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Contextual Fear after Signalled versus Unsignalled Shocks: Effect of Extent of Prior Experience with Context and Signal

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In the first two experiments, rats were differentially familiarized with a discrete stimulus and/or a context prior to receiving either shocks signalled by that stimulus or unsignalled shocks in that context. As indexed by freezing, in none of the pre-exposure conditions did the signalled-shock rats consistently acquire less contextual fear than the unsignalled-shock animals. Both pre-exposure to the stimulus and relatively short pre-exposure to the future conditioning context resulted in more contextual fear in the signalled-shock than in the unsignalled-shock subjects. In a third experiment, freezing in the target conditioning context was especially enhanced in rats that had been familiarized with a stimulus, conditioned with the stimulus as a signal for shock, and subsequently further conditioned to the stimulus in a different, non-target context. The level of freezing to the stimulus in a neutral test context was positively related to the level of freezing in the target conditioning context in all experiments. These results were discussed in terms of context–shock, stimulus–shock, and context–stimulus associations.

In the literature on Pavlovian conditioning, there is disagreement as to whether the presence of a discrete Pavlovian signal or conditioned stimulus (CS) interferes with the formation of an association between static background stimuli and the unconditioned stimulus (US). The results of several studies indicate that the presence of a predictive, discrete CS during conditioning interferes with the acquisition of a direct context–US association (e.g., Fanselow, 1980; Odling-Smee, 1975a, 1975b, 1978a, 1978b). The

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outcome of these studies is consistent with formal models of associative learning that are based on the notion of associative competition between stimuli paired with a US (e.g. Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972).

However, other research suggests that learning about context proceeds independently from learning about discrete stimuli. That is, the presence or absence of a discrete stimulus has no effect whatsoever on the formation of a context-US association (e.g. Balsam & Gibbon, 1988; Williams, Frame, & LoLordo, 1992). These studies are in accordance with models of associative learning that assume that discrete stimulus-US and context-US associations are acquired independently (e.g. Gibbon & Balsam, 1981; Miller & Matzel, 1988).

Recently, Maes and Vossen (1993; Experiment 1) reported results that were interpreted as being consistent with a competitive account. One group of rats was pre-exposed to an auditory stimulus that was subsequently paired with a shock US. On reexposure to the conditioning context after the conditioning session, these rats showed more contextual fear than did a second group of animals that had not received non-reinforced preexposure to the auditory stimulus. This result is predicted by associative competition models if it is assumed that the stimulus preexposure resulted in a reduced saliency or associability of the auditory stimulus (latent inhibition [LI]; Lubow, 1973), so that it competed less with the contextual stimuli for association with the shock during the conditioning session than did the non-preexposed CS in the control group.

The purpose of our first experiment was to eliminate a shortcoming of the above-described experiment. There were no control groups that received the same treatment as the aforementioned two groups, except that the shocks were not signalled by the auditory stimulus. Thus, overshadowing was assumed, but not demonstrated. Such control groups permit an assessment of the level of context conditioning in the case of un signalled presentations of the US. Accordingly, they provide a “baseline” against which the effect on context conditioning of signalling the US by either a preexposed or a non-preexposed CS can be more directly assessed.

EXPERIMENT 1

Two groups of rats received a treatment that was similar to that received by the two groups in Maes and Vossen (1993; Experiment 1). Thus, one group was pre-exposed to a non-reinforced tone, prior to tone-shock pairings. The pre-exposure and conditioning phase occurred in one and the same context. A second group of animals received the same treatment as the first group, except that the tone was not presented during the pre-exposure phase. These two groups enabled us to determine whether the enhanced contextual freezing previously found in the group pre-exposed to tone could be replicated.

The present experiment also included two control groups that received exactly the same treatment as the first two groups, except that the shock USs were un signalled. Thus, one group was pre-exposed to the context and tone prior to receiving un signalled shocks; the other group was pre-exposed to only the context prior to receiving un signalled shocks. This design permits an additional comparison that bears on the notion of associative competition. Associative competition predicts that context conditioning would be
weaker in a group pre-exposed to context and then conditioned to tone in that context than in a group pre-exposed to context and then conditioned with the US alone in the context.

A comparison between the context-pre-exposed and the context-and-tone-pre-exposed groups also allows an examination of the viability of an alternative account of greater contextual fear in the context-and-tone-pre-exposed/context-and-tone-conditioned group than in the context-pre-exposed/context-and-tone-conditioned group. It might be that the presence of the tone during pre-exposure to the context in the context-and-tone-pre-exposed group attenuates LI of the context, thereby enhancing contextual freezing relative to the context-alone-pre-exposed group (e.g. Lubow, 1989). This effect should occur whether the tone was present during conditioning or not.

To complete the experimental design, which is summarized in the top part of Table 1, two additional control groups that were given neither pre-exposure to the context nor to the tone were included. One of these control groups subsequently received tone-signalled shocks, whereas the other group received unsignalled shocks. It is conceivable that pre-exposure to the context alone alters the observable effect of the discrete cue on conditioning to context, relative to a non-pre-exposure condition. For instance, context pre-exposure in the context-pre-exposure control groups might result in the contextual cues losing saliency or associability (LI of context). As a result, the level of contextual fear in the context-pre-exposed, unsignalled-shock group may turn out to be too low for an additional attenuation of fear due to overshadowing in the tone-signalled group to be detectable (floor effect). Inclusion of non-pre-exposed groups permits the assessment of the effect of a signal on context conditioning under conditions where such conditioning is not already attenuated by a possible LI effect.

Inclusion of a non-pre-exposed, signalled-shock control group also permits examination of the effect of a reduction of the saliency or associability of contextual cues on conditioning to a discrete CS in the presence of those cues. In Maes and Vossen (1993; Experiment 3), one group of animals was first exposed to Context 1 for an extended period of time. Subsequently, a tone was conditioned in that context. A second group received, instead, exposure to Context 2 prior to being conditioned to the tone in Context 1. During an unreinforced test session for responding to the tone in a novel Context 3, no difference was observed between the two groups. Hence, there did not seem to be a competitive relationship between context and signal; diminished conditioning to the context as a result of LI did not result in enhanced conditioning to the tone. However, it is possible that, because of generalization between Contexts 1 and 2, conditioning to the tone in the second group occurred against a background that had some generalized associative strength and thus itself overshadowed the tone. In the present experiment, the control group, against which the effect of prior experience of a context on the formation of a signal-US association is assessed, has no prior experience with the conditioning context or similar contexts.
Method

Subjects

The subjects were 60 naive male Sprague-Dawley rats obtained from Charles River, Canada. The animals had a mean weight of 332 g and were individually housed in wire-mesh hanging cages with *ad lib* food and water. The rats were maintained on a 16-h/8-h light/dark cycle, and all experimental
Manipulations were conducted during the light portion of the cycle. During the week prior to the start of the experiment, the animals were handled daily for approximately 1 min.

**Apparatus.**

Two distinctively different contexts were used. Two copies of Context X (dimensions: 23 × 16 × 24 cm) each had a back wall and two side walls made of aluminium. On one side wall, a jewelled light was mounted that was not used. The front wall and the ceiling were clear Plexiglas. The floor consisted of stainless-steel rods (diameter: 2 mm), spaced 1.9 cm apart. Through these rods, a 0.8-mA, 1-sec scrambled electric footshock US could be presented by a Grason-Stadler shock generator. The grids were cleaned with a water/ammonia solution after each rat’s session. A 7-kHz, 82-dB (C) tone could be presented through a speaker that hung on the ceiling of the experimental room at a distance of 1.3 m from the centre of the box. Context X was located in a room that was dimly illuminated by overhead lights. A 65-dB (C) masking noise was provided by a ventilation fan. A Panasonic WV-1550 low-light videocamera, positioned 1 m in front of Context X and connected to a Panasonic AG-2500 videorecorder, enabled recording of the animals’ behaviour on videotape. An auditory signal, presented once every 5 sec, was superimposed on the videotapes and paced the scoring of the rats’ behaviour (see Dependent Measure).

