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Immediate Shock Deficit in Fear Conditioning: Effects of Shock Manipulations

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Pavlovian contextual fear conditioning occurs when an aversive unconditional stimulus (US), such as a footshock, is presented to a rat shortly after it is placed in an experimental context. Contextual fear conditioning does not occur when the shock is presented immediately upon placement of the rat in the novel chamber. In the present study, the authors report that increasing either the number of immediate shock sessions (Experiment 1) or the immediate shock duration (Experiment 2) did not reverse this deficit. However, immediate shock seems to sensitize subsequent context conditioning (Experiment 3). These findings suggest that the associative deficit produced by immediate shock is not related to the rat's ability to process the footshock US.

Keywords: context fear conditioning, immediate shock deficit, freezing, footshock, classical conditioning

Contextual fear conditioning is probably one of the simplest and most rapid procedures for producing associative learning. For example, through pairing of a context with a single, brief (0.75-s), and moderate (0.5-mA) unsignaled electric footshock, the context becomes capable of eliciting detectable conditional fear responses, that is, freezing in rats (e.g., Fanselow & Bolles, 1979). In a typical context-conditioning procedure, shock presentation is delayed for a few minutes after placement of the rat in the chamber (e.g., Fanselow, 1980). However, when the shock is presented simultaneously with the rat's placement in the chamber, no contextual fear conditioning is observed (Blanchard, Fukunaga, & Blanchard, 1976; Fanselow, 1986, 1990). This phenomenon has been termed the immediate shock deficit (ISD), and it appears to be caused by a deficiency in association formation between contextual stimuli and the shock (Fanselow, 1986, 1990; Landeira-Fernandez, 1996; Landeira-Fernandez, Fanselow, DeCola, & Kim, 1995).

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This associative deficit interpretation of the ISD is based on the fact that contextual stimuli paired with the immediate shock (IS) fail to produce several conditional responses besides freezing (e.g., passive avoidance; Kiernan, Westbrook, & Cranney, 1995), potentiation of the startle response (Kiernan et al., 1995; Young, Rabchenuk, Landeira-Fernandez, Helmstetter, & Leaton, 1990), conditional analgesia (Fanselow, Landeira-Fernandez, DeCola, & Kim, 1994), and defecation (Fanselow, 1986). Also, IS does not affect neuronal changes observed during conditioning, such as immediate early gene expression in the amygdala (Rosen, Fanselow, Young, Sitcoske, & Maren, 1998) or the temporary decrease in neurogenesis in the dentate gyrus of the hippocampus generally observed in traditional contextual fear conditioning (Pham, McEwan, Ledoux, & Nader, 2005).

Two possibilities can account for the failure to form a context–shock association with IS: One is based on the rat's failure to process the contextual stimuli prior to the shock (*context processing deficit*), and the other is based on the rat's inability to properly perceive the IS as an effective aversive stimulus (*unconditional stimulus* [US] *processing deficit*). Several results in the literature favor the former interpretation of the ISD (Fanselow, 1986, 1990; Kiernan & Cranney, 1992; Kiernan & Westbrook, 1993; Kiernan et al., 1995; Rudy, Barrientos, & O'Reilly, 2002). For example, the ISD tends to disappear as the interval between the exposure to the context and the occurrence of the shock increases (Fanselow, 1986, 1990; Kiernan & Westbrook, 1993; Westbrook, Good, & Kiernan, 1994). Moreover, preexposure to the contextual stimuli 24 hr prior to shock delivery reduces the delay necessary to produce context conditioning (Fanselow, 1990).

Therefore, it appears that two processes are involved during the processing of the contextual stimuli: one responsible for forming the contextual representation and the other responsible for retriev-

ing it before the shock (Fanselow, 1990). An elegant demonstration of these two independent processes was provided by Rudy and colleagues (Matus-Amat, Higgins, Barrientos, & Rudy, 2004), who showed that the ISD can be eliminated in rats that had context preexposure if they were presented with a retrieval cue associated with transport to the context just prior to an IS.

