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The effect of context change upon long-term memory of CS duration

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Abstract

An experiment with rats investigated forgetting of inhibition of delay in the conditioned suppression paradigm. The combined effects of contextual change and retention interval were tested. After a reliable temporal discrimination was reached, half of the rats received a test in the training context after a retention interval of 3 or 20 days. The other half received it in a different but equally familiar context at either retention interval. The longest retention interval flattened the temporal discrimination gradient and increased suppression to the CS. A similar but weaker pattern was found with the change of context; this effect was independent of the retention interval. The implications for retrieval and interference theory [Bouton, M.E., 1993. Psychol. Bull., 114: 80–99] and hypotheses concerning the forgetting of specific features of stimuli over time [Riccio, D.C., Richardson, R. and Ebner, D.L., 1984. Psychol. Bull., 96: 152–165] are discussed. © 1997 Elsevier Science B.V.

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1. Introduction

When a long conditioned stimulus (CS) is followed by an aversive unconditioned stimulus (US) in a conditioned suppression paradigm, the conditioned emotional response (CER) develops first to the whole CS. As training progresses, the CER to the first part of the CS becomes weaker, while the CER to the end of the CS tends to remain unchanged (e.g., Hendry and Van-toller, 1965; Millenson and Hendry, 1967). Pavlov (1927) named the final pattern of responding inhibition of delay. He assumed that the first part of the CS acquires inhibitory properties, because it is not directly followed by the US (e.g., Rescorla, 1967).

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Rosas and Alonso (1996) have shown that forgetting in this situation occurs in reverse of the way learning does. That is, as the retention interval increases, the temporal discrimination gradient becomes flatter because of an increase in the conditioned suppression to the first part of the CS. If the first part of the CS had acquired inhibitory properties, one could say that inhibition was forgotten faster than excitation, as has been shown in other conditioning paradigms (e.g., Hendersen, 1978). In more general terms, and without the assumption of acquired inhibition, it could be said that the information learned second was more easily disrupted by the retention interval (as has been pointed out by Bouton, 1993). From this perspective, forgetting of inhibition of delay could be considered akin to spontaneous recovery after extinction (Pavlov, 1927). In both cases the second learned information (extinction) is forgotten relatively quickly over time. Making this assumption, and knowing that contextual change effects on extinction are similar to retention interval effects (e.g., Bouton, 1991; Bouton, 1993), one might expect that the effect of a context switch on inhibition of delay will resemble the effect of retention interval. That is to say, a context change should flatten the temporal gradient. With this background, the first aim of the experiment presented here was to test the effect of a contextual change on the retrieval of the temporal discrimination. We were interested in knowing whether the effect of switching the context resembles that of the retention interval, as it does in the case of extinction.

The assumption of equivalence between context change and retention interval effects is a basic point in some retrieval theories of long-term memory (e.g., Bouton, 1993; Spear, 1973). According to these views, spontaneous forgetting is caused by unavoidable changes in the context (internal and external environment) that occur over the retention interval. However, there is evidence in the literature suggesting that context effects may become smaller with longer retention intervals (e.g., Riccio et al., 1984; Zhou and Riccio, 1994). This pattern has been emphasized by Riccio and colleagues (Riccio et al., 1992; Riccio et al., 1994), who have suggested that context is forgotten over time. According to these authors, since context is subject to forgetting, it cannot be claimed at the same time as causing it. On the other hand, if spontaneous forgetting is caused by implicit contextual changes (e.g., Bouton, 1991; Spear, 1978), the effect of an explicit contextual change should become bigger instead of smaller with the retention interval. That is, the effect of context change and retention interval should be additive (Bouton, 1993). This issue is unresolved, although some experiments have shown that context effects can be observed after quite long retention intervals (e.g., Bouton and Brooks, 1993; Zentall, 1970). Therefore, it is worth asking whether any context effect on the temporal discrimination changes with the retention interval. This was the second objective of the experiment.

2. Method

2.1. Subjects

Thirty-two naive male Wistar rats provided by Letica Instruments were used. They ranged in ad lib. weight from 175 to 249 g just before the experiment began. They were housed individually in acrylic plastic cages located in a room with constant temperature (23°C) and humidity (50%) kept on a 12 h light/dark cycle with light on at 2:30 a.m. The experimental procedures were conducted in a room next to the home room during the dark portion of the cycle. Water was available throughout the experiment. Access to dry food was limited: first, rats spent two days without food, and then they received a food ration daily until they reached 80% of ad lib. weight. This weight was maintained throughout the experiment. However, a correction procedure was used to be sure the level of deprivation was no further that the 80% even with the natural growth of the rat. Rats were handled each day before the experiment began.