The other context, Context Y, measured 30 × 25 × 28 cm. The front and back walls were clear Plexiglas, and the two sides were aluminium. One side wall contained a recessed food tray and a jewelled light that were not used. The floor was composed of stainless-steel rods (diameter: 4 mm), spaced 1.9 cm centre-to-centre. The 7-kHz, 82-dB (C) tone could be presented through a speaker, just as in Context X. The speaker hung from the ceiling at approximately the same distance from the box as in the other context. A distinctive odour was provided by placing a piece of tissue scented with a 10% acetic acid solution between the two copies of Context Y. The boxes were housed in an experimental room different from that used for housing Context X. The room was illuminated by red overhead lights, and a ventilation fan provided a 65-dB (C) masking noise. The rats’ behaviour was videotaped as described for Context X. The experiment was controlled by an Apple IIe computer located in an adjoining room.

**Dependent Measure**

Once every 5 sec during specific periods of experimental sessions (see Results), the behaviour of each rat was scored as freezing or not freezing (time sampling). Freezing was defined as the absence of visible movement of the body and vibrissae, except for movement necessitated by respiration. The scoring of freezing by the primary observer was checked for reliability by a second observer, who was not informed of the purpose of the experiments. Across experiments, observers agreed on 92.1% of a total of 81,960 samples.

**Procedure**

The experiment was run in two replications, with 30 animals in each. The second replication started the day following termination of the first.

**Pre-exposure.** Six matched groups were formed (n = 10) on the basis of the animals’ weights. Groups XT−/XT+ and XT−/X+ (the part of the groups’ names preceding the slash refers to the pre-exposure condition; the second part designates the conditioning treatment) received a tone-pre-exposure session in Context X on each of 10 successive days. On each session, rats were individually
placed in Context X for 20 min and received 4 non-reinforced 30-sec tone presentations. The interstimulus interval (ISI) was quasi-random (mean: 226 sec). Group $X^{-}/XT^{+}$ and group $X^{-}/X^{+}$ were treated like groups $XT^{-}/XT^{+}$ and $XT^{-}/X^{+}$, expect that the tones were not presented in the first phase. The remaining groups, group $-/XT^{+}$ and group $-/X^{+}$, were handled in the same manner as the animals in the other groups, but they were pre-exposed neither to the tone nor to Context X.

**Conditioning and Testing in Context X.** All animals received two shocks on the day following the pre-exposure phase. For the animals of groups $XT^{-}/XT^{+}, X^{-}/XT^{+}$, and $-/XT^{+}$, each of these shocks was signalled by a 30-sec tone. The first tone was presented 120 sec after placement in Context X, and the shock was delivered in the last second of the tone presentation. The second tone–shock trial commenced 60 sec after the previous shock. The subject was removed from Context X 60 sec after the last shock. The rats in the remaining groups, groups $XT^{-}/X^{+}, X^{-}/X^{+}$, and $-/X^{+}$, received the same treatment as the other three groups', except that the tone was not presented.

One day after the first conditioning session, a test for contextual freezing was performed. Each rat was placed in Context X for 5 min, and no events were planned to occur during this session.

Because freezing levels were relatively low in some groups (see Results), it was decided to perform another conditioning session in order to allow group differences to occur. This session was performed one day after the non-reinforced Context X test session and was exactly like the first conditioning session. Then test sessions for contextual freezing just like the first one were performed on the next seven days.

**Exposure to Context Y and Test Tone in Y.** Finally, freezing in response to tone was assessed in a neutral Context Y. To eliminate any possible fear in Context Y caused by generalization from Context X to Context Y, all animals were simply placed in Context Y for 20 min on the day following testing in Context X. On the next day, four non-reinforced tone presentations occurred in Context Y. The mean ISI was 245 sec.

**Statistical Analyses**

Freezing scores of this and the following experiments were included in analyses of variance (ANOVAs), and analyses of covariance (ANCOVAs). All analyses were first conducted with the inclusion of a replication factor. In none of the analyses of the present and subsequent experiments did this factor reliably interact with the other factors. Therefore, for each of the analyses of the experiments reported in this paper, the replication factor was deleted from each model under investigation. Specific hypotheses about group differences in the tests for responding to Context X were examined using planned contrasts. Post-hoc comparisons were performed using the Newman–Keuls method. Interactions between main factors were further analysed using tests for simple main effects, with the error term and degrees of freedom based on the overall analysis (Winer, 1971). All statistical tests using a rejection criterion set at $p < 0.05$.

**Results**

Figure 1 shows the results of the tests for freezing in Context X. The different pre-exposure groups are depicted in separate panels. The figure indicates that the pattern of freezing observed during the first test day remained largely unchanged on subsequent test sessions. In the non-pre-exposed groups, group $-/X^{+}$ versus group $-/XT^{+}$, the
presence of the tone during conditioning attenuated freezing, whereas in the tone-and-context-pre-exposed groups, group XT−/X+ versus group XT−/XT+, the tone enhanced contextual freezing.

The data obtained during the first test session—that is, after two conditioning trials—were analysed separately from the data obtained on Tests 2–8, which were performed after each animal had received a total of 4 conditioning trials. Separate analyses of the first ten day's freezing scores permit a better comparison with the results of Experiment 2, in which the total number of conditioning trials was restricted to 2. Specific hypotheses involved the following comparisons. (1) Freezing was compared in the context-and-tone-pre-exposed/context-and-tone-conditioned group (group XT−/XT+) and the context-pre-exposed/context-and-tone-conditioned group (group X−/XT+) to examine whether the enhanced contextual freezing in the former found in Maes and Vossen (1993) would be replicated. A planned comparison revealed that group XT−/XT+ froze marginally significantly more than did group X−/XT+, $F(1, 54) = 3.82$, $p = 0.056$, thereby replicating the effect found in Maes and Vossen (1993). (2) Groups XT−/X+ and X−/X+ were compared to examine whether the presence of a tone during context pre-exposures attenuates the development of LI with respect to that context. The analysis revealed that the presentations of the tone during context-pre-exposure (XT−/X+) did not enhance contextual fear as compared to the group receiving only context pre-exposure (X−/X+). (3) Within each pre-exposure condition, the tone-signalled and unsignalled groups (−/X+ vs. −/XT+, X−/X+ vs. X−/XT+, and XT−/X+ vs. XT−/XT+) were compared to assess the effect of the tone in each of the pre-exposure conditions. The analyses revealed that in the non-pre-exposed subjects the presence of the tone during conditioning attenuated contextual freezing, $F(1, 54) = 4.73$; in the context-pre-exposed animals, the presence versus absence of the tone did not
make a reliable difference, and in the tone-and-context-pre-exposed rats, the presence of the tone during conditioning enhanced later contextual freezing, $F(1, 54) = 6.67$.

