

Temporal Discrimination and Forgetting of CS Duration in Conditioned Suppression

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Two experiments with rats investigated a temporal discrimination, and the forgetting of it, using the conditioned suppression paradigm. Experiment 1 showed that the conditioned emotional response (CER) increased as a function of time in the conditioned stimulus (CS), with a maximum near the unconditioned stimulus (US), when a long CS was immediately followed by the US. Location of the maximum response was taken as an index of the expected time of US. When the CER was recorded in time-proportional units (every fifth of the CS), the temporal discriminations found with CS durations of 50, 100, 150, and 200 s superposed. Experiment 2 showed forgetting of the temporal discrimination (flattening of the temporal discrimination gradient) after a retention interval of 20 days, but not after 3 or 7 days. The forgetting of the temporal discrimination resulted in an increase in the CER at CS onset. Thus, a high level of suppression to the whole CS was found after the retention interval of 20 days. Results were consistent over each of the CS durations employed. © 1996 Academic Press, Inc.

The capacity of animals to process information about time is well reflected in the literature (see Church, 1984, 1989; Richelle & Lejeune, 1980). It is well known that the duration of an event or the interval between events may be perceived by animals in a variety of situations, resulting in behavior that changes systematically over time. Traditional examples of this type of temporal discrimination may be found in situations such as temporal conditioning (e.g., Pavlov, 1927; Williams, Frame, & Lolordo, 1992) and the fixed-interval schedule (e.g., Ferster & Skinner, 1957; Lejeune & Wearden, 1991).

Temporal discrimination also occurs when a long conditioned stimulus (CS) is followed by an unconditioned stimulus (US) in a Pavlovian conditioning situation. In that case, the conditioned response (CR) appears with either a long

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latency or maximum strength at the end of the inter-stimulus interval, i.e., at the expected time of the US. Pavlov (1927) found the phenomenon using salivary conditioning in dogs, and he called it inhibition of delay. The effect has also been found with other paradigms and animals: eyeblink (e.g., Boneau, 1958) and galvanic skin response conditioning (e.g., Rodnick, 1937) in humans, nictitating membrane conditioning in rabbits (e.g., Schneiderman & Gormezano, 1971), autoshaping in pigeons (e.g., Fernandez Serra, 1990), leg flexion response conditioning in dogs (e.g., Lynch, 1973), and conditioned suppression in rats (e.g., Hendry & Van-Toller, 1965; Schachtman, Channel, & Hall, 1987), among others.

Using the conditioned suppression paradigm, temporal discrimination has been obtained when the inter-stimulus interval has ranged between 30 and 360 s in different experiments (Davis, McIntire, & Cohen, 1969; Hammond & Maser, 1970; Hendry & Van-Toller, 1965; Holmes, Jackson, & Byrum, 1971; Libby & Church, 1975; Millenson & Hendry, 1967; Schachtman *et al.*, 1987; Zielinsky, 1966; Zielinsky & Grazyna, 1977). However, as far as we know, no study has compared temporal discrimination of the conditioned emotional response (CER) with CSs of different durations. Timing studies with other procedures suggest that animal behavior is equivalent with different event durations when the behavior is recorded in units of time that are proportional to the total event duration (e.g., Church & Gibbon, 1982). This is known as the superposition result, and it is a basic prediction of the scalar expectancy theory of timing (Church & Gibbon, 1982; Gibbon, 1977). Superposition has usually been found when operant behaviors (lever pressing, computer key pressing or key pecking) are involved (e.g., Church & Deluty, 1977; Gibbon & Church, 1990; Wearden, 1992). It has only occasionally been tested in classical conditioning, specifically with a temporal conditioning procedure (Killeen, 1975; LaBarbera & Church, 1974). Superposition theoretically results from a decision making process based on a comparison between estimated and stored time which is done in proportional rather than absolute terms (e.g., Church, 1984, 1989). To understand the generalizability of the phenomenon, it is valuable to know whether a similar result is found in other classical conditioning situations. This could further contribute to an understanding of the cognitive processes mediating Pavlovian conditioning and whether these processes are shared with operant conditioning. We therefore examined inhibition of delay as it developed to CSs of different duration in the conditioned suppression paradigm. According to the theory, if the CER to the CS of different durations is recorded in proportional units (for instance, every fifth of the CS), the CER in each period will be equivalent for all CS durations.

The present research also tested the effect of the passage of time on the memory of the temporal discrimination. Memory for time has enjoyed a large amount of interest in the last twenty years. However, researchers have focused almost exclusively on short-term memory for time (e.g., Church, 1980; Spetch, 1987). We know relatively little about long-term memory for time. Most of the few studies that have addressed it have been centered on memory formation and

storage processes, paying little attention to the retrieval process (e.g., Meck, Church, & Olton, 1984).