2.2. Apparatus

Eight operant boxes (31 × 25.5 × 33 cm) made by Coulbourn Instruments were used. The front panel, ceiling and rear wall were made of aluminum, whereas the side walls and door were made of clear Plexiglas. A food cup (magazine) was 2 cm from the floor in the center of the front wall. An external pellet dispenser delivered 45 mg food pellets (provided by Letica Instruments) into the food cup through a plastic tube. To the right of the magazine was a lever, 6 cm above the floor. The auditory stimulus was provided by a speaker located to the right of the bulb, 25.5 cm above the floor. The floor of the box was composed of stainless steel rods 6 mm in diameter and spaced 1.5 cm apart center-to-center. The floor could be electrified by an AC shock generator. Each box was housed in a sound-attenuating cubicle equipped with a fan that supplied a background noise of 40 dB. All experimental contingencies and response recording were controlled by a Fujitsu AT microcomputer. Two different contexts were used. Four operant boxes were used as context A, which was characterized by ambient light supplied by a 15 W bulb, sepiolite bed in the tray under the floor, and a distinctive olfactory cue provided by a glass containing 15 ml of red wine vinegar (6 degree acidity) made by Vinagrerías Riojanas. Both light bulb and vinegar were placed on the roof of the operant chamber. The other four boxes were used as context B, which was characterized by no ambient light, sawdust bed in the tray, and a distinctive odor from an open pot of Vicks VapoRub (Procter and Gamble) placed on the roof of the chamber.

2.3. Procedure

All sessions lasted 60 min, except for those involved in magazine training, and were conducted daily.

Magazine training. Rats initially received magazine training sessions. Each session had a maximum duration of 30 min. In each, food pellets were delivered on a variable-time (VT) 60 s schedule; lever press responses were continuously reinforced. Each rat finished magazine training after a cumulative total of 100 lever press responses were made.

Training of the lever press response (baseline). Rats then received 20 sessions of lever press training. Two sessions daily were given with an interval of about 4.5 h between them. Half of the animals (randomly assigned) had the morning session in context A and the afternoon session in context B, while the other half had the reverse. The lever press response was reinforced with one food pellet on a variable interval (VI) 30 s schedule in the first day (two sessions). In the remaining sessions, reinforcement was delivered according to a VI 60 s schedule.

Aversive classical conditioning. Sixteen on-baseline classical conditioning sessions in the morning and fifteen operant baseline sessions in the afternoon were then conducted. Context exposures (A then B or B then A) were kept as before to continue to equate exposure to them. Rats received 3 conditioning trials during each morning session. On each trial, a 4.5 kHz tone CS (85 dB) was presented 5 times per second for 150 s, followed immediately by an electric shock of 0.5 mA and 0.5

s duration. The intertrial interval (ITI) was variable around a mean of 780 s. The first trial appeared a mean of 600 s after the beginning of the session. Afternoon baseline sessions were the same as the previous ones. At the end of conditioning, rats were assigned to four groups of 8 subjects each with contexts counterbalanced. They were matched on the mean rate of lever press responding and on suppression to the CS during the last conditioning session.

Test. Rats then received a test session either 3 or 20 days after the end of training. Half the rats were tested at each retention interval. The test session was the same as a conditioning session. Half of the rats at each retention interval received the test session in the same context, and at the same hour of the day (morning) that was used in the conditioning sessions (groups S3 and S20). The other half (groups D3 and D20) received the test session in the different context, and at a different hour of the day (afternoon), than where they had received conditioning (i.e., in the context where they had received the operant lever-press training sessions). During the retention interval, rats remained in their home cages except for being weighed daily. They received one baseline recovery session (VI 60 s training) the day before the test session in the same context and time (afternoon) that they had received the previous lever press training sessions. The rats were equally familiar with context A and B before the test began. Only the data of the first trial of the test were analyzed.

Data analysis. Lever press responses were recorded and suppression ratios to the CS were calculated. Five ratios were obtained in each trial, each corresponding to a fifth of the CS duration. Ratios were computed with the $A/(A+B)$ formula proposed by Annau and Kamin (1961) with a slight modification. A was the number of lever press responses during a period equal to a fifth of the CS duration, and B was the number of lever press responses made during the same duration period without the CS (the mean response rate for that period during the session when the CS was not on). Analyses of variance (ANOVAs) were conducted. For statistical analyses, we adopted a rejection criterion of $p < 0.05$.