A Group $\times$ Session repeated-measures ANOVA using the freezing scores of Test Sessions 2–8 revealed a reliable main effect of group, $F(5, 54) = 4.46$, and of session, $F(6, 324) = 54.99$, as well as a significant interaction between the main effects, $F(30, 324) = 1.85$. The group main effect was examined further. The same planned comparisons as specified above were also used to evaluate the data of Test Sessions 2–8. None of the five comparisons revealed significant results, although the comparison between groups $\text{X}_- / \text{XT}^+$ and $\text{XT}^- / \text{XT}^+$ was again marginally significant, $F(1, 54) = 3.83, p = 0.056$. The Group $\times$ Session interaction was examined further by tests for simple main effects. There was a significant difference between groups on every test session except the second, $F(s)(5, 89) > 2.79$. Separate planned comparisons using the data of each of Sessions 2–8 revealed that on each of Sessions, 4, 5, 6, and 8, group $\text{XT}^- / \text{XT}^+$ froze more than did group $\text{X}^- / \text{XT}^+$, $F(s)(1, 54) > 4.10$, and on Session 7 the difference between these groups was marginally significant, $F(1, 54) = 3.83, p = 0.056$. Only on Session 3 did group $\text{X}^- / \text{X}^+$ freeze less than did group $\text{XT}^- / \text{X}^+$, $F(1, 54) = 5.00$.

Figure 2 depicts the mean percentages of observations that were scored as freezing for the various groups during the 30-sec periods prior to the tone presentations in Context Y (pre-CS freezing), and during the tone presentations in that context (CS freezing). The figure shows that responding during pre-CS periods was relatively low in all groups and that among groups conditioned to the tone, group $\text{X}^- / \text{XT}^+$ responded most to the tone, followed by group $\text{XT}^- / \text{XT}^+$; group $\text{XT}^- / \text{XT}^+$ responded least. A Group $\times$ Period (preCS/CS) repeated-measures ANOVA performed on these data revealed significant main effects for group, $F(5, 54) = 9.67$, and period, $F(1, 54) = 89.05$, and a significant Group $\times$ Period interaction, $F(5, 54) = 19.20$. The interaction was due to the effect of group being significant during CS periods, $F(5, 82) = 22.81$, but not during pre-CS periods. Furthermore, the difference between pre-CS and CS freezing was significant in all tone-conditioned groups, groups $\text{X}^- / \text{XT}^+$, $\text{X}^- / \text{XT}^+$, and $\text{XT}^- / \text{XT}^+$, $F(s)(1, 54) > 7.23$, but not in the remaining groups. In order to examine the difference between groups in responding to the tone, relative to their pre-CS responding, a difference score
was computed of the form: CS freezing score − pre-CS freezing score. Groups differed on this measure, $F(5, 54) = 19.20$, and Newman-Keuls tests revealed that within the context–pre-exposure and no-pre-exposure conditions, the tone-conditioned group responded more to the tone than did the unsignalled group, but that in the tone-and-context–pre-exposed groups this was not the case. Furthermore, group X− /XT+ had a higher difference score than did either groups − /XT+ or group XT− /XT+, and group − /XT+ had a reliably higher difference score than did group XT− /XT+.

The data of all three experiments reported in the present paper were analysed by ANCOVAs to examine the contribution of differences in freezing in response to the tone to the variance in contextual freezing. For Experiment 1, the results of the ANCOVA, with the percentage of observations scored as freezing during the tone presentations as a covariate, group as a factor, and contextual freezing on the first test day as the dependent variable, were as follows: The Group × Covariate interaction, which tests for different slopes of the regression line relating the tone-test scores to the first test-day scores in X in the different groups, was not significant. Deletion of the interaction from the model revealed a significant effect of the covariate, $F(1, 53) = 12.70$, as well as the group factor, $F(5, 53) = 6.82$. The significant covariate effect reflects the fact the tone-test scores significantly and positively contributed to the variance in freezing in Context X. For each of the tone-conditioned groups, there was a positive correlation between these two measures, mean $r = 0.50$.

Discussion

Experiment 1 replicated the enhanced contextual freezing observed in a group that was first pre-exposed to a tone and subsequently conditioned to that tone in the same context, relative to a group that was pre-exposed to only the context prior to tone conditioning. However, the results of the present experiment cannot simply be explained by referring to the notion that this enhanced contextual freezing was caused by a reduction in overshadowing of context by the tone in the tone–pre-exposed group, as was suggested by Maes and Vossen (1993). Contextual freezing in the context-and-tone–pre-exposed/context-and-tone–conditioned group, group XT− /XT+, was significantly enhanced relative to its own control group, group XT− /X+. If the tone–pre-exposure treatment only resulted in the tone competing less, or not competing at all, with the context for association with the shock, contextual freezing in group XT− /XT+ at maximum should have equalled that in group XT− /X+. Furthermore, overshadowing of context by the tone was absent in the context-only–pre-exposure condition, as indicated by the comparison of group X− /X+ with group X− /XT+. This indicates that, given the present parameters, there was no overshadowing of context by the tone to begin with that could be reduced in group XT− /XT+. The only sign of overshadowing of context by the discrete cue was in the non-pre-exposed animals, group − /XT+ versus − /X+, on the first test day in Context X.

An explanation for the enhanced contextual freezing in group XT− /XT+ solely in terms of a reduced LI of contextual cues is also found wanting. There was one indication that the presence of the tone during context pre-exposure attenuated LI of the context. Freezing in group X− /X+ was less than in group XT− /X+ during the third test session
in Context X. However, on all other Context X test sessions there was no such difference, whereas the difference between groups X−/XT+ and XT−/XT+ continued to be significant. In sum, it seems unlikely that the strong response-enhancing effect of the tone–re-exposures is solely due to the attenuation of LI with respect to the context.

In the present experiment, as well as in the following two experiments, the tone CS was consistently tested after tests for freezing to the conditioning context. One could argue that this potentially confounds obtaining a “pure” measure of the associative strength that this stimulus had acquired immediately after the conditioning phase. It may be that, apart from a direct CS–US association, freezing to the CS in the novel test context reflects the strength of a CS–conditioning–context association, and the strength of a conditioning-context–US-association (conditioning-context mediated CS freezing). However, although conditioning context-alone presentations could very well extinguish a context–US association, there is no reason to think that the context extinction manipulation during the context tests should alter the ordering of the groups on the strength of context–US association and, hence, on amount of CS freezing. In the present experiments, significant differences in CS freezing were obtained, despite test exposure to the conditioning context (see also further on).

An ANCOVA found that the level of freezing shown in response to the tone presented in a neutral context significantly and positively contributed to the level of freezing in the conditioning Context X. This positive relationship may simply reflect a general tendency to freeze as a specific trait of a given rat. Thus, for instance, an animal that shows a strong tendency to freeze to the tone after conditioning will also have a strong tendency to freeze in the conditioning context, and vice versa. Alternatively, or in addition to the foregoing, the positive relationship may reflect the potential of Context X during the test sessions to evoke a representation of the tone (context–tone association; see, e.g. Marlin, 1982; Miller, McCoy, Kelly, & Bardo, 1987; Rescorla, 1984; Williams and LoLordo, 1995). Hence, if, for some reason, conditioning to the tone had been particularly successful in a given subject, and/or the association between the context and the tone was strong (e.g. because of a tone–pre-exposure treatment), a strong freezing response was also evoked by the context in the absence of the tone. Experiment 3 further addresses the potential contribution of a context–tone association to group XT−/XT+’s enhanced contextual freezing.