Alternatively, it is possible that the ISD is a consequence of difficulty in processing the shock US when it is presented in an immediate fashion. Support for this view comes from two sources. First, preexposure to the aversive stimuli alleviates the occurrence of the ISD (Fanselow, DeCola, & Young, 1993; Frankland et al., 2004). Second, increasing the intensity of the IS might reduce the ISD (Bevins, McPhee, Rauhut, & Ayres, 1997; Lattal & Abel, 2001). However, Kiernan and Cranney (1992) used a loud noise as a US and found that although this stimulus caused the same magnitude unconditional startle response whether it was presented immediately after placement in the chamber or after a short delay, context conditioning occurred only in the delayed condition. Thus, it is unclear whether US possessing plays a role in the ISD.

The purpose of the present study was to further examine the possibility that the ISD is due to a failure of the rat to properly process the electric shock when it is presented immediately. Two approaches were used to this end. In Experiment 1, the number of IS sessions was increased. In Experiments 2 and 3, the IS duration was extended. If the ISD is related to a defect in processing aversive stimuli, then the deficit should be alleviated by these manipulations that increased shock exposure.

Experiment 1

In this experiment, the prediction that the ISD is a product of incomplete processing of the shock was tested by exposing a group of rats to daily IS sessions for 5 days. The ISD has usually been demonstrated with a single trial. If IS affects the processing of the US, then a single trial might not be sufficient to foster conditioning. If this is the case, then increasing the number of trials might overcome the deficit. Conditioning in the IS group was compared with two other groups that received daily sessions of delayed shock (DS) or no-shock (NS) procedures for 5 days.

To further assess whether the five sessions of IS resulted in an undetectable context–shock association, we conducted a savings test. Savings tests are used to detect small amounts of associative learning to conditional stimuli (CSs) that are not sufficiently strong to produce a conditional response on their own. In this particular case, savings were used to detect whether rats exposed to multiple ISs had associative learning that was otherwise undetectable. Therefore, after the last IS session, all groups received four DS sessions. If the five IS sessions did in fact produce some amount of learning that was not detected during training, then the IS group should exhibit a faster acquisition curve than the NS group during the four DS sessions. Freezing served as the measure of context conditioning because this response is most commonly used to investigate the ISD. Freezing level is very sensitive to the severity of the shock, and it is differentially controlled by the contextual stimuli of the place where shock was presented (e.g., Fanselow, 1980).

Method

Subjects. Twenty-four naive male Long-Evans rats between 90 and 110 days old and weighing 450–550 g were used as subjects. They were born and raised in the University of California, Los Angeles, Department of Psychology colony room. Animals were individually housed in hanging stainless cages with ad libitum food and water. There was a 12:12-hr light–dark cycle, and subjects underwent fear conditioning during the light phase. Each rat was handled daily for 5 days before the start of the experiment; rats were transported in their home cages to a holding room next to the experimental room, and two experimenters handled the same rats throughout the experiment.

Apparatus. All experiments took place in four identical observation chambers (28 cm × 21 cm × 10.5 cm; Lafayette Instrument, North Lafayette, IN) that were placed inside of sound-attenuating chests. A white light bulb (1820 bayonet bulb, 28 V) that illuminated the chamber allowed the experimenter to observe and videotape the subject's behavior. A video camera was mounted in front of the observation chambers, and experimenters observed animals through a monitor placed outside of the experimental room. A ventilation fan attached to each chest supplied background noise (78 dB, A scale).

The floor of each chamber was composed of 18 stainless rods (4-mm diameter), spaced 1.5 cm center to center and wired to a shock generator and scrambler (Lafayette Instrument, North Lafayette, IN). A foot switch and a timer allowed the experimenter to present a 1-mA electric shock. Ammonium hydroxide solution (5%) was used to clean the chambers before and after each subject.

Procedure. Twenty-four rats were randomly assigned to three groups containing 8 subjects each. The experiment was composed of two phases. During the first phase, one group (IS) received 5 daily IS sessions. In each session, subjects were placed in the experimental chamber, and a 1-s 1-mA electrical shock was delivered as soon as the chamber's door was closed. Four minutes after the shock, subjects were returned to their home cage. The second group (DS) was exposed to 5 daily DS sessions. DS consisted of the presentation of the shock 2 min after subjects were placed in the experimental chamber. Two minutes after the shock, subjects were returned to their home cage. The third group (NS) was exposed to the experimental chamber for 4 min during each of the 5 days, but no shock was presented. The second phase started on the day after the last session of Phase 1. During this phase, all subjects were submitted to 4 daily DS sessions that were identical to the procedure of the DS group of the previous phase.

