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Conditioning of fear and conditioning of safety in rats

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Abstract. In separate groups of rats forward and backward procedures for classical defensive conditioning were superimposed on on-going bar pressing for food. The forward conditioned stimulus elicited suppression of bar presses, indicating acquisition of fear. The backward stimulus paired with identical shock elicited behaviour typical for rats in a condition of safety and caused an increase of bar press rate. Enhancement of bar presses acquired in the course of backward conditioning was stable, immune to influences from unsignalled shocks presented in the same experimental context, and resistant to extinction when all shocks were discontinued. Properties of the employed variety of the backward conditioning procedure are discussed. When a brief shock overshadowed the onset of a backward stimulus, the remaining portion of the stimulus became a signal of safety.

Key words: fear, safety, backward procedure, overshadowing, extinction, stimulus modality, rat

INTRODUCTION

The basic law of learning by Pavlov mentions two indispensable requirements for conditioning: the temporal coincidence of the stimuli and the specific order of their presentation, with the neutral stimulus starting before the unconditioned stimulus (Pavlov 1927, p. 26). This generalization was grounded on numerous data from forward conditioning studies and on experiments by Krestovnikov (1921) with the backward conditioning procedure. Subsequent studies changed Pavlov's initial radically negative position about the possibility of excitatory conditioning resulting from the backward procedure. He concluded that a conditioned stimulus (CS) can acquire some excitatory effect early in backward training and an inhibitory effect when overtrained (Pavlov 1927, p. 393). The notion about "double effect" of the backward conditioning was shared by other authors (see reviews by Razran 1956, Spetch et al. 1981). Similarly, the contingency models of classical conditioning predicted that if the backward procedure continued long enough, the backward CS would eventually become inhibitory, eliciting a conditioned response opposed to the excitatory conditioned response (Siegel and Domjan 1971, Wagner and Rescorla 1972).

The extensive relevant literature indicates that backward conditioning is used as an aggregate term including a variety of procedures by which a CS is superimposed on an unconditioned stimulus (US) or given shortly thereafter. A common denominator of all these procedures is a long period of CS presentation during which the US is not applied (Zieliński, in press).

Traditionally, in Pavlovian laboratories a short action of the US alone (short backward delay) was followed by a long period of the US-CS combination. In contemporary backward conditioning studies simultaneous US and CS presentation is either omitted or very brief. Comparison of the effects from different varieties of the backward procedure suggests that discriminability of the period during which the US will not be applied should be the main factor influencing the subject's behaviour. It may be expected that in some varieties of the backward conditioning procedure the behaviours typical for the US-free period be limited to the CS itself, whereas in other varieties these behaviours may extend to a substantial portion of the intertrial interval. Discriminability of the US-free period depends on salience of the stimulus and on time parameters.

In the present study, the effectiveness of noise and darkness as CS for classical defensive conditioning were compared, using the Estes-Skinner (1941) method of conditioned suppression of bar presses for food. The forward and the backward conditioning procedures were used in separate groups of rats. In a third group of control rats, the shock was embedded in the CS and given in the middle portion of its presentation.

METHODS

Subjects

The subjects were 24 experimentally naive male hooded rats, all from the Nencki Institute colony and approximately 90 days old at the start of training. They were housed individually with free access to water and reduced to 80% of their free-feeding weight. During the experiments, a 22 h schedule of food deprivation was applied and a daily supplement of food was given just after the experimental session. A natural light/dark cycle from external illumination was maintained. Rats were trained once a day in the same order and at the same time in the morning or early afternoon.

Apparatus

The experiments were carried out using eight rat operant chambers, housed inside sound- and light--attenuating shells. One wall of each chamber contained a bar and a food receptacle into which 45 mg Noyes food pellets could be delivered. A pilot light centred on the top of the back chamber wall provided illumination in the vicinity of the bar equal to 205±5 lx. Below the food receptacle, under an electrifiable grid floor, a speaker was mounted through which 70 dB (re: 20 μN/m^2) wide-band noise could be presented. The ambient noise level in the absence of the auditory stimulus was 46±2 dB. The subjects' behaviour was watched on a TV monitor in an adjoining room in which equipment for automatic programming and data recording was located.