A final point of interest is the enhanced conditioning to the tone in group X−/XT+ relative to group −/XT+. This result is contrary to that found in Maes and Vossen (1993), Experiment 3, in which the control group was pre-exposed to another context. It could, in principle, point to a competitive relationship between context and tone. Latent inhibition of the context could have reduced its saliency and, thereby, its ability to overshadow the tone during conditioning. In order to assess the generality of this phenomenon, a second, parametric, experiment was performed in which the extent of familiarization with the context prior to conditioning with or without the tone was systematically manipulated. This experiment also permitted further assessment of the overshadowing of context by tone.
EXPERIMENT 2

The results of the previous experiment suggest that the effect of the presence versus absence of a discrete cue on conditioning to a context depends on the extent of prior familiarization with the context. When there was no prior exposure to the conditioning context, tone-conditioned animals showed less contextual freezing than unsignalled-shock rats. Pre-exposure to the conditioning context for a total of 200 min abolished this effect: There was no longer a significant difference between signalled-shock and unsignalled-shock subjects. It is unlikely that this failure of overshadowing can be attributed to a floor effect; for instance, on the second test session group X− /X+ showed 51% freezing.

It is noteworthy that Williams et al. (1992), who in a series of experiments failed to detect overshadowing of context by a tone, started each experiment by pre-exposing all animals to the future conditioning context for 5 min. Perhaps a short context pre-exposure is sufficient to reduce subsequent overshadowing of contextual cues by a discrete CS.

Experiment 1 also showed an effect of pre-exposure to a context on subsequent conditioning to a tone in that context. Rats that were pre-exposed to Context X for 200 min showed a stronger freezing response to the tone after conditioning than did animals that had not received any pre-exposure to that context.

The purpose of Experiment 2 was to examine further the effect of the extent of pre-exposure to a context on conditioning to context and discrete signal. A parametric study was performed in which there were five different levels of context pre-exposure. The experimental design is outlined in the middle portion of Table 1. Different groups of rats received 0-, 5-, 10-, 20-, or 60-min pre-exposure to Context X. Relatively more values were included on the lower end of the scale to permit a more powerful test of the hypothesis that even minor variations in relatively short-duration pre-exposures can significantly alter the effect of the presence versus absence of a discrete cue during conditioning on conditioning to context. After the context–pre-exposure manipulation, one half of each pre-exposure group was aversively conditioned with the tone as a discrete CS; the other half received unsignalled USs. Subsequently, both freezing to the context and freezing to the tone in a neutral context were assessed in unreinforced test sessions.

Method

Subjects and Apparatus

One hundred and sixty naive male Sprague-Dawley rats obtained from Charles River, with a mean weight of 321 g at the start of the experiment, served as subjects. They were housed and maintained as described for Experiment 1. The apparatus used in the present experiment was identical to that used in Experiment 1.

Procedure

The experiment was run in a series of replications. The first two replications included all 10 groups (see further on). An additional two replications were run involving only groups − /X+, − /XT+, 10X− /X+, 10X− /XT+, 60X− /X+, and 60X− /XT+. 
Pre-exposure to Context X. Context-pre-exposed rats received a single pre-exposure session. Groups 5X− /X+ (n = 10) and 5X− /XT+ (n = 10) were exposed to Context X for 5 min, with no stimuli being presented. Groups 10X− /X+ (n = 20) and 10X− /XT+ (n = 20) were exposed to X for 10 min. Groups 20X− /X+ (n = 10) and 20X− /XT+ (n = 10) were placed in Context X for 20 min, and Groups 60X− /X+ (n = 20) and 60X− /XT+ (n = 20) were exposed to X for a total of 60 min. Finally, Groups − /X+ (n = 20) and − /XT+ (n = 20) were handled in the same manner as were the other animals, but these were not exposed to Context X. These animals were simply returned to their home cages after the handling manipulation.

Conditioning. On the following day, all animals were individually (re-)placed in Context X. Groups − /XT+, 5X− /XT+, 10X− /XT+, 20X− /XT+, and 60X− /XT+ received two tone-shock conditioning trials. The conditioning parameters were exactly the same as described for Experiment 1. For the remaining groups, groups − /X+, 5X− /X+, 10X− /X+, 20X− /X+, and 60X− /X+, each of the two shocks was unsignalled. The shocks occurred at the same time as in the tone-conditioned groups.

Tests in Context X. After the conditioning session, the rats received 5 daily Context X exposure sessions, during which no specific events were planned to occur. Each session lasted for 5 min.

Exposure to Context Y and Test Tone in Y. Each animal was exposed to Context Y for 20 min on the day following the last Context X exposure session. On the next day, the animals were again placed in Y, and four tones were presented. The same intertrial intervals were employed as during the tone test in Experiment 1.

Results

Figure 3 shows the levels of freezing observed in each group during the tests for fear of Context X. The figure shows that in the 5- and 10-min pre-exposure condition, the tone-conditioned animals showed enhanced contextual freezing relative to the unsignalled-shock rats. In each of the other pre-exposure conditions, the signalled-shock animals did not differ from the unsignalled-shock animals.

A separate analysis was performed on the data of the first test day to permit specific comparisons between the results of Experiments 1 and 2. Planned comparisons, in which the tone-conditioned group was compared with the unsignalled-shock group within each pre-exposure condition, revealed that group 5X− /XT+ froze more than did group 5X− /X+, \( F(1, 150) = 4.31 \), and that group 10X− /XT+ froze more than did group 10X− /X+, \( F(1, 150) = 4.91 \). The other comparisons did not reveal any significant differences, \( Fs < 1 \).

An analysis using the data of all tests in Context X by means of a Group \( \times \) Test ANOVA revealed a significant main effect of group, \( F(9, 150) = 2.59 \). Planned comparisons contrasting the tone and no-tone groups in each pre-exposure condition revealed, across test sessions, a significantly higher level of freezing in group 10X− /XT+ than in group 10X− /X+, \( F(1, 150) = 11.61 \). Within each of the other pre-exposure conditions and across sessions, the difference between signalled-shock and unsignalled-shock rats was not significant, \( Fs(1, 150) < 3.31 \). In addition to the main effect of group, the main effect of test was also reliable, \( F(4, 600) = 220.18 \). This reflects the diminishing freezing...
in each group across test sessions. The Group × Test interaction was not reliable, $F(36, 600) = 1.12$.

Figure 4 depicts the groups’ mean percentages of observations scored as freezing during the pre-CS and CS periods of the test for responding to the tone in Context Y. The figure shows that the tone-conditioned animals froze more to the tone than did unsignalled-shock animals. Furthermore, group 5X-/XT+ and especially group
10X− /XT+ appeared to freeze more to the tone than did the other tone-conditioned subjects.

A Group × Period (preCS/CS) repeated-measures ANOVA revealed a significant main effect of group, $F(9, 150) = 13.68$, and period, $F(1, 150) = 161.96$. The interaction between these two factors was also significant, $F(9, 150) = 17.14$. Simple main effect analyses revealed that the groups differed in CS freezing, $F(9, 259) = 28.61$, but not in pre-CS freezing, $F < 1$. Furthermore, the tone-conditioned groups froze more during CS periods than they did during pre-CS periods, $F_{(1, 150)} > 20.50$, whereas the unsignalled-shock groups did not, $F_{s} < 1$. Differences scores were computed in the form CS freezing – pre-CS freezing, and a one-factor ANOVA using these scores revealed a reliable group effect, $F(9, 150) = 17.14$. Subsequently, Newman-Keuls post-hoc comparisons revealed that group 10X− /XT+ showed more differential freezing to the tone than did any of the other tone-conditioned groups, groups − / XT+, 5X− /XT+, 20X− /XT+, and 60X− /XT+. All other comparisons between tone-conditioned groups revealed insignificant differences. Thus, conditioning to the tone had been most successful in group 10X− /XT+.