3. Results

Rats pressed the lever in a consistent and systematic way. The mean response rates during the last two sessions of baseline training were 36 and 37 responses per minute in context A and B, respectively, in the morning session, and 34 and 37 in the afternoon session. A 2 (context) × 2 (time of day) ANOVA found no significant effect of context, time of day, or interaction, $Fs < 1$. There were also no differences between the groups. On the last session of conditioning, the mean rate for groups S3, D3, S20 and D20 were, respectively, 35, 45, 35, and 34 responses per minute. During the test, the mean rates were 25, 34, 27 and 24 responses per minute for the same groups. None of these differences were significant, $Fs < 1$. The absence of differences among rates of bar pressing during the test suggest that, even though the subjects in the long retention interval groups were tested later than the ones in the short retention interval groups, their motivation level during the test was comparable.

Conditioning proceeded uneventfully and in the same way as has been described elsewhere (e.g., Millenson and Hendry, 1967). A reliable temporal discrimination had developed by the end of training. The left panel of Fig. 1 shows the mean suppression ratios plotted across fifths of the CS during the last conditioning trial for the four groups. Conditioned suppression was clearly higher at the end of the CS than at the beginning of it in all groups. Consistent with this impression, a 2

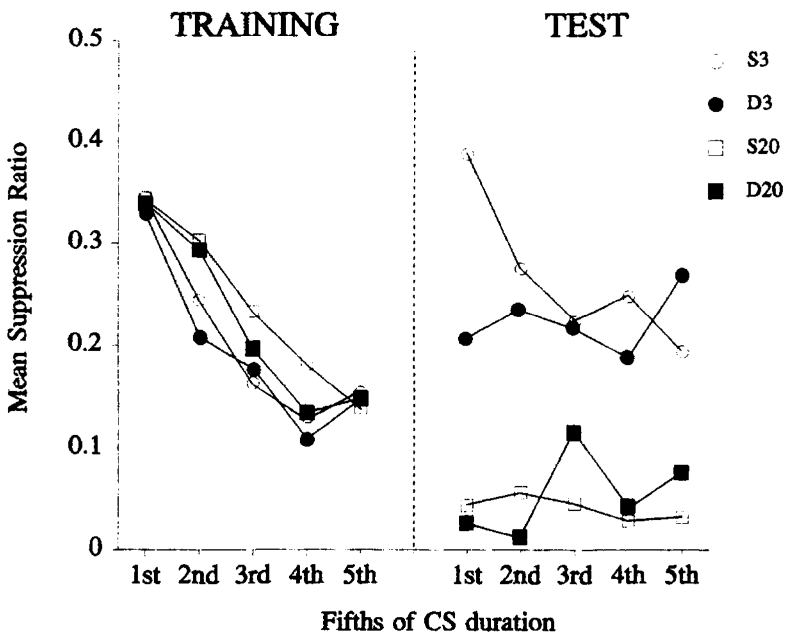

Fig. 1. Mean conditioned suppression ratios plotted across fifths of the CS duration during the last trial of training (left panel) and the first test trial (right panel) for groups S3, D3, S20 and D20.

(context same versus different) × 2 (retention interval) × 5 (fifths) ANOVA only found a significant main effect of fifths, $F(4, 112) = 18.3$. The remaining main effects and interactions were not significant, $Fs < 1$.

The right panel of Fig. 1 shows the mean suppression ratios plotted across fifths of the CS during the first test trial. At the 20 day test (groups S20 and D20), there was a general increase in suppression to the CS accompanied by a flattening of the temporal discrimination gradient. Contextual change yielded a similar flattening of the temporal gradient in the 3 day test (group D3); this was primarily a consequence of an increase in the suppression to the beginning of the CS. A 2 (context same versus different) × 2 (retention interval) × 5 (fifths) ANOVA found a main effect of the retention interval, $F(1, 28) = 17.1$, and a significant context by fifths interaction, $F(4, 112) = 3.4$. The rest of the main effects and interactions were not significant, $Fs \leq 1.9$. Subsequent analyses exploring the context by fifths interaction found a significant simple effect of context in the first fifth, $F(1, 112) = 8.6$, but not in the others, $Fs(1, 112) \leq 3.1$. Moreover, only the subjects tested in the same context where they were trained showed a significant simple effect of fifths, $F(4, 112) = 2.7$.

4. Discussion

These results demonstrate an increase in conditioned suppression to the CS accompanied by a loss of the temporal discrimination gradient with the 20 day retention interval. The forgetting of the temporal discrimination over time without apparent loss of the CS–US association replicates the results previously reported by Rosas and Alonso (1996). It also resembles the loss of temporal discrimination that is observed with long retention intervals after training with fixed interval (e.g., Gleitman and Bernheim, 1963) or differential low-rate (Lejeune, 1989) reinforcement schedules. In the present experiment, such an effect was evident regardless of the test context.