Procedure

Rats were trained to press the bar for food reinforcement. Preliminary training consisted of initial presentation of 40 "free" 45 mg food pellets on a 1 min variable interval (VI) schedule of reinforcement, followed immediately by a period with continuous reinforcement of bar presses until 120 food pellets were delivered in a single session. The next day rats were split into three groups of 8 subjects each. All following sessions were of 2 h duration and bar presses were reinforced by food according to a 2.5 min VI schedule. The 5th (last) session of preliminary training constituted a so called Dummy day (D-day) in which no sporadic stimuli were presented, but the number of bar presses during blank trials were recorded and analysed in the same way as in the subsequent experimental sessions.

Preliminary training was followed by 22 daily experimental sessions divided into several phases (Table I). Phase I consisted of two Pretest sessions (P1 and P2) during which unconditioned effects of the stimuli, 1 min of house light offset (darkness, D) or 1 min of a wide-band noise of 70 dB intensity (noise, N), were tested. Stimuli were presented in the same order for each subject; namely, at 22 min after the start of the session, the D stimulus was presented and then at regular 10 min intertrial intervals the N and the D stimuli were given alternatively, each stimulus four times daily.

Conditioning was then started with trials presented according to the same sequence as during Pretest sessions. The backward conditioning procedure was applied for Group BACK, and the forward conditioning procedure for Group FOR. The unconditioned stimulus (US) was presented simultaneously with the onset of the 1 min CS for Group BACK, while it was given in the last second of the 1 min CS for Group FOR. In the control rats (Group EMB) the US was given at the 30th second of the 1 min CS. During Phase II (Sessions 1-7), the US delivered to the grid floor was a nominal 1 mA scrambled, pulsed DC shock of 1 s duration, and during Phase III (Sessions 8-14) the US intensity was increased to nominal 2 mA intensity. Then two phases

TABLE I

Design of experiment

Phase: Session:	I P1, P2	II 1 - 7	III 8 - 14	IV 15 - 17	V 18 - 20
Group BACK	4D 4N	4 sh-D 4 sh-N	4 SH-D 4 SH-N	8 SH	4 D 4 N
Group FOR	4D 4N	4 D-sh 4 N-sh	4 D-SH 4 N-SH	8 SH	4 D 4 N
Group EMB	4D 4N	4 D-sh-D 4 N-sh-N	4 D-SH-D 4 N-SH-N	8 SH	4 D 4 N

D for darkness, N for noise, sh for shock of 1.0 mA and SH for shock of 2.0 mA nominal intensity. Single symbols denote unpaired and double or triple symbols denote paired presentations of stimuli and their order. Number of trials in each session are given in front of symbols.

of extinction followed. During Phase IV (Sessions 15-17), the 2 mA US not accompanied by any CS was presented eight times daily at the same times as previously. During Phase V (Sessions 18-20), the auditory and visual CSs were reintroduced and presented four times daily at the same times as during phases I-III, but without the US.

Measures

The number of bar presses was recorded for each 30 s period of the D-day and of each of the subsequent sessions. The raw counts were used to calculate individual mean rates of bar presses per 1 min immediately before the CS onset (period A), during the presentation of the CS (period B), and immediately after termination of the CS (period C). For each subject, stimulus modality, period, and session, the number of responses was summed and mean daily rates of responses were calculated for use in statistical tests. The results for Group BACK and Group FOR were compared to assess different effects of the contrasted time relations between the same pair of stimuli, the CS and the US. A mixed-design analysis of variance (ANOVA) considering both between- and within-subjects factors (Lindquist 1953) was employed for statistical evaluations of the results followed, when appropriate, by Newman--Keuls test.

Additionally, changes of bar presses in consecutive 30 s periods for each group of rats were compared.

RESULTS

Unconditioned effects of stimuli

The daily response rates in consecutive 1 min periods before, during, and after each stimulus were compared by 3 (groups) x 2 (stimuli) x 3 (periods) ANOVA's for mixed data, with stimuli and periods as within-subject effects. In contrast to the D-day, where no difference in response rate between groups or periods was observed, the introduction of stimuli elicited marked changes in responding: the noise enhanced and the darkness suppressed response rate. At the P1 session this resulted in stimulus effect, $F(1,21)=6.57$, $P<0.02$, and stimulus x period interaction, $F(2,42)=10.16$, $P<0.001$. At the P2 session these effects were accompanied by period effect, $F(2,42)=5.84$, $P<0.01$.