In order to examine the statistical contribution of freezing to the tone to the variance in freezing in Context X, an ANCOVA was performed using the data of the first test day in X, with group as a factor and freezing during the tone presentations in Y as a covariate. As in Experiment 1, the interaction between the main factor and the covariate was not significant and was, therefore, deleted from the model. The analysis without the interaction term revealed only a significant effect of the covariate, $F(1, 149) = 13.10$. This means that differences in freezing to the tone were predictive of freezing to the conditioning context.

**Discussion**

On the first three days of the experiment (handling, conditioning, and testing in Context X), groups − /XT+ AND − /X+ in Experiment 2 were treated exactly the same as were groups − /XT+ and − /X+ in Experiment 1. Yet in Experiment 1 the tone-conditioned group did show attenuated contextual freezing relative to the unsignalled group, whereas this effect could not be replicated in Experiment 2. The reason for this inconsistency between experiments is not clear. It may be related to the large individual differences between animals in the tendency to freeze (large within-group variances) that, perhaps, resulted in a Type I error (incorrect rejection of the null hypothesis of no difference between groups) in Experiment 1, or in a Type II error (incorrect failure to reject the null hypothesis of no difference) in Experiment 2. Increasing the number of subjects within each group to 30 by pooling the data from the first Context X test session of the no-pre-exposure groups from Experiments 1 and 2 and performing a 2 (Group) × 6 (Replications) ANOVA on these data just failed to reveal a significant effect of group, $F(1, 48) = 3.81$, $p = 0.057$, and no main effect of replication, or of the Group × Replication interaction, $F_{s}(5, 48) < 1.12$.

In Experiment 1, conditioning to the tone was enhanced in the tone-conditioned group that had received 200 min of pre-exposure to Context X, group X− /XT+, as compared to the 0-min pre-exposure group in that experiment, group − /XT+. Furthermore, the
200 min of context pre-exposure resulted in attenuated contextual freezing, revealing LI of context. On the first Context X test session, group X−/X+ froze less than did group X−/X+, \( F(1, 18) = 26.48 \). Therefore, the results of the first experiment suggest that latent inhibition of contextual cues reduces the extent to which those cues compete with a discrete stimulus for association with the shock. Experiment 2 showed that differences in conditioning to a discrete tone can also occur if one uses context pre-exposure parameters that do not support LI of context. There was no significant difference between the unsignalled-shock groups in freezing in Context X in this experiment, \( F(4, 75) = 1.11 \), indicating that none of the different context pre-exposure conditions was sufficiently long to cause LI of context. However, group 10X−/XT+ still showed a higher level of conditioning to the tone than did any of the other tone-conditioned groups.

The combined results of Experiment 1 and 2 suggest a complex relationship between the extent of pre-exposure to a future conditioning context and the rate at which a discrete stimulus acquires excitatory associative strength in that context. Pre-exposure to the context for 5 or 10 min increases conditioning to the CS, relative to a no-pre-exposure condition. A pre-exposure that lasts longer than 10 min but is shorter than the duration that is necessary to obtain LI of context reduces conditioning to a level that is comparable to a no-pre-exposure condition. Finally, a long pre-exposure that supports LI of context again increases conditioning to the stimulus relative to a no-pre-exposure condition. At present, one can only speculate about the underlying mechanism(s) of this pattern.

Whatever the reason(s) for this differential conditioning to the tone, as in Experiment 1, freezing to the tone was predictive of freezing to the context. Indeed, in Experiment 2 freezing to the tone was the only element in the ANCOVA that could significantly account for the variance in freezing to context. This contribution may reflect a context–tone association, with the groups in the present experiment only differing in the strength of the excitatory property of the tone and not in the strength of the association between context and tone as such. This issue is further discussed in the General Discussion.

**EXPERIMENT 3**

In the first experiment of Maes and Vossen (1993), as well as in Experiment 1 of the present paper, a group that was pre-exposed to both tone and context before tone–shock pairings showed a particularly high level of contextual freezing (group XT−/XT+). The level of freezing was higher than in a control group that received identical treatment, except that it was pre-exposed to only context prior to conditioning with the tone (group X−/XT+).

One process that might have contributed to group XT−/XT+’s high level of contextual freezing is the acquisition of a strong association between Context X and the tone during the pre-exposure phase. On this view, excitatory conditioning of the tone after the pre-exposure treatment resulted in Context X having a response-eliciting potential that was based on two sources: a context–tone association acting in concert with a tone–shock association, and a context–shock association. The latter association may or may not have been affected by the tone–shock association that was also formed (overshadowing), but
the focus of Experiment 3 is solely on the potential contribution of a context–tone association.

Maes and Vossen (1993) addressed this issue in their Experiment 2, in which they pre-exposed one group of rats to 40 tones in Context X and subsequently presented two tone–shock trials in a different Context Y. Finally, the animals were replaced in Context X to test whether or not this context would elicit freezing because it evoked a representation of the excitatory tone. The experiment found no evidence for a context–CS association; the animals showed the same low levels of freezing in X as a control group that had only received pre-exposures to Context X prior to receiving tone–shock trials in Context Y.

One factor that might have worked against the detection of a difference between the two groups in that experiment is the contribution of contextual occasion setting. When a stimulus is reinforced in Context 1 and on another occasion is non-reinforced in a different context, Context 2, then Contexts 1 and 2 come to retrieve or signal stimulus–reinforcer and stimulus–no-consequence relationships, respectively (Bouton, 1993). That is, whether or not the animal responds to the ambiguous stimulus depends on the context in which it is presented. Context 1 “sets the occasion” for reinforcement following the stimulus, and Context 2 sets the occasion for non-reinforcement following that same stimulus.

In the specific procedure used in Experiment 2 of Maes and Vossen (1993), Context X might well have become a negative occasion setter that signalled or retrieved a tone–no-consequence relationship. If so, then the excitatory training of the tone in the other context, Context Y, would not have resulted in Context X acquiring a response-evoking potential. Even though Context X might have become able to evoke a representation of the tone (context–tone association) as a result of the pre-exposure treatment, that context at the same time signalled that the tone would not be followed by shock.

Experiment 3 was intended to circumvent the potential negative effect of contextual occasion setting on the ability to detect a context–tone association in a tone–pre-exposed group of animals. The experimental design is summarized in the bottom part of Table 1. One group of subjects was first pre-exposed to a tone in Context X. In the next phase, the animals received tone–shock conditioning trials, also in Context X. In a third phase, the animals were placed in a novel context, Context Y, and received additional tone–shock pairings. The rationale for the third phase was to increase further the excitation conditioned to the tone. Finally, the animals received a series of test trials in Context X in order to assess X’s excitatory potential. If Context X, because of the tone–pre-exposure phase, has developed the potential to evoke a representation of the tone (Context X–tone association), the additional tone–shock trials in the third phase should result in Context X having a particularly strong potential to evoke a freezing response. Context X is strongly associated with the tone, and the tone, in turn, is well conditioned. This line of reasoning holds even though the additional tone–shock conditioning trials were conducted in a context that differed from the context employed during the initial two stages of the experiment. This is because the pre-exposure phase and the first tone-conditioning phase were performed in one and the same context. Under these circumstances, Context X continues to retrieve a tone–shock association during the critical tests for freezing in that context (or at least it does so to the same extent as it does in the first control group discussed below).
Two control groups were included. One, like the experimental group, also received a tone–pre-exposure and a tone–shock treatment in Context X. However, for this group, the additional phase in Context Y involved un signalled shocks instead of tone-signal led shocks. Therefore, prior to the critical test sessions in Context X, the tone should have been less strongly associated with shock than was the case in the experimental group. This would imply a weaker response to Context X in the control group than in the experimental group, even though the groups should have equally strong Context X–tone associations.