Subjects were tested in sets of 4. A time-sampling procedure was used to assess conditioning to the chamber during the 2 min that preceded the shock presentation of Phase 2. Every 8 s, a rat was observed, and freezing, defined as the absence of any visible movement of the body, head, and vibrissae except for movement necessary for respiration, was scored by a well-trained observer who was unaware of the experimental conditions.

Data analysis. Previous experiments dealing with IS have shown an absence of freezing when subjects are exposed to IS but not when they are exposed to DS (Fanselow, 1986, 1990). This implies no variance in the IS group as well as heterogeneity of between-group variance among different treatments. Therefore, nonparametric statistics were used to analyze the results in all the experiments presented here. The Kruskal–Wallis test was used to determine overall differences among groups, followed by the Mann–Whitney test for pairwise comparison.

Results

Figure 1 displays the median percentage of time spent freezing during the four sessions of the second phase. The freezing behavior of the IS group during the preshock period of the first session was zero, indicating that the previous five ISs did not produce any conditioning. In contrast, the DS group showed strong condition-

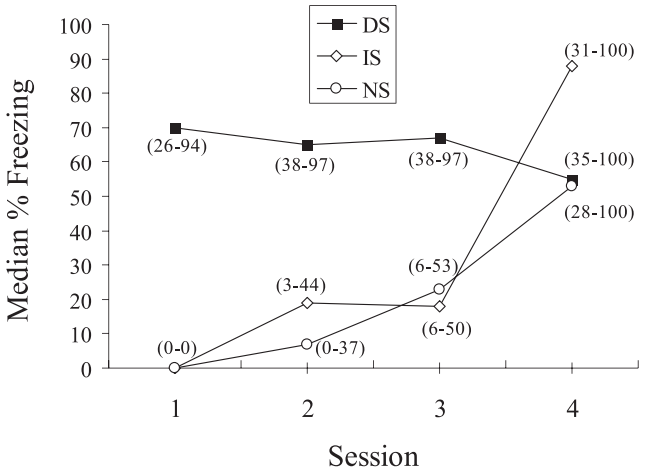

Figure 1. Median percentage of freezing during the delayed shock (DS) savings test across the four sessions of Experiment 1. During the first phase, rats received DS, immediate shock (IS), or no shock (NS). Numbers in parentheses represent the range (minimum and maximum) of each group.

ing during the first session of Phase 2, indicating that they acquired high levels of fear during the first phase. In fact, because the DS group showed no further increment in freezing during Phase 2, the five shocks of Phase 1 drove performance to asymptotic levels. On the other hand, IS and NS groups had the same acquisition curve during the four sessions of the second phase. This suggests that the five ISs presented during Phase 1 did not lead to any context conditioning that could be detected by the savings test of Phase 2.

These impressions are supported by statistical analysis. An overall difference among groups in the first three sessions, but not in the fourth, was found: Session 1, $H(2) = 21.82$, $p < .001$; Session 2, $H(2) = 9.24$, $p < .001$; Session 3, $H(2) = 5.8$, $p < .05$; Session 4, $H(2) = 4.17$, $p > .10$. Pairwise comparisons between the IS and NS among the first three sessions failed to show a reliable difference (all ps $>.10$). To evaluate the trend toward more freezing in the IS group on Session 4, we conducted a pairwise comparison of the IS and NS groups on Session 4, but it fell short of statistical significance ($U = 14$, $p > .05$).

Discussion

Experiment 1 increased the number of shock trials to determine whether the ISD is related to a possible deficit in processing the US. However, the five IS sessions produced absolutely no conditioning at all as indicated on the first trial of Phase 2. Furthermore, five ISs did not produce a savings effect when the rats were transferred to a DS procedure. Note that five trials of DS during Phase 1 were sufficient to bring conditioning among those rats to an asymptotic level of performance, yet this same number of IS trials produced no detectable acquisition. This finding speaks to the robustness of the ISD and makes an account in terms of reduced US processing unlikely. It is interesting to note that despite the fact that rats in the IS group remained in the context after the occurrence of the IS over the five IS sessions, no context conditioning was observed in the first session of the savings test. This indicated that context processing after the occurrence of the shock is not sufficient for context conditioning. This finding is similar to that with context preexposure (Fanselow, 1990). Preexposure to a chamber that is discontinuous with shock reduces the amount of time needed between placement in the chamber and shock that is necessary to support conditioning but cannot produce conditioning with IS unless a retrieval cue is provided (Fanselow, 1990; Matus-Amat et al., 2004).