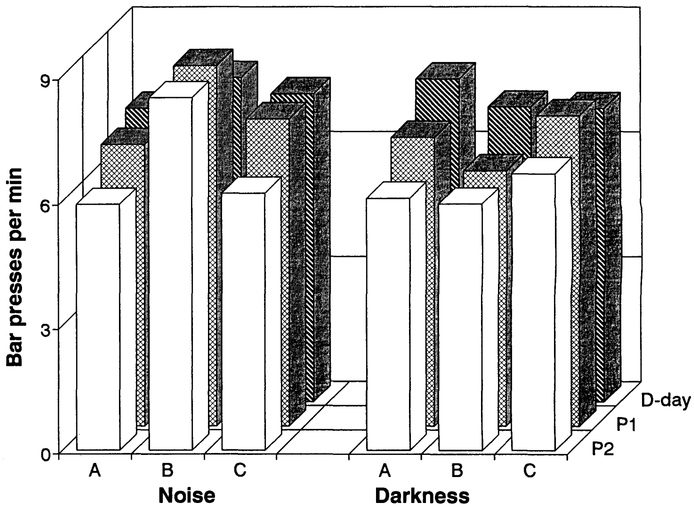

Fig. 1. Mean bar press rate before (A), during (B), and following (C) stimuli presentations on D-day (blank trials), P1 and P2 days. Data for the noise stimulus on the left, data for the darkness stimulus on the right.

Since no group effect was observed, the data for all groups were combined; mean response rates for each session, stimulus modality, and 1-min period are presented in Fig. 1, illustrating all of the effects revealed in ANOVA tests. Visual inspection of the data for A periods suggests some decrease of the overall level of bar presses after the introduction of auditory and visual stimuli prior to any shock experience. A 3 (groups) x 2 (stimuli) x 3 (sessions) ANOVA yielded a day effect, $F(2,42)=5.36$, $P<0.01$, in the absence of other effects. The Newman--Keuls test, however, failed to identify a difference between any pair of group means.

Conditioning with mild shock (Sessions 1-7)

Introduction of the 1 mA shock did not change the relations between bar press rates before, during, and after the stimuli. A 2 (groups) x 2 (stimuli) x 3 (periods) ANOVA for Groups FOR and BACK and

Session 1 revealed a period effect, $F(2,28)=21.77$, $P<0.001$, in the absence of other effects. The period effect was due to an increase in the rate of bar presses during the action of stimuli. In subsequent sessions the enhancing effect of the darkness stimulus decreased. No other effects were observed during this phase of the experiment, indicating failure of conditioning with low intensity of US.

Introduction of the mild shock resulted in an overall decrease of bar press rate and in an increase of daily fluctuations of this index. The largest decrease of bar press rate was noted on Session 2 and full recovery was observed only for Group FOR. In fact, a 3 (groups) x 2 (stimuli) x 7 (sessions) ANOVA on daily A scores yielded the expected session x group interaction, $F(12,126)=2.61$, $P<0.005$.

Conditioning with more intense shock (Sessions 8-14)

As early as the first day of training with the 2 mA shock, some effects related to the conditioning procedures were observed. In rats subjected to the backward conditioning, the noise and the darkness stimuli increased response rate like in previous sessions. Thus, the more intense shock presented concurrently with the CS onset in Group BACK did not modify the enhancement of bar press rate during the CS. By contrast, the similar enhancement in Group FOR was readily attenuated by shock of the same intensity but given at the last second of the CS. A 2 x 2 x 3 ANOVA for Session 8 yielded a significant group x period interaction, $F(2,28)=4.28$, $P<0.05$, and a significant stimulus x period interaction, $F(2,28)=4.20$, $P<0.05$, without other effects.

After short training with 2 mA shock, the forward conditioning procedure resulted in stable suppression of bar presses during CS presentations, while the effect of backward conditioning was just the opposite (Fig. 2). This was confirmed by 2 x 2 x 3 ANOVA's performed for Groups FOR and BACK separately for each session. The ANOVA for Session 14, in particular, yielded a group x period interaction, $F(2,28)=39.03$, $P<0.001$, and a stimulus x period interaction, $F(2,28)=6.14$, $P<0.01$. It should be also noted that in the BACK condition the noise CS had a more marked response-enhancing effect than the darkness CS; by contrast, both CSs were equally effective as suppressor in the FOR condition, which is likely due to a floor effect. This profile was supported by the finding of a stimulus x group x period interaction in the above-mentioned ANOVA, $F(2,28)=6.68$, $P<0.01$.