A second control group was treated exactly like the first control group, except that it did not receive pre-exposures to the tone in the first phase. Hence, this group had no opportunity to form a strong association between Context X and the tone. In case of a significant contribution of such an association to responding to Context X in both the experimental group and the first control group, this group should demonstrate the lowest level of responding during the Context X test sessions.

The experiment was concluded by a test session in which the tone was presented (non-reinforced) in a third context, Context Z, in order to assess the level of conditioning that had taken place to the tone in each of the three groups.

Method

Subjects and Apparatus

The subjects were 30 experimentally naive male Sprague-Dawley rats that were housed and maintained like the subjects in Experiments 1 and 2.

The same boxes described for the previous experiments were used. Context X (see further on) refers to the box that was previously used as the pre-exposure and conditioning box. Context Y (see below) refers to the box previously used as the tone–test context. In addition to these contexts, a third context, called Context Y, was employed in the present experiment. It consisted of a relatively small box (20 × 13 × 18 cm) with three matt-black plywood walls, one mat-black plywood wall that had an opening that was covered by a clear Plexiglas sliding door (not used in the present experiment), a clear Plexiglas lid, and a grid floor made of 12 2-mm stainless-steel rods. This floor could be used for presenting 0.8-mA, 1-sec shock USs. The box was located in a room that differed from the rooms that contained Contexts X and Z. Context Y was dimly illuminated by a red overhead light, and a background noise was provided by a ventilation fan. A distinctive odour was introduced in this context by placing a wad of paper scented with wine vinegar underneath the grid floor. The same tone CS used in the previous experiments could be presented through a speaker that hung on the ceiling of the room at a distance of approximately 2 m above the box.

Procedure

Three matched groups were formed on the basis of weight: group XT−/XT+/YT+, group XT−/XT+/Y+, and group X−/XT+/Y+. Each group’s name designates (1) the pre-exposure treatment—either pre-exposure to tone and Context X (XT−), or only to Context X (X−); (2) the first conditioning treatment in Context X—all groups received tone–shock trials in Context X (XT+); and (3) the conditioning treatment in Context Y—either further tone–shock trials (YT+) or un signalled shocks (Y+).
Pre-exposure. Both group XT− /XT+/YT+ and group XT− /XT+/Y+ received 10 daily sessions in each of which there were four 30-sec non-reinforced tone presentations. The sessions took place in Context X, and, as in Experiment 1, they each lasted 20 min. The mean ISI was 226 sec. Group X− /XT+/Y+ was merely placed in Context X for 10 20-min sessions; no tones were presented.

Conditioning 1. On the day following the last pre-exposure session, all animals received a single session in Context X, during which there were two tone–shock trials. The conditioning parameters were identical to those employed in the first conditioning session of Experiment 1 and the conditioning session of Experiment 2.

Conditioning 2. The animals of group XT− /XT+/YT+ received an additional tone-conditioning session in Context Y. The session was 20 min in duration, and there were four tone–shock trials. Tones were 30 sec in duration, and the shock was the same as used during the first conditioning phase. The mean intertrial interval was 245 sec. Groups XT− /XT+/Y+ and X− /XT+/Y+ received identical treatment, except that the shocks were not signalled by the tone.

Tests in Context X. All animals received five daily test sessions in Context X. Each session was 5 min in duration, and no events were planned to occur. The rats’ behaviour was scored as either freezing or not freezing, using the same time-sampling method as in the previous two experiments.

Exposure to Context Z and Test Tone in Z. The day after the last Context X test session, each animal was placed in Context Z for 20 min. Four non-reinforced 30-sec tones were presented in Context Z on the following day, during which pre-CS and CS freezing were recorded. As in the previous experiments, the mean ISI was 245 sec.

Results and Discussion

Before evaluating the results of the tests for freezing in Context X, conditioning to the tone is examined. Figure 5 shows the groups’ mean levels of freezing during the pre-CS and CS periods of the test for freezing to the tone in Context Z.

The figure shows that group X− /XT+/Y+ showed the strongest response to the tone, followed by group XT− /XT+/YT+, which showed a higher response than did group XT− /XT+/Y+. A 3 (group) × 2 (period: preCS/CS) repeated-measures ANOVA revealed a significant effect of group, $F(2, 27) = 12.84$, of period, $F(1, 27) = 49.36$, and of the interaction between these two main factors, $F(2, 27) = 11.23$. The effect of period was significant in groups XT− /XT+/YT+ and X− /XT+/Y+, $Fs(1, 27) > 18.13$, but not in group XT− /XT+/Y+. Furthermore, groups differed on CS freezing, $F(2, 48) = 23.12$, but not on pre-CS freezing.

A one-factorial ANOVA of the form CS freezing score – pre-CS freezing score was performed on the difference score. The analysis revealed a significant difference between groups. Subsequent Newman–Keuls post hoc tests revealed that group X− /XT+/Y+ froze more to the tone than did either group XT− /XT+/YT+ or group XT− /XT+/Y+, $ps < 0.05$. Furthermore, group XT− /XT+/YT+ froze more to the tone than did group XT− /XT+/Y+, $p < 0.05$.

The fact that group XT− /XT+/YT+ showed a higher level of responding to the tone than did group XT− /XT+/Y+ indicates that the additional tone-conditioning trials in
the former group had indeed strengthened the tone–shock association. The finding that responding to the tone in group $X^-/XT+/YT+$ was lower than responding in group $X^-/XT+/Y+$ reflects LI with regard to the tone in the former group. Furthermore, the additional four tone-shock trials in group $XT^-/XT+/YT+$ could not fully compensate for a similar detrimental effect of the tone pre-exposures on subsequent conditioning to the tone. Responding to the tone in this group was still lower than responding in the group that had not been pre-exposed to the tone, group $X^-/XT+/Y+$, even though the latter group had received only a total of two tone-shock trials instead of six.

The left panel of Figure 6 depicts the freezing percentages across the five tests for freezing in Context X. The overall impression from this figure is that group $X^-/XT+/Y+$—the only group that had not received non-reinforced tone exposures in the first

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**FIG. 5.** Groups’ mean percentages of observations (+ SEM) scored as freezing during the pre-tone periods (preCS) and during the tone presentations (CS) of the tone test of Experiment 3. Groups differed on whether or not they had received tone pre-exposures ($XT^-$ versus $X^-$) and whether they had received tone–shock trials or unsignalled shocks in Context Y ($YT+$ versus $Y+$).

**FIG. 6.** Left: groups’ mean percentage of observations scored as freezing during each of the five tests for freezing in Context X of Experiment 3. Right: groups’ mean percentages of observations scored as freezing during each of the 10 30-sec time intervals of the first Context X test session of Experiment 3.
phase—froze less in X than did either of the other two groups. Groups XT− /XT+/YT+ and XT− /XT+/Y+ did not seem to differ much in contextual freezing, except for the first test session, during which the former group appeared to freeze more than the latter.