With respect to retrieval processes, it has usually been found that temporal information is at least partially forgotten with retention intervals ranging between 10 and 90 days (e.g., Campbell, Krauter & Wallace, 1980; Gleitman & Berheim, 1963; Gleitman, Steinman, & Berheim, 1965; Lejeune, 1989). However, the CR itself is remembered well over the same retention intervals. Animals seem to forget when the behavior should be done but not what the behavior is. There are, nevertheless, a few studies in which temporal discrimination was retained after 21 (Hamm, Dixon & Knisely, 1984) or 27 days (Crouse & Cohen, 1987). For Crouse and Cohen (1987), the temporal memory may have been unusually strong because a within subjects design was used; the rats were retrained repeatedly prior to testing different retention intervals. For Hamm *et al.* (1984), the absence of forgetting may have been because the retention interval was too brief; forgetting was obtained by others (Lejeune, 1989) using the same procedure with a longer retention interval (90 days).

As far as we know, the only study of the long-term memory of CS duration using the conditioned suppression paradigm was conducted by Hammond and Maser (1970). Consistent with the results of other procedures, they found that discrimination of the CS duration disappeared when a retention interval of 25 days was inserted between training and testing. Apparently, the overall conditioned suppression to the CS was not affected by the retention interval. However, a careful review of their results indicates that the overall level of CER at the test was actually quite low (the mean suppression ratios were around 0.4), and most important, lower than that found even to the last part of the CS at the end of the training for the majority of the subjects. This may suggest that the subjects had forgotten that the CS was followed by the US after the retention interval. This unusual result may have been due to an specific aspect of the procedure: To obtain inhibition of delay, the authors found it necessary to present weak shocks in the absence of the CS. This could have made excitatory conditioning too weak to be remembered with the passage of time. The result is somewhat surprising, as conditioned suppression is usually not affected by retention intervals even larger than 90 days (e.g., Gleitman & Holmes, 1967; Hoffman, Selekman & Fleshler, 1966). Even when an inhibitory process is also involved (e.g., Hendersen, 1978), forgetting of fear excitation does not occur after retention intervals of 25 or 35 days. However, it is possible that when a temporal discrimination is involved, a different effect of retention interval may be found. To assess this possibility, we examined forgetting of the temporal discrimination after different retention intervals.

EXPERIMENT 1

The main purpose of the first experiment was to compare the temporal discrimination that developed with different CS durations (50, 100, 150, and 200s). According to scalar expectancy theory (see Church & Gibbon, 1982; Gibbon,

1977), a superposition result should be obtained when the response is recorded in proportional time units. That is, if the CER is recorded for each fifth of the CS duration, then a similar pattern of temporal discrimination should be obtained with each duration of the CS.

Method

Subjects

Thirty-two naive male Wistar rats were used. They were provided by Leticia Instruments. They ranged in *ad lib* weight from 195 to 241 g just before the experiment began. They were housed individually in makrolon cages located in a room with constant temperature (23°C) and humidity (50%) that was maintained 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 2 days without food, and then they received a food ration daily until they reached 80% of *ad lib* weight. This weight level was maintained throughout the experiment. However, a correction procedure was used to adjust for the natural growth of the rat. All the rats were weighed before deprivation started and the proportional deviation from the mean weight was then calculated for each rat. Using the natural growth curve provided by the breeders, the 80% target weight was calculated by multiplying 80% of the mean expected weight by the proportional deviation corresponding to each rat. Rats were handled each day before the experiment began.

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 Leticia Instruments) into the food cup through a plastic tube. To the right of the magazine was a lever, 6 cm above the floor. Ambient illumination was provided by a 2-lux white incandescent bulb placed 20.5 cm above the food cup. The CS 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 (E 13-08). 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.

Procedure

All sessions lasted 60 min, except for 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 one, food pellets were delivered on a variable-time (VT) 60-s schedule; lever press responses were continuously reinforced (CRF). Each rat finished magazine training after 100 lever press responses were made.

Training of the lever press response. Rats received eight further training sessions of lever press response. The lever press response was reinforced with one food pellet on a variable interval (VI) 30-sec schedule in the first session. In the remaining sessions, reinforcement was delivered according to a VI 60-s schedule. At the end of the training, rats were distributed into four groups of eight subjects each that were matched on the mean rate of lever pressing in the last three sessions.

Aversive classical conditioning. Thirty on-baseline classical conditioning sessions were then conducted. After every five sessions, a rest day and a lever press recovery session were inserted. Rats received three conditioning trials per session. On each trial, a 4.5 KHz tone CS (85 dB) was presented 5 times per second (5Hz), immediately followed by an electric shock of 0.5 mA and 0.5 s duration. The CS duration was different in each group: 50 (group 50), 100 (group 100), 150 (group 150) and 200 s (group 200). 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.