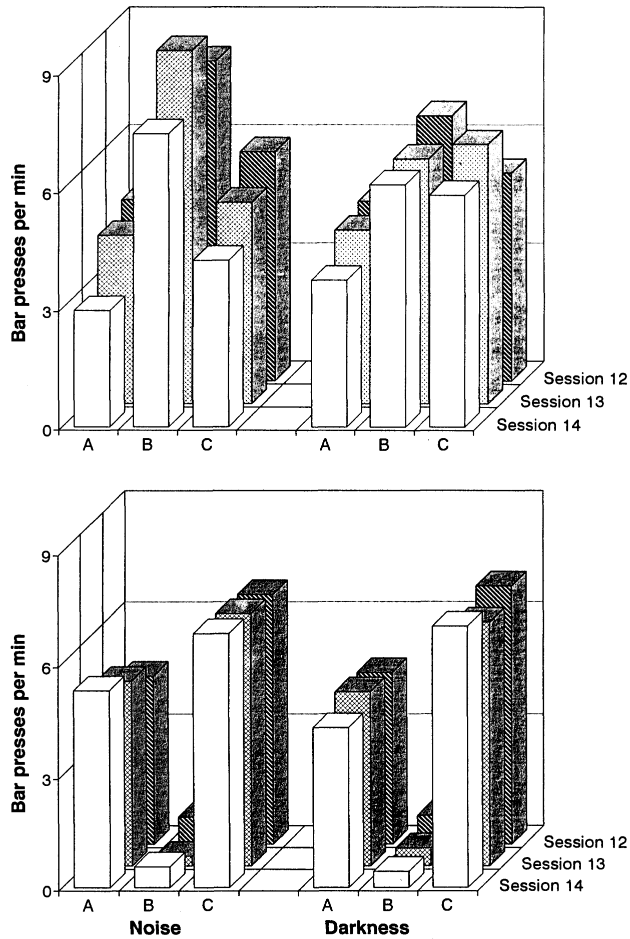

Fig. 2. Mean bar press rate before (A), during (B) and following (C) stimuli presentations on Sessions 12-14. Upper panel for Group BACK, bottom panel for Group FOR. Data for the noise and for the darkness CSs on the right and on the left, respectively.

Graphs presenting response rates in consecutive 30 s periods of the CS action and the intertrial interval in Sessions 12-14 independently for each group (Fig. 3) allowed a more detailed analysis of

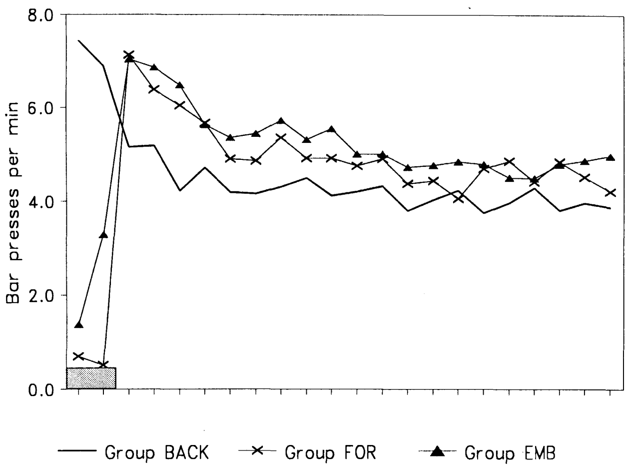

Fig. 3. Mean bar press rate in consecutive 30 s periods during 1 min CSs presentations (marked in the bottom left corner of the panel) and subsequent 10 min intervals on Session 12-14 for each group. Solid line for Group BACK, line with x for Group FOR, and line with triangles for Group EMB.

the data. Toward the end of training there was more suppression elicited by CSs in Group FOR than in Group EMB. The difference was pronounced in the second half of the CS action, when only moderate suppression was observed in Group EMB. Since a difference in response rate between the first and the second half of the CS in Group EMB emerged in the course of training, acquisition of signalling properties by the shock US must be suspected. This was confirmed by 2 (groups) x 2 (stimuli) x 7 (sessions) ANOVA's on mean daily response rate in 30 s periods. The groups FOR and EMB did not differ in mean daily response rate either before or after stimuli presentations. A session effect emerged only for response rates during stimuli presentations indicating acquisition of suppression. Analysis of response rates during the second half of CSs yielded also group effect, $F(1,14)=20.18$, $P<0.001$, and a group x stimulus interaction, $F(1,14)=11.30$, $P<0.005$. In Group EMB less suppression occurred during the noise than during the darkness stimulus.