Importantly, the change of context led to an increase in suppression to the beginning of the CS and consequently a flattening of the temporal discrimination gradient. This effect, without being as intense, resembles a major effect of the retention interval observed here and elsewhere (Rosas and Alonso, 1996). The flattening of the temporal gradient that now appears to result from both a context switch and a retention interval suggests that context switches and retention interval have similar effects. Such a conclusion is consistent with the view that spontaneous forgetting (the one that happens with the retention interval) can be attributed to a contextual change (e.g., Bouton, 1993; Spear, 1978) — retention interval is a context switch.

The idea that a retention interval is a context switch also suggests that the effect of the change in the context might be greater with the long retention interval: The switched group tested at the long retention interval effectively received two context switches. Additivity of the two effects was not found in this experiment, but this is likely attributable, at least in part, to the floor effect that was evident in suppression at the 20 day interval. On the other hand, it is true that statistical analyses suggested that the context effect was independent of the retention interval. The interpretation of forgetting given by Riccio and colleagues (Riccio et al., 1984; Riccio et al., 1992; Riccio et al., 1994) would predict an interaction between these two factors — the context switch effect should have decreased with the long retention interval — and the absence of it could be taken as evidence against this hypothesis. However, once again the floor effect in the 20 day test must constrain our conclusions in this respect.

As has been pointed out above, the context effect at the 3 day retention interval resembled the 20 day retention interval effect in the sense that the temporal discrimination disappeared in both cases. However, the two effects were not exactly alike: The long retention interval also yielded a general increase in conditioned suppression that the contextual change did not. This difference might suggest that the effects are not really equivalent and, thus, that retention interval effects cannot be exclusively explained as a consequence of a change in the context. In fact, this result was not entirely unexpected. In this procedure, we usually find both a strong decrease in the suppression to the beginning of the CS, and a smaller decrease in the suppression to the end of the CS over training. The later effect is similar to other non monotonic learning curves that are known to occur in conditioned suppression (e.g., Annau and Kamin, 1961; Hendry and Van-toller, 1965; Millenson and Dent, 1971). This effect is often attributed to US habituation; that is, the US may become less aversive over training. This possibility sets the stage for two possible effects of the retention interval: Forgetting of inhibition to the first part of the CS (Rosas and Alonso, 1996) plus recovery from habituation over time (e.g., Carew et al., 1972; Hall and Schachtman, 1987; Leaton, 1974). As habituation has been shown to transfer well between equally familiar contexts (e.g., Hall and Channell, 1985), the contextual change effect should have only affected the retrieval of the associative information (temporal discrimination), as indeed it did. The main implication of this argument is that retention intervals can be expected to produce complex effects; some of them are associative and some are non associative. Retrieval theories that emphasize the parallel between retention intervals and context switches have usually addressed only their associative effects.

In this regard, it is also worth noting that context switches can also lead to complex effects, not all of which are memory retrieval effects (e.g., Devenport, 1989). The effect of context in this experiment was mainly an increase in the suppression to the first part of the CS. It is worth considering the possibility that the presentation of the CS in a context where it was not expected could lead to either dishabituation or disinhibition (Wagner, 1981). For example, an increase in suppression to the first part of the CS could reflect a loss of habituation of unconditioned suppression in the new context. Although this explanation is not easy to rule out, it is worth noting several results that challenge it. First, habituation usually transfers well between contexts whenever these contexts are familiar to the subject, as was the case here (e.g., Hall, 1991; Hall and Channell, 1985). Dishabituation or disinhibition usually occurs when the subject is exposed to a novel stimulus before testing the habituated stimulus (e.g., Groves and Thompson, 1970; Pavlov, 1927). Obviously, in the present experiment, the changed context was not new to the subject, since the rats were exposed to both contexts equally throughout the experiment. However, it could be argued that the new stimulus here was the relationship between the test context and the CS. In other words, perhaps the rats did not perceive the CS in the test context as the same CS as the one in the training. This possibility seems unlikely because the fact that habituation transfers across familiar contexts is often taken as an indicator that the rats perceived the CS as the same in different contexts (e.g., Hall and Honey, 1989).

In summary, the results of this experiment shows that a context switch abolishes inhibition of delay. This effect was similar, but not identical, to the retention interval effect. The difference between the effects is a challenge for retrieval theories, but it cannot be explained either by the hypothesis concerning the forgetting of specific features of stimuli (e.g., Riccio et al., 1984).

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