The present results are also relevant to an interpretation of the IS in terms of a retrieval deficit. This notion stems from the finding that performance often reflects a failure in retrieval or expression rather than a failure of association formation (Spear, 1973). Cueing either prior to or concurrent with the retention test has been suggested as a valuable technique to discriminate between association and retrieval failure. The basic cueing procedure consists of exposing the subject to some components of the learning episode, such as the training context or the US before or during the retention test. The more features that resemble the original training occasion with which subjects are cued, the better the ability of the technique to detect a failure to retrieve acquired information (Spear, 1973). In this regard, the DS savings test incorporates all the features of IS experience, but the shocks are given in a manner that fosters strong performance. Therefore, it should provide a very strong assay of any information that was acquired during IS that subjects failed to retrieve. The failure of this savings test to detect an influence of the previous IS suggests that these rats did not form a context–shock association despite five immediate context–shock pairings. It also argues against any performance-based account of the ISD (Blanchard et al., 1976).

Experiment 2

In the second experiment, we adopted a different strategy to further investigate the idea that the ISD resulted from inadequate exposure to the shock. Instead of several IS sessions, the duration of a single IS was manipulated. Increasing the duration of the IS should increase the ability of the rats to process the aversive stimulus. The basic procedure consisted of a 3×2 factorial design. The first factor comprised the three intervals between placement in the chamber and shock termination (5, 10, and 20 s). The second factor determined whether the shock was presented as soon as the rat was placed in the experimental chamber and continued throughout the assigned interval (IS) or just during the last 3 s (DS) of the assigned interval.

The three different intervals of the present experiment were based on a previous study (Fanselow, 1986). In that study, it was found that rats exposed to a 3- or 7-s DS showed a complete ISD, whereas a context–shock interval of 17 s resulted in some context conditioning. Therefore, we expected a complete ISD in the 5- and 10-s DS groups, but the 20-s delayed group should exhibit appreciable context conditioning. Shock begins immediately upon placement in the chamber in all the IS subjects, so all these groups are IS groups.

The hypothesis that the ISD reflects a lack in processing the US predicts that the 10-s continuous shock group should display more context conditioning then the DS subjects assigned to the same interval. There is another comparison of interest. This is between the two groups trained at the 20-s interval. On the basis of previous results, the DS subjects should show some conditioning because they have 17 s of context exposure before shock presentation. The

continuous group had the same treatment except that the 17 s of shock-free time was filled with shock. If the immediate and continuous 20-s shock conditioning procedure produces more conditioning than the 20-s DS conditioning, then it would suggest that the shock exposure is the critical factor producing the ISD. However, if the continuous group freezes less than the delayed group, it suggests that the ISD is, at least in part, caused by shock interfering with processing of the context.

Method

Subjects and apparatus. Seventy-two naive male Long-Evans rats were used. They were housed and handled in the manner described above. The fear-conditioning apparatus was the same as in Experiment 1.

Procedure. The experiment was conducted in a series of two separate replications. The 72 rats were equally and randomly divided into six groups. Three of the six groups were exposed to a continuous electric shock of 5-, 10-, or 20-s duration. Rats were placed in the chamber, and the shock was delivered as soon as the chamber's door was closed. The other three groups were exposed to a 3-s shock, which occurred 2, 7, or 17 s after rats were placed in the experimental chamber. Thirty seconds after the delivery of the shock, all the rats were returned to their home cage. The next day, all the rats were placed in the same chamber where the shock was administered the day before for 4 min. No stimuli were presented during this test session, and behavior was videotaped and scored in the same way as in the previous experiment.

Results

Results of the two replications revealed the same patterns and thus were collapsed. Table 1 presents the median percentage of samples scored as freezing. The results are clear. None of the groups, with the exception of the group that received the 17-s DS, exhibited freezing during the 4-min testing period. A Kruskal–Wallis test indicated an overall difference, $H(5) = 30.47$, $p < .001$. A pairwise comparison between all six groups confirmed what is evident from the table. The 20-s delayed group showed reliably more conditioning than all the other groups (all ps $< .05$), which did not differ among them.

Discussion

The results of the DS groups replicate a previous study by Fanselow (1986). Rats shocked 3 or 7 s after placement in the chamber did not condition, whereas shock presented 17 s after the rats were exposed to the chamber produced a considerable amount of context conditioning. The novel result of this experiment is the fact that rats exposed to a continuous 5-, 10-, or 20-s IS still displayed the ISD. Clearly, this result argues against an account based on the assumption that the IS reflects a deficit in processing the IS.