The general pattern of response rate changes was similar in Group FOR and Group EMB, and opposite to that in Group BACK. The time arrangements employed in Group FOR and in Group EMB resulted in suppression during the CSs' action and subsequent enhancement of response rate lasting for about 2 min after a trial. In Group BACK the CSs elicited an enhancement of bar press rate which decreased shortly after termination of a trial. In all groups, bar press rate was higher during the final training sessions just after a trial than at the end of the intertrial interval. Data of Fig. 3 indicate that response rate just after the forward trial, and similarly, after the control trial was comparable to that observed during the backward trial.

Introduction of more intense shock produced a further decrease of the overall bar press rate. The lowest daily A scores were observed on Session 10. A 3 (groups) x 2 (stimuli) x 7 (sessions) ANOVA for Phase III (sessions 8-14) yielded a session effect, $F(6,126)=4.90$, $P<0.001$, and a group x stimulus interaction, $F(2,21)=4.88$, $P<0.02$. This interaction was related to the higher response rate before the darkness than before the noise CS observed in Group EMB only.

Stimulus effects during extinction (Sessions 18-20)

A weakening of the signalling properties of stimuli was achieved by two procedures applied subsequently. Neither noise nor darkness stimuli were presented during Phase IV of the experiment, but shock alone was administered eight times daily at appropriate times. This should have consolidated fear conditioned to contextual (non-discrete) cues. Next, the regular extinction procedure was applied during three sessions of Phase V, presenting the noise and the darkness stimuli in the appropriate sequence but without shock.

Comparison of data from the last session of Phase III and the first session of Phase V provides information about effectiveness of unsignalled shock presentations. Response rates collected either before (period A) or after (period C) CSs showed no difference between Sessions 14 and 17. This suggests an absence of change in fear conditioned to contextual stimuli. A similar 2 (groups) x 2 (stimuli) x 2 (sessions) ANOVA on response rates during

CSs presentations (period B) yielded significant effect of each factor and two interactions: group x session, $F(1,14)=10.87$, $P<0.005$, and stimulus x session, $F(1,14)=16.23$, $P<0.002$. These interactions reflect attenuation of the contrasting effects of CSs in the two compared groups of rats.

The extinction procedure resulted in a weakening of the suppressant effects of the forward CSs and of the enhancing effects of the backward CSs (Fig. 4), but CS modality had a marked influence on this trend. The suppressant effect of the noise forward CS was lost almost completely, whereas that of the darkness CS was more resistant to extinction.