Freezing to Context X in group XT− /XT+/YT+ was compared with freezing to that context in group XT− /XT+/Y+ to test whether the separate reinforcements of the tone in Y in the first group resulted in enhanced freezing. A planned comparison, in which the data of the five tests were pooled, failed to detect a significant difference, \( F(1, 27) < 1 \). The data for groups XT− /XT+/YT+ and XT− /XT+/Y+ were pooled and contrasted with the Context-X freezing data of group X− /XT+Y+ to assess the influence of the tone pre-exposures in the first phase. The contrast revealed a significant difference, \( F(1, 27) = 4.26 \). This result replicates the enhanced contextual freezing previously found for subjects that were pre-exposed to a tone before being conditioned with that same tone acting as a CS relative to subjects that did not receive tone pre-exposures.

In order to examine further whether the additional reinforcements of the tone in Context Y in group XT− /XT+/YT+ yielded enhanced contextual freezing, the pattern of freezing in Context X was evaluated in a more detailed manner. The right side of Figure 6 shows freezing during each 30-sec time bin of Test 1 in Context X. The figure suggests that, especially during the fourth 30-sec period, which was the period that corresponded with the time period immediately prior to the first tone presentation of the earlier conditioning session in that context, group XT− /XT+/YT+ froze more than did either of the other two groups. Planned comparisons using the data from this fourth 30-sec period revealed that group XT− /XT+/YT+ froze more than did group XT− /XT+/Y+ or group X− /XT+Y+, \( F_s(1, 27) > 5.05 \); the latter groups did not differ.

The final analysis performed was a Group × Tone Freezing in Context Z × Test repeated-measures ANCOVA to evaluate the contribution of differences in tone conditioning to freezing in Context X. As in the previous two experiments, the analysis did not reveal a significant interaction between the group main factor and the covariate. A subsequent analysis, in which this interaction term was not included, revealed a significant effect of the covariate, \( F(1, 26) = 6.83 \), in addition to a significant effect of group, \( F(2, 26) = 6.13 \).

The results of Experiment 3 indicate that there was enhanced contextual freezing, albeit short-lived, in a group that was pre-exposed to a tone and that had formed a relatively strong tone–shock association, relative to a group that had also received tone pre-exposures but that had acquired a less strong tone–shock association. Furthermore, each of the two groups that were pre-exposed to the tone showed more contextual fear than the group that was not pre-exposed to the tone.

GENERAL DISCUSSION

The goal of the present experiments was two-fold. (1) The experiments sought to assess the effect of differences in the extent of prior familiarization with a discrete stimulus and/or a context on conditioning of a freezing response to that context in animals that received footshocks with or without the stimulus as a CS. (2) Possible mechanisms underlying observed differences in contextual fear in different groups were evaluated further.
In Experiments 1 and 2, groups of rats differed in the extent of familiarization with a tone and/or a context, prior to receiving tone-signalled or unsignalled shocks in that context. In Experiment 1, one group received a total of 200 min of pre-exposure to the to-be-conditioned context. A second group also was pre-exposed to the future conditioning context for 200 min, but in addition it received 40 non-reinforced exposures to a tone. Finally, a third group did not receive any pre-exposures to tone or context. In Experiment 2, rats received one context pre-exposure session for a duration of 0, 5, 10, 20, or 60 min. In none of the above-mentioned exposure groups was there a consistent attenuation of contextual freezing in the tone-signalled-shock groups, relative to the unsignalled-shock groups. If anything, given some pre-exposure conditions, the presence of the tone during conditioning enhanced contextual freezing.

Turning now to the second goal of the present studies, a variety of contemporary associative learning theories predict that the presence of the tone during conditioning should attenuate contextual fear, relative to the unsignalled condition (e.g. Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). This prediction is based on the assumption that contextual stimuli and discrete stimuli compete for association with a US, with the latter stimuli overshadowing the former. The present findings are clearly at odds with this prediction and can be added to previous failures to detect overshadowing of context by a discrete stimulus in which a procedure similar to the present one was adopted (Sigmundi & Bolles, 1983; Williams et al., 1992). Collectively, these studies suggest that, despite manipulations of a number of conditioning parameters, such as number of conditioning trials per day, total number of conditioning trials, and extent of prior familiarization with context, no consistent overshadowing of context by a CS can be detected.

The absence of overshadowing of context by a CS is predicted by so-called comparator models (Gibbon & Balsam, 1981; Miller & Schachtman, 1985). In these models it is assumed that context-US and CS-US associations are independently formed during conditioning. But Gibbon & Balsam (1981) argue that the strength of the conditioned response to the CS is a function of the ratio of the expectancy of the US in the presence of the CS relative to the expectancy of the US during the entire session. Miller and Schachtman (1985) extended this notion by providing evidence that the extent of conditioned responding to the CS is determined by a comparison of the CS with its training context and not its test context. In our experiments, the tone-test context, Context Y, had a similar low associative strength in all groups, as is reflected in the absence of differences in the (low) pre-CS freezing levels. This means that, if the test context is the comparator stimulus that determines CS responding, no differences in responding to the tone should emerge between the groups that had been conditioned with the tone but that had not been pre-exposed to that tone. The fact that these groups differed among themselves is clearly not in accord with such a version of a comparator account.

In Experiment 1, differences did exist between the tone-conditioned groups in the associative status of the conditioning context, Context X, at the time the test for responding to the tone was performed in Context Y, $F(2, 27) = 8.89$. Group X− /XT+ froze more than did group − /XT+, Newman–Keuls, $p < 0.05$. This means that if the current associative value of the conditioning context is the critical variable that determines responding to the tone, group − /XT+ should have frozen more as a response to the
tone in Context Y than group X−/XT+. However, group X−/XT+ froze more to the tone than did group −/XT+. In Experiment 2, the levels of freezing in the conditioning Context X also still differed between tone-conditioned groups on the last test session, Session 5, $F(4, 75) = 3.82$, with group −/XT+ showing a lower level than group 5X−/XT+, Newman–Keuls, $p < 0.01$. However, instead of finding a lower freezing response to the tone in Y in group 5X−/XT+, as would have been the case if Context X is the critical comparator stimulus, groups −/XT+ and 5X−/XT+ did not differ on this measure. These results are inconsistent with the predictions based on Miller and Schachtman’s (1985) comparator model, according to which the conditioning context is the critical comparator stimulus.

An alternative account of the present results is that the contextual stimuli were overshadowed in the various tone-conditioned groups but that, to varying extents, the reduced contextual fear as a result of an attenuated context-shock association was compensated for by tone-mediated contextual freezing. The consistent finding that freezing to the tone in a neutral test context was predictive of freezing to the conditioning context suggests such an association. In principle, there are two basic mechanisms that might underlie such tone-mediated freezing. First, Context X might have acquired additional excitatory strength (in addition to being directly associated with shock) through second-order classical conditioning. On this view, after the first tone-shock conditioning trial, Context X was reinforced by the presentation of the (now) aversive tone (e.g. Helmstetter & Fanselow, 1989). One implication of a second-order conditioning account is that post-conditioning manipulations of the excitatory property of the tone should most probably have no effect on the excitatory potential of the context in which it was trained. This is because second-order conditioning of fear is probably based on S–R rather than S–S learning (see, e.g., Rizley & Rescorla, 1972). Consequently, enhancing the excitatory strength of the tone after conditioning in X, as was done in Experiment 3, should not have resulted in the observed enhanced contextual freezing in group XT−/XT+/YT+ (see also Helmstetter & Fanselow, 1989). For additional arguments against this second-order conditioning mechanism, see Williams and LoLordo (1995).