Table 1
Median Percentage of Freezing in the Six Conditions of Experiment 2

	Interval (s)		
Nature of shock	5	10	20
Immediate	0.0%	0.0%	0.0%
Delayed	0.0%	0.0%	21.8%*

Note. Rats were exposed to an immediate or delayed shock according to a 5-, 10-, or 20-s exposure to the context. Rats in the immediate shock condition were exposed to the shock for the whole 5-, 10-, or 20-s interval. Rats in the delayed shock condition received a 3-s duration shock 2, 7, or 17 s after being placed in the experimental context. The asterisk indicates that this group was statistically different from all others.
* $p < .05$.

It is interesting to compare the two 20-s interval groups: These rats spent the same total time in the chamber, and both received at least 3 s of shock after being exposed to the chamber for 17 s. Despite this procedural similarity, the rats exposed to a 20-s continuous IS showed the ISD. This suggests that it is the onset of the shock with respect to placement in the chamber that is the critical variable; shock onset interferes with the rat's processing of the context stimuli.

Experiment 3

The previous two experiments suggest that the ISD does not involve a deficiency in processing the shock. If rats are capable of processing the IS, there should be some way of detecting the shock's effect on subsequent behavior. Because the IS procedure is not producing significant associative learning, one possibility is to look for a nonassociative effect of the IS. One relevant form of nonassociative learning is sensitization. Sensitization tends to be most apparent with a small number of presentations of stimuli that have a strong emotion-arousing content (Groves & Thompson, 1970). The IS procedure certainly meets these requirements for sensitization. If the IS causes sensitization, it may be detectable as enhanced conditioning to a DS that occurs after the IS.

An alternative account of these data is that some aspect of receiving IS prevents further processing of shock. This account predicts that an IS should actually reduce conditioning to a DS that was presented shortly after the IS. That is, it makes a prediction opposite to the sensitization account. Therefore, Experiment 3 tested these two possibilities.

This was accomplished by comparing a group that received an IS followed 17 s later by a second shock with a group that received just the 17-s DS. A third group received an IS 7 s after being exposed to the chamber and a second shock 7 s after the termination of the first shock. The interesting feature of this group is that these rats were exposed for 17 s to the context before the presentation of a shock, but a 7-s DS, which should not produce conditioning, was delivered in the middle of this interval. Again, if the IS disturbs the processing of contextual stimuli, then an absence of context conditioning is expected in this group. Finally, on the basis of the results of the previous experiment, we decided to have the 20-s continuous IS as a no-conditioning control group. This group received an equivalent amount of time in the context and substantial exposure to shock but in a manner that Experiment 2 showed does not produce significant context conditioning. Thus, this seems to be a conservative control with which to compare the other three groups.

Method

Subjects and apparatus. Forty-eight naive male Long-Evans rats served as subjects. Again, the subjects were similarly housed and handled, and the fear-conditioning apparatus was the same as previously described in Experiment 1.

Procedure. The experiment was carried out in two separate replications. The 48 rats were randomly divided into four groups, each one containing 12 rats. The first group (IMM) was exposed to a 20-s shock immediately after the rats were placed in the chamber. The second group (DEL) received a 3-s shock 17 s after being placed in the chamber. Rats in the third group (I/D) received a 3-s shock immediately after being placed in the chamber; 14 s after termination of this shock, another 3-s shock was delivered. The fourth group (D/D) received a 3-s shock 7 s after being placed in the chamber; 7 s after this shock, another 3-s shock was presented. Figure 2 presents a schematic diagram of this procedure. Thirty seconds after the last shock, all the rats were returned to their home cages. The next day, all rats were returned to the chamber for 4 min, and behavior was videotaped throughout the session. Freezing was scored in the same manner as in the previous experiments.

Results and Discussion

Figure 3 presents the median percentage of time rats spent freezing. A Kruskal–Wallis test revealed an overall difference among groups, $H(3) = 12.89$, $p < .004$. Pairwise comparisons indicated that the group exposed to the 20-s continuous immediate shock (IMM) was different from all the other groups (all ps $< .05$). There was a trend for the two groups (I/D and D/D) that received the two shocks to freeze more than the other groups. The pattern of the trend is more consistent with the sensitization alternative than the shock-processing account provided above. If IS interfered with processing of the DS, then the I/D group should have frozen less than the DEL group. As can be observed in the figure, this was not the case. The fact that the IS was not able to prevent future context conditioning is consistent with the work of Westbrook, Good, and Kiernan (1994), who found that an IS does not distract the rats from conditioning to a subsequent shock.