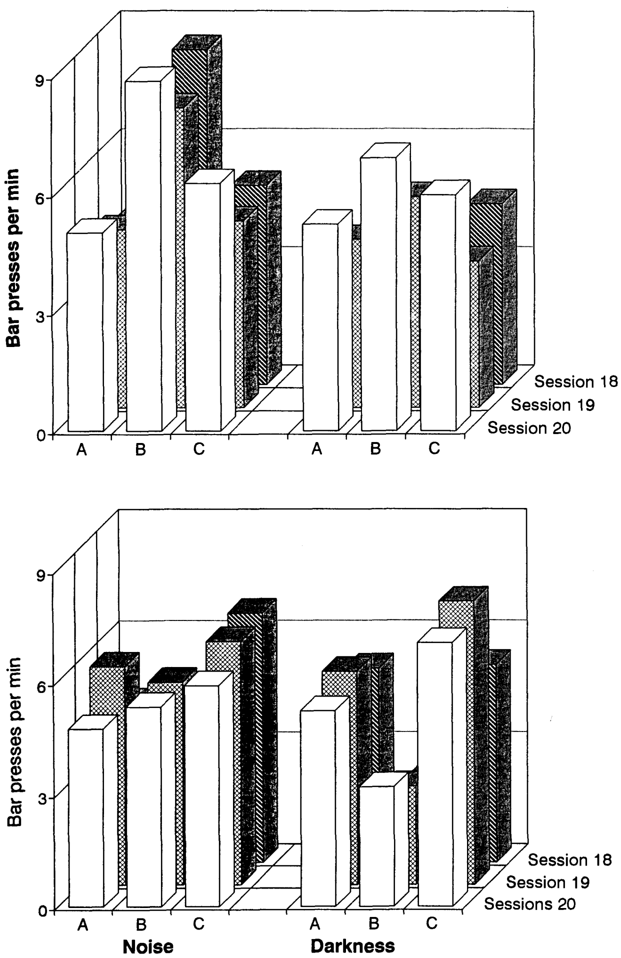

Fig. 4. Mean bar press rate before (A), during (B) and following (C) stimuli presentations on Sessions 18-20. Upper panel for Group BACK, bottom panel for Group FOR. Data for the noise and for the darkness CSs on the right and on the left, respectively.

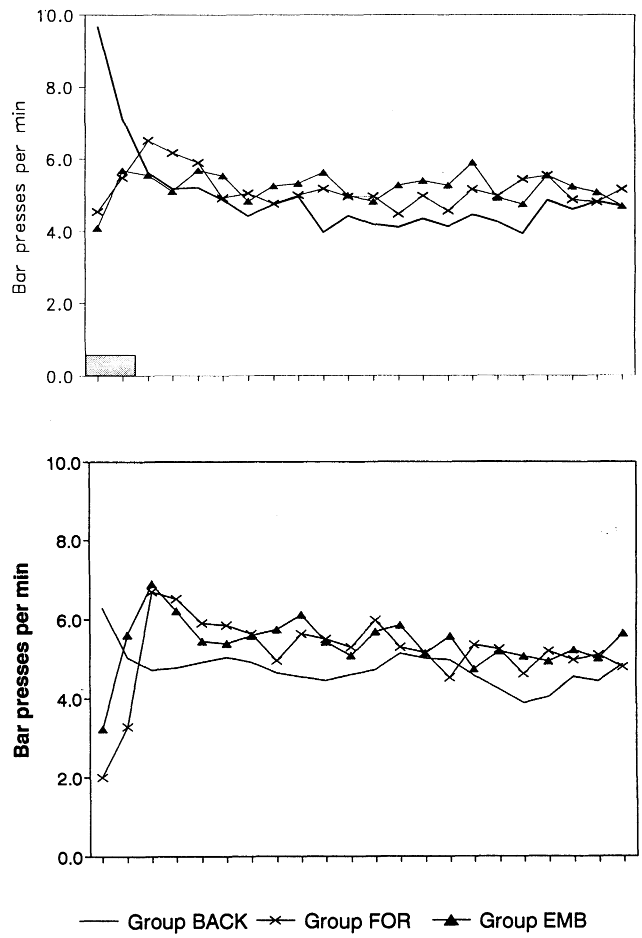

Fig. 5. Mean bar press rate in consecutive 30 s periods during 1 min CSs presentations (marked in the bottom left corner of the panel) and subsequent 10 min intervals on Sessions 18-20 for each group. Solid line for Group BACK, line with x for Group FOR, and line with triangles for Group EMB. Upper and bottom panels for the noise and the darkness CSs, respectively.

On the contrary, the enhancing effect of the darkness backward CS was weakened more than that of the noise CS. In fact, independent 2 (groups) x 2 (stimuli) x 3 (periods) ANOVA yielded significant group x period and significant stimulus x period interactions for each session of the Phase V. These stimulus effects were especially pronounced during the first session of extinction.

The perfect retention of the enhancing effect of the noise backward CS is clearly shown by the graphs presenting mean response rates in consecutive 30 s periods of Sessions 18-20 for each stimulus modality and group independently (Fig. 5). The suppressing properties of the noise CS in Groups FOR and EMB were devastated by the extinction procedures. On the other hand, the suppressing effects of the darkness CS was retained in these groups, whereas the enhancing effect of the darkness CS in Group BACK was strongly attenuated.

DISCUSSION

The present experiment showed that the contingencies created by the time relationships between two discrete stimuli, the CS and US, are critical for the classically conditioned modulation of motivational states underlying overt responding. The forward CS paired with a shock US elicited suppression of bar presses for food, indicating acquisition of fear. The backward CS paired with identical shock US caused enhancement of bar presses, indicating acquisition of a symmetrically opposite motivational function.