A second mechanism that might be responsible for the observed positive relationship between freezing to CS and freezing to context is a context–CS inter-element, or within-compound association (e.g. Marlin, 1982; Miller et al., 1987; Rescorla, 1984). According to this view, two factors determine responding to the context. The first is the strength of the association between context and CS. This may at least partly be determined by the number of presentations of the CS in the context. The extended non-reinforced tone pre-exposures in some of the groups of Experiments 1 and 3 may have resulted in a particularly strong context–CS association (sensory preconditioning—e.g. Marlin, 1982). The second factor is the level of excitation conditioned to the CS. Accordingly, the post-conditioning enhancement of the tone’s excitatory strength in group XT−/XT+/YT+ of Experiment 3 should result in the observed enhanced contextual freezing, relative to a group for which the tone was less excitative (group XT−/XT+/Y+).

The results of the present experiments can be evaluated in terms of different strengths of Context X–tone, tone–shock, and Context X–shock associations. Table 2 presents an overview of the possible strengths of these associations within each of the tone-conditioned groups of Experiments 1–3. The following assumptions are made: (1) The relative
strengths of the context-shock association are inversely related to the strengths of the tone-shock association (overshadowing of first-order conditioning). (2) The strength of the context-tone association depends on the number of occasions that the tone has been presented in Context X (2–4 for all groups, except for the tone-pre-exposed groups, which received a total of 42–44 presentations). (3) The net tone-mediated associative strength that Context X acquires in the various conditions is determined by multiplying the strength of the context-tone association and the strength of the tone-shock association. This multiplication formalizes the following chain of associations: Context X evokes a representation of the CS to a certain extent, and the tone, in turn, has the potential to evoke a representation of the US to a degree that corresponds with the tone’s own associative strength with regard to the US. (4) As these experiments included a rather limited number of tone-shock trials, the overshadowing-of-context-by-tone effect was probably rather small (overshadowing of first-order context-shock association, see, e.g. Odling-Smee, 1978b). Instead, the larger freezing score in Context X in some tone-conditioned animals relative to their unsignalled counterparts implies that, given the present conditioning parameters, a context’s associative strength that is mediated by the tone contributes more to the overall level of contextual fear than does its direct association with shock. This notion is formalized by weighing the outcome of the context-tone × tone-shock associations multiplication with the factor 2, and the context-shock association with the factor 1. It should be noted that the theoretical strengths derived from this calculation have only ordinal properties. Furthermore, giving the mediated context-tone, tone-shock association twice the weight of the context-shock

<table>
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<th>Group</th>
<th>Type of Association</th>
<th>Theoretical Strength (Sum)</th>
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<tr>
<td>−/XT+</td>
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Note: Context refers to Context X in Experiments 1–3. The sum of the associative strengths to determine Context X’s excitatory potential is computed according to the formula: 2 * (Context–Tone strength * Tone–Shock strength) + 1 * Context–Shock strength. The relative strength of the Tone–Shock association was empirically determined in a neutral test context.
association is also entirely arbitrary. However, it is also important to note that any ratio greater than 1:1 would give the same ordinal predictions.

With these assumptions it is possible to explain the observed pattern of contextual freezing in Context X. In Experiment 1, group XT− /XT+ showed the highest level of fear, because of the presence of both a strong context–tone association and a strong context–shock association. In group X− /XT+, the relatively strong tone–shock association resulted in a reduced context–shock association (overshadowing), but this very same tone–shock association also compensated for the reduced direct context–shock association because the context could, to a relatively weak extent, evoke a representation of the tone (context–tone association). Finally, in group − /XT+, none of the associations was strong, resulting in the lowest net associative strength of the three tone-conditioned groups of Experiment 1.

In Experiment 2, the differences in contextual freezing were completely caused by differences in conditioning to the tone. This conditioning proved to be more successful in group 5X− /XT+, and especially in group 10X+/XT+. Hence, these groups were the only groups for which an overshadowed context–shock association was “overcompensate” by context–tone and tone–shock associations, with a resultant higher level of freezing in X than that shown by unsignalled-shock control subjects.

Finally, in Experiment 3 context freezing in group XT− /XT+/YT+ was particularly strong. This was the only group in the present experiments for which there was not a complete inverse relationship between the strength of the context–shock association and the tone–shock association. The context–shock association was strong because the tone suffered from LI at the time it was reinforced in X (reduced overshadowing). The tone was further excitatory conditioned after the first conditioning phase, but the additional tone–shock trials occurred in another context and had, therefore, no effect on the context–shock association. Group XT− /XT+/Y+ had formed a strong context–tone association (because of the tone pre-exposures), but the tone–shock association was weak. Instead, in group X− /XT+/Y+, the context–tone association was weak and the tone–shock association was strong.

Regardless of the foregoing theoretical speculations, the present experiments show that, despite manipulations of the familiarization with the discrete cue and/or context in an aversive classical conditioning preparation, signalled shocks did not result in more contextual freezing than did unsignalled shocks. On the contrary, both relatively short pre-exposures to the context and prior familiarization with the CS enhanced rather than diminished the acquisition of contextual conditioned responding in signalled-shock rats.

REFERENCES


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Peur du contexte après des chocs signalés vs non signalés: effet de l’étendue de l’expérience antérieure du signal et du contexte

Lors des deux premières expériences, des rats sont différemment familiarisés avec un stimulus discret et/ou un contexte, avant de recevoir dans ce contexte des chocs signalés par le stimulus ou non signalés. Estimée par l’immobilisation [freezing], autant de peur contextuelle est acquise dans les conditions de préexposition par les rats dont le choc est signalé que par ceux pour lesquels le choc n’est pas signalé. La préexposition au stimulus et une préexposition relativement courte au contexte futur de conditionnement produisent plus de peur du contexte chez les sujets dont le choc est signalé, par rapport aux sujets dont le choc n’est pas signalé. Lors d’une troisième expérience, l’immobilisation dans le contexte de conditionnement cible est particulièrement accrue chez les rats familiarisés avec un stimulus, conditionnés avec ce stimulus signalant le choc, et ultérieurement encore conditionnés à ce stimulus dans un contexte non cible différent. Dans toutes les expériences, le niveau d’immobilisation en présence du stimulus dans un contexte neutre est positivement lié au niveau d’immobilisation dans le contexte de conditionnement cible. Ces données sont expliquées en termes d’associations contexte–choc, stimulus–choc et contexte–stimulus.

Miedo contextual después de la exposición a descargas señaladas o no señaladas: efecto de la duración de la experiencia previa con el contexto y la señal

En los dos primeros experimentos, unas ratas recibieron diferentes grados de exposición a un estímulo discreto y/o a un contexto, antes de recibir descargas señaladas por el estímulo o descargas no señaladas en el contexto. Según medidas de paralización, ninguna de las condiciones de preexposición hizo que las ratas que recibían descargas señaladas adquirieran menos miedo contextual que las que recibían descargas no señaladas. Tanto la preexposición al estímulo como la preexposición breve al futuro contexto de condicionamiento originaron más miedo contextual en los sujetos con descargas señaladas que en aquellos expuestos a descargas no señaladas. En un tercer experimento, la paralización en el contexto de condicionamiento se intensificó especialmente en las ratas que habían sido familiarizadas con un estímulo, condicionadas con el mismo como señal de la descarga y posteriormente vueltas a condicionar en otro contexto diferente. En todos los experimentos, el nivel de paralización al estímulo en un contexto de prueba neutro mostró una relación positiva con el nivel de paralización en el contexto de condicionamiento. Finalmente, se analizan estos resultados en relación con el papel de las asociaciones contexto–descarga, estímulo–descarga y contexto–estímulo.