General Discussion

Conditional fear to contextual cues paired with shock assessed with freezing is a rapidly acquired conditional response that has become a mainstay in the analysis of associative learning and emotional behavior. That the same shocks that support this learning result in no freezing when shock occurs immediately upon placement in the chamber is a striking finding that has influenced much of the thinking about contextual fear learning (O'Reilly & Rudy, 2001). The current findings that this deficit is present even with multiple IS trials (Experiment 1) and when shock is very prolonged (Experiment 2) provide further evidence for the robustness of this phenomenon.

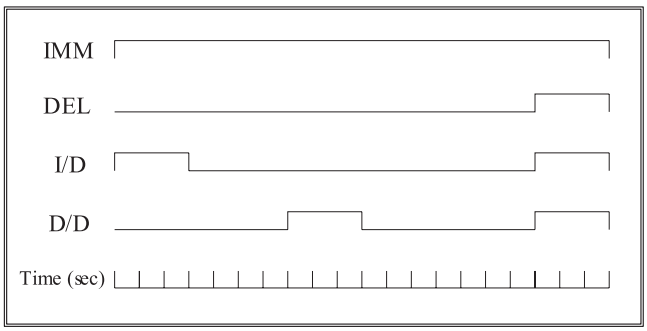

Figure 2. Schematic diagram representing the procedure of Experiment 3. Rats in the IMM group were exposed to an immediate shock for the entire 20 s. Rats in the DEL group received a 3-s shock 17 s after being placed in the experimental context. Rats in the I/D group received two shocks of 3-s duration. The first shock was immediate, and the second occurred 17 s after the rats were placed in the experimental context. Rats in the D/D group received two 3-s shocks 7 s and 17 s after being placed in the experimental context.

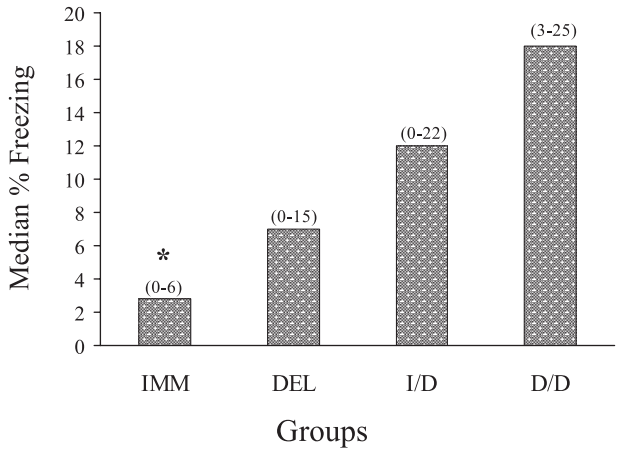

Figure 3. Median percentage of freezing in the four conditions of Experiment 3. The asterisk indicates that the IMM group froze less reliably than the other three groups (*$p < .05$). Numbers in parentheses represent the range (minimum and maximum) of each group.

Three general accounts of this deficit have been proffered: (a) It is a performance deficit that occurs because fear is expressed in a response other than freezing (e.g., escape); (b) it reflects an associative deficit that occurs because of a failure of shock (US) processing; and (c) it reflects an associative deficit that occurs because of a failure of context (CS) processing. We will discuss each of these in turn. In brief, the current findings provide strong evidence against the former two accounts. We will conclude with a description of how these and past results can be accommodated within a context-processing view.