The motivational value of the CSs was evaluated by the summation (combined-cue) test. The Estes--Skinner (1941) method of conditioned suppression employed for Group FOR and Group EMB has been considered as the most widespread application of the summation test for demonstration of the opposite response tendencies conditioned to an aversive sporadic CS and to appetitive contextual stimuli (Dickinson and Pearce 1977). Similarly, the summation test may be applied for demonstration of the concerted action of the two response tendencies acquired by different contingencies (Rescorla 1969, Hearst 1972). Enhanced bar press responding for food in Group BACK indicated a compatibility of the motivational value of the backward CS and the appetitive contextual stimuli of the experimental situation.

It has to be asked, why in the present experiment the backward stimulus regularly paired with shock did not evoke fear but resulted in a state of safety. It may be even in doubt whether the stimulus, whose onset coincided with brief shock, is a backward stimulus. An analysis of the time arrangements employed in contemporary backward conditioning studies may help to answer these questions.

Backward conditioning procedures

Independently of the effector system involved, during the last decades three basic varieties of the backward procedure have been used: (1) onset of a backward CS coinciding with termination of an US; (2) a backward CS presented shortly after termination of an US; (3) a short joint action of US and CS followed by a long backward CS.

The first variety constitutes the most unambiguous procedure for backward conditioning (e.g., Memmott and Reberg 1977, Bouton and Bolles 1979, Van Willigen et al. 1987, Bevin and Ayres 1992). The second variety may be labeled trace backward conditioning, since there is a pause between US termination and CS onset (e.g., Plotkin and Oakley 1975, Heth 1976). The third variety has been used earlier by Siegel and Domjan (1971, 1974) in the conditioned suppression situation. Brief shock at the beginning of a longer CS was also presented in some studies involving shock-negative discrimination of conditioned suppression (e.g., Reberg and Memmott 1979), in which backward arrangement of stimuli signalled that shock would not be given at the end of the CS presentation. In all experiments employing this variety of the backward procedure, the ratio between the length of a joint US-CS action and the subsequent CS alone presentation ranged from 1:30 (Reberg and Memmott 1979) to 1:240 (Siegel and Domjan 1971). It seems that contrasting durations of the two phases of a trial are crucial for effectiveness of this variety of backward conditioning.

In a spaced trial procedure, the environmental and temporal stimuli immediately following shock US never closely precede the next US. Thus, they may acquire fear-inhibiting properties (Siegel and Domjan 1971, 1974, Ayres et al. 1976). In other words, the backward CS signals a US-free period. It has been postulated that in classical defensive conditioning the temporally "backward" CS acquires fear-inhibiting properties due to the forward-associative process (Barlow 1956, Moscovitch and LoLordo 1968). Numerous data indicate that a stimulus, even explicitly unpaired with a shock US but presented in the same experimental situation, can acquire punishing properties (e.g., Mowrer and Aiken 1954). The fear-inhibiting backward CS may restore the earlier bar press response rate observed after habituation to the experimental environment and consolidation of acquired appetitive instrumental behaviour, prior to the first punishment experience.

It has to be stressed that in our experiment backward CS did not suppress the alimentary behaviour even at the very beginning of conditioning. Such an outcome might be expected for noise, since this stimulus elicited enhancement of bar presses during the Pretest sessions. By contrast, the early unconditioned response to darkness was a decrease of bar press rate; a similar difference in unconditioned effects of darkness and noise stimuli has been observed previously (Walasek et al. 1994). In spite of this intrinsic (unconditioned) suppressant property, pairing of the darkness backward CS either with mild or with stronger shock resulted in enhanced bar pressing in all phases of training. The Pavlovian notion about the "double effect" of backward conditioning (Pavlov 1927, p.393) is not supported by these findings.

Shock-free period discrimination

In earlier studies employing conditioned suppression procedures, backward conditioning typically resulted in a general lowering of the bar press rate during intertrial intervals. Such "overall suppression" (Matthews et al. 1974) was more pronounced with backward than with forward conditioning (Kamin 1963, James 1971, Davis et al. 1976). Data contaminated by augmented fear conditioned to the contextual non-discrete stimuli make interpretation of the CS effects more difficult (Hall 1984). The backward conditioning procedure, in which onset of a short US coincides with the onset of a much longer CS, provides an effective method to overcome such difficulties. In the present experiment, the pre-CS response rates for separate groups of rats to which forward, backward, and control conditioning procedures were applied did not differ. Elimination of the between-group differences in on-going appetitive responding did not preclude a consistent enhancement of bar presses during the backward CS.

