appear to be deficient in terms of short-term contextual fear. Specifically, Rudy [36] reported that 18- and 23-day-old rats exhibited different levels of long-term (i.e. 24-h retention interval) contextual fear, with the older rats exhibiting more, but did not differ in levels of short-term contextual fear when tested immediately after the shock. Because the shock sensitization of startle effect involves short-term contextual fear, one might then predict that preweanling rats would exhibit the sensitization effect to the same extent as older rats.

We recently examined the ontogeny of the shock sensitization of startle effect [34]. Using the same general procedures as were used in our context change and latent inhibition experiments (see above), we found that 75-day-old (i.e. adult) rats exhibited a pronounced shock sensitization effect but that 16-day-old rats did not (see left panel of Fig. 3). Indeed, at 16 days of age, shocked rats responded at test like non-shocked rats. In contrast to this result with the startle procedure, we also found that the shock procedure was very effective in producing contextual fear, as measured by freezing, at both 16 and 75 days of age (see right panel of Fig. 3). Indeed, there were no age differences in the level of conditioned freezing during the post-shock period.

These results show that even if shock sensitization of startle is mediated by contextually conditioned fear, it is not necessarily the case that all rats acquiring fear of the context will also exhibit the sensitization of startle effect. Furthermore, these results are strikingly similar to those previously reported with discrete CSs [22]. That is, rats exhibit conditioned freezing to a discrete CS at a younger age than they exhibit conditioned fear potentiation of startle to that same CS (see [21] for a more thorough review of this area of research). The results depicted in Fig. 3 could be evidence of this dissociation with contextual cues. One possible interpretation of these results is that the threshold for conditioned freezing is lower than that for conditioned fear potentiation of the startle response (see [31]). Another possible interpretation of these results is that the neural mechanisms involved in conditioned freezing mature at a younger age than do the mechanisms involved in potentiation of the startle response. Both of these interpretations are testable, and future research should directly investigate them.

5. Other models of unlearned fear

Given all the evidence reviewed above, it seems clear that the shock sensitization of startle effect is mediated by learned, rather than unlearned, fear. Therefore, this simple procedure is appropriate for studying contextually mediated learned fear, but is inappropriate for studying the neural and pharmacological bases of unlearned fear. Other procedures are required for this purpose. Because the startle probe procedure has been used so effectively to examine the neural and pharmacological bases...
of learned fear [8,11], it would seem reasonable to use this procedure to explore the neural and pharmacological bases of unlearned fear as well. In the final section of this paper, I briefly consider two potential models of unlearned fear.

5.1. Light potentiation of startle

Rats are nocturnal animals. Recently, Davis and his colleagues took advantage of this in a series of experiments on what they termed light potentiation of startle (LPS) [12,41]. Specifically, they reported that rats exhibited a potentiated startle response when tested in a brightly illuminated environment (70 or 700 footlamberts) compared with a dark or dim (0 or 8 footlamberts) environment. Interestingly, humans exhibit a larger startle response when tested in the dark [18]. The idea offered for the larger magnitude startle response in rats tested in the light and in humans tested in the dark is that these settings have an evolutionary history of being potentially dangerous. In other words, the LPS effect in rats is thought to be due to unconditioned fear being elicited by the bright light. The LPS effect is blocked by pre-test injection of buspirone, a clinically-used anxiolytic. Further, there appears to be a dissociation in the neural mechanisms responsible for the unconditioned LPS effect and the conditioned potentiation of the startle response produced by a light CS [41]. That is, infusion of an AMPA receptor antagonist into the central nucleus of the amygdala blocked conditioned fear potentiation of startle by a light CS but did not block the unconditioned LPS effect. Infusion of the AMPA antagonist into the bed nucleus of the stria terminalis, in contrast, blocked the unconditioned LPS effect but did not block the conditioned fear potentiation of startle produced by a light CS. From these data, it seems that the LPS effect in rats is indeed mediated by unlearned fear. Future research with this procedure should substantially increase our understanding of the neural and pharmacological bases of unlearned fear.

5.2. Predator odors

There is substantial evidence that predator odors elicit a variety of fear-like behaviors (e.g. freezing, hiding) in rats as well as various physiological responses (e.g. elevations in serum corticosterone levels) that are usually taken as indicative of fear-like states [2,13,17,42]. Although no one has yet systematically examined the effects of predator odors on the startle response, we have recently shown that a biologically-neutral odor (i.e. grape) previously paired with shock substantially enhances the startle response [35]. Further, this conditioned odor potentiation of startle effect is blocked by pre-test injections of diazepam [38]. Therefore, it should be possible to use predator odors and the startle probe procedure to explore the neural and pharmacological bases of unlearned fear.

There are several potential advantages of using predator odors in examining unlearned fear. First, these stimuli have obvious ecological validity. Second, conditioned fear responses occur at much younger ages to olfactory than to visual cues [21]. Therefore, unlearned fear responses to predator odors may emerge earlier in development than does the unlearned light potentiation of startle effect. Third, the test procedures used in our conditioned odor potentiation of startle experiments remove one potential confound that occurs in comparing LPS and conditioned FPS to a light CS. That is, as noted by Walker and Davis [41], the LPS effect involves a light stimulus that is continually present throughout testing while the light CS used in the conditioned FPS procedure is a discrete stimulus (on for only a few seconds each time). Therefore, findings of different neural structures being involved in these two situations may reflect differences in the neural bases of learned and unlearned fear, or they may reflect differences in the neural structures involved in the processing of long-versus short-duration stimuli. Because our conditioned odor CS is of a long duration, we would not have this interpretative difficulty when comparing startle potentiation produced by a conditioned odor or by an unconditioned odor. In any case, it would be very useful to have at least two different stimuli, preferably from different sensory modalities, for eliciting unlearned fear. At the least, this would permit us to test the generality of any conclusions reached.

6. Summary and conclusions

There has been an increasing interest in the past few years in developing model preparations for studying unlearned fear. Davis [9] proposed that shock sensitization of startle could be used for this purpose. Given the success that has been achieved in delineating the neural circuits of learned fear through the use of the startle probe procedure, it would appear reasonable to have a model preparation of unlearned fear that also involved the startle probe procedure. However, explicit empirical tests of the role of contextual conditioning in the shock sensitization procedure have shown that this effect is due to learned, rather than unlearned, fear. Fortunately, there are other potential model preparations for studying unlearned fear. Davis and his colleagues have documented an unconditioned potentiation of the startle response in rats tested in bright light. Further, in their initial studies of the neural bases of this effect, they have reported evidence suggesting that this effect is mediated by a different neural structure than that involved in learned fear potentiation of startle. These results are very promising, and support the possibility
that the neural bases of unlearned fear may be different from the neural bases of learned fear. Understanding these differences may be critical in our continued understanding of anxiety disorders and phobias in humans. A second potential model preparation for studying unlearned fear involves using predator odors. Although these odors have been shown to elicit a variety of fear-like behaviors, no one has yet examined them systematically in the startle probe procedure. However, if these odors do produce an unconditioned potentiation of the startle response, then they will provide a very useful procedure for studying the neural substrates of unlearned fear.

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