Blanchard et al. (1976) provided the first account of the ISD in terms of a hypothetical defensive response hierarchy. They suggested that rats prefer to escape and freeze only if they learn that escape exits are unavailable. They suggested that a long enough preshock period provides time for rats to learn that such exits are not present. This learning leads to selection of the less preferred freezing response. With IS, there is no time to learn about the absence of an exit, and the rat chooses the preferred escape response. Blanchard et al.'s experiments provided no direct tests of this account, and no measures of alternate behaviors were provided. Fanselow (1986) tested this possibility more directly by manipulating the availability of exits and measuring behavior directed at those exits and could not find any evidence supporting the view that occurrence of freezing could be modulated by the presence or the absence of exits in the context where the shock was presented. Furthermore, a parallel deficit was detected in fear-induced defecation, which is not amenable to an account in terms of escape behavior. Therefore, Fanselow (1986) proposed an account in terms of context processing. The current data provide further evidence against performance-based accounts. Experiment

1 provided the rats with many opportunities to look for escape exits during each of the 4 min that followed the five ISs. This 4-min interval should have been adequate time to search for exits as the DS rats had just 2 min to look for exits in the DS condition. Indeed, the Blanchard et al. (1976) account suggests that the IS rats should have been highly motivated to search for these exits during the postshock period as such a search is the hypothesized reason for the ISD following shock. Therefore, it seems that a performance account of the ISD is inconsistent with the majority of the available data.

The ISD could result if rats fail to process the IS. Support for this view comes from two sources. First, increases in shock intensity can lead to more freezing in immediately shocked rats (Bevins et al., 1997; Lattal & Abel, 2001). The second line of evidence comes from Fanselow et al.'s (1994) report that exposure to shock prior to an IS can alleviate the ISD. Frankland et al. (2004) replicated this effect and suggested that shock preexposure helps the rat form a memorial representation of the shock, which is not adequately formed with IS. Here, we show that the IS is not attenuated by the use of multiple shocks or extremely long shocks. It seems unreasonable to assume that the rats trained under these conditions had no opportunity to process the shock. Indeed, Experiment 3 shows that the rats did process the IS to some extent, as it seemed to cause a nonassociative sensitization of learning provoked by a second shock. Despite this processing, IS did not support conditioning per se. Thus, it does not seem that the ISD results from a failure to process the US.

There is widespread support for the context-processing account of the ISD; this has been reviewed elsewhere (e.g., Fanselow, 2000; Rudy, Huff, & Matus-Amat, 2004). Therefore, we will not review that evidence here. Rather, we will try to show how changes in US intensity or shock preexposure may be integrated into a context-processing account of the ISD.

The first question is if the ISD reflects a contextual CS-processing deficit, why should increasing US intensity increase freezing? This can be best addressed by considering an analogy to a situation that unarguably reflects a reduction in the effectiveness of the CS. Less intense auditory CSs do not condition as well as more intense auditory CSs (Kamin & Schaub, 1963). If shock intensity is increased, fear to the weak CS will also increase (Sigmundi, Bouton, & Bolles, 1980), but no one would accept this as evidence that the difference between the weak- and intense-tone CSs was a US-processing deficit. In this regard, Lattal and Abel (2001) found that increasing shock intensity increased freezing in both the IS and DS mice. Furthermore, the absolute magnitude of the difference between the IS and DS groups was greater in the strong (3 mA) than in the weak (0.5 mA) groups. Thus, the data provided by Lattal and Abel (2001) are entirely consistent with a context-processing deficit.

The second question is why shock preexposure alleviates the ISD (Fanselow et al., 1994; Frankland et al., 2004). Fanselow et al (1994) suggested that shock has two opposing effects. One is the obvious ability to support conditioning to such CSs as tones, lights, and contexts. However, it also has the ability to temporarily disrupt context processing, and this is why massed unsignaled shocks support less context conditioning than do spaced unsignaled shocks (e.g., Fanselow et al., 1994; Fanselow & Tighe, 1988). In support of this, lesions of the dorsal periaqueductal gray, which attenuates the unconditional reaction to shock, reduce both the ISD and the deficit seen with massed shocks (Fanselow, DeCola, DeOca, & Landeira-Fernandez, 1995). Fanselow et al. (1994) further suggested that shock preexposure habituates the disruptive effects of the shock. Consistent with this hypothesis, Rau, DeCola, and Fanselow (2005) demonstrated that shock preexposure facilitates fear conditioning in a nonassociative manner. Experiment 2 provides very direct support for the disruptive effects of shock on context processing. Both the IS and the delayed 20-s shock groups spent an equal amount of time in the context (20 s). When more of this time was occupied by shock, less conditioning occurred. Shock is clearly disrupting context processing, and it does so in a manner that overwhelms any benefit that increased exposure to the long US offers. Thus, the ISD results from inadequate time to process the context (e.g., Fanselow, 1990, 2000), and the detrimental effects of shock exacerbate this context-processing deficit.

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