The special properties of the procedure in which onset of a long CS coincided with a brief aversive US may be related to the fact that the early portion of the CS was overshadowed by the more salient aversive stimulation. If a brief US overshadowed the CS onset, the remaining portion of the CS would be paired with the US absence, the next US being presented only after a relatively long intertrial interval which in our experiments was of constant duration.

Originally, the mechanism of overshadowing was proposed to account for interrelations between simultaneously presented elements of compound stimuli (Palladin 1906, Pavlov 1927, p. 141). Theoretical bases of the mechanism of overshadowing were extensively developed and incorporated in contemporary learning theory within the concept of selective attention (Kamin 1969, Mackintosh 1975, 1976). We propose an application of this concept to the situation where two stimulus events occur simultaneously, as a brief US and a CS onset, but one stimulus continues for an extended period of time after termination of the other one.

Support for such an extension was provided by studies analysing the possibility of establishing associations between stimuli presented with very short CS-US intervals. Experiments conducted on different species employing a variety of responses showed little or no conditioning with CS-US intervals close to zero (see reviews by Kimble 1961, Gormezano and Moore 1969). Early in training with simultaneous presentations of CS and aversive US some conditioned responses may be noted, but they soon extinguish (Spooner and Kellogg 1947, Cohen 1950). The level of responding observed during training with a CS-US interval of zero duration did not differ significantly from that produced by pseudo-conditioning (White and Schlosberg 1952, Fitzwater and Trush 1956, Pakovich 1956, Bierbaum 1958, Bitterman 1964). This effect was obtained independently of whether two short stimuli were given simultaneously, or with simultaneous onset of CS and US followed by long action of the CS [1]. On the contrary, CS presented simultaneously with shock US of longer duration acquires punishing properties (e.g., Mowrer and Aiken 1954, Heth and Rescorla 1973).

The time arrangement employed in Group BACK of the present experiment made it possible for the backward CS, but not for the contextual stimuli, to become a safety signal. In this respect, our results are more convincing than those reported previously by Moscovitch and LoLordo (1968). In the latter study, dogs were trained in classical defensive conditioning with a 5 s tone backward CS started 1 s after termination of a shock US. During the test trials in a shuttle-box, the backward CS suppressed continuous (Sidman) avoidance responding. However, the graphs presented by the authors clearly indicate that suppression of the on-going defensive instrumental behaviour was even more pronounced after termination of the backward CS (Moscovitch and LoLordo 1968).

CS-US contingency and stimulus modality interaction

Another significant finding of the present experiment was the enhancement of on-going alimentary bar press responding after termination of the forward CS. Such an enhancement of appetitive behaviour may indicate that the temporal and contextual stimuli after termination of the forward CS became a safety signal. In Group FOR and in Group EMB, a high response rate continued for few minutes after a trial; the rise of expectancy of the forthcoming US within an intertrial interval of constant duration subsequently abated this enhancement of bar presses rate. The duration of the post-trial high response rate period was not influenced by the CS modality. In contrast, enhancement elicited by the action of backward stimuli was more pronounced during noise than during darkness presentations.

The stimulus modality effect was especially pronounced during extinction in our experiment. Shocks not signalled by CSs elicited an increase of fear elicited by contextual cues. Such a change exerted a limited influence on the effect of the noise backward CS, but markedly attenuated the response enhancing properties of the backward darkness CS. The subsequent dissipation of contextual fear when the shock US was discontinued resulted in a gradual recovery of the enhancing effect of the backward darkness CS. In the other groups unsignalled shocks resulted in nearly complete loss of the suppressing properties of the noise forward CS. On the contrary, the darkness forward CS elicited substantial suppression of bar presses even on the last extinction session.

Previously, an interaction of the conditioned stimulus modality and the contingency used has been reported for suppression of the licking response in rats (Van Willigen et al. 1987). Our data on the resistance to extinction clearly demonstrate an interaction between the two variables investigated in the present experiment: the contingency employed during training and the modality of the conditioned stimulus.

[1]It is worth noticing that the simultaneous procedure seems to be ineffective also in alimentary conditioning. Krestovnikov in one variation of his experiments presented a metronome exactly at the moment when the dog's mouth touched food presented in a bowl. After 226 such pairings, the metronome continued to be a neutral stimulus as revealed by the subsequent application of a forward conditioning procedure (Krestovnikov 1921, p. 234).

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