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 by 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 in the absence of the CS (calculated from the mean response rate during the session when the CS was not on). Analyses of variance (ANOVAs) were conducted. For statistical analyses, we adopted a rejection criterion of .05, except when differences were not expected a priori; in this case, a Bonferroni correction procedure was used to minimize Type 1 error ($p < .05/\text{number of comparisons}$).

Results and Discussion

Training of the Lever Press Response. Rats pressed the lever in a consistent and systematic way. The mean rates were 34, 33, 34, and 30 responses per minute for groups 50, 100, 150, and 200, respectively, during the three last sessions of baseline training. The differences among groups were not statistically significant [$F(3,28) = 0.09$].

Aversive Classical Conditioning. Figure 1 shows the mean conditioned suppression ratios plotted across fifths of the CS duration and over the six blocks of five sessions for Groups 50, 100, 150, and 200. Starting with a high level of conditioned suppression to the whole CS, a differential level of the CER across

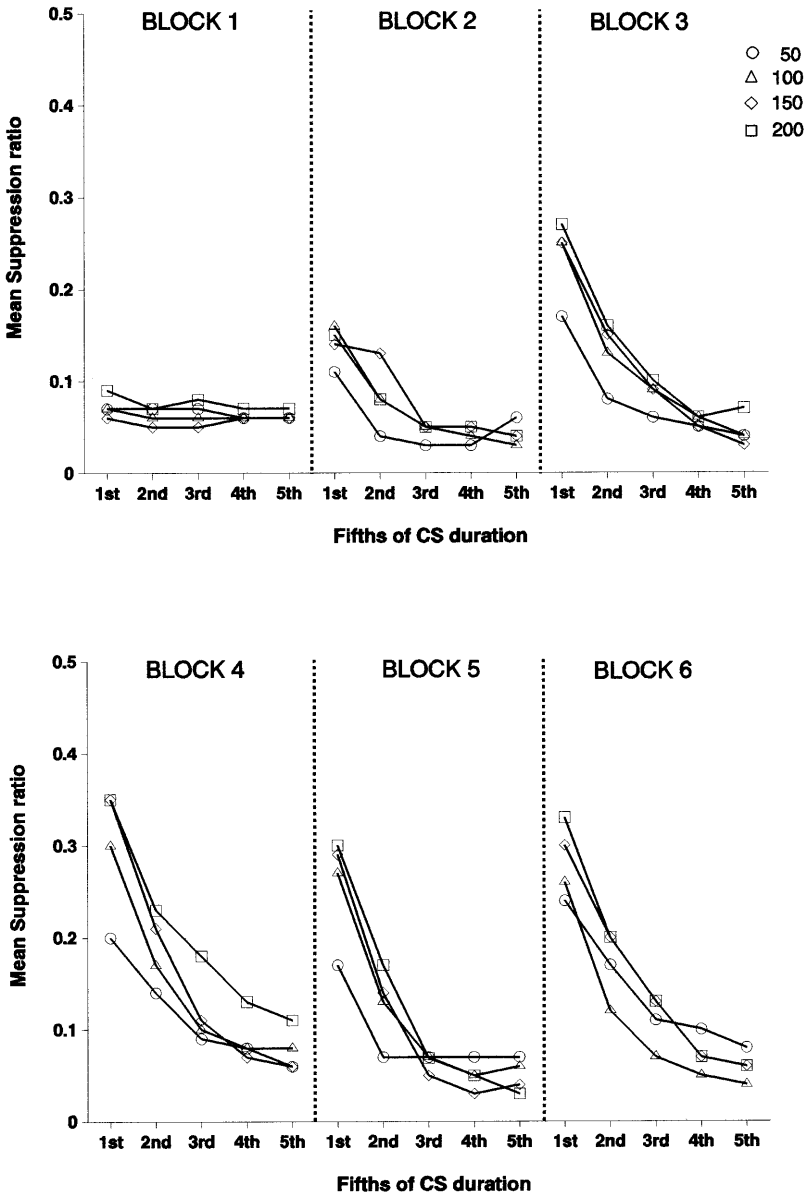


FIG. 1. Mean conditioned suppression ratios plotted across fifths of the CS duration and over the six blocks of five sessions for Groups 50, 100, 150, and 200.

the CS duration emerged as training progressed. Suppression to the CS onset decreased, whereas it remained constant toward the end of the CS. At the end of conditioning, the CER was increased over the CS duration in a manner that appeared to be independent of the CS duration.

Statistical analyses confirmed the visual impression. A 4 (groups) \times 5 (fifths) \times 6 (blocks) ANOVA was conducted. It found a significant main effect of fifths [$F(4,112) = 108.3$] and blocks [$F(5,28) = 20$], and also significant interactions of groups by fifths [$F(12,112) = 2.03$], fifths by blocks [$F(20,560) = 27.88$] and groups by fifths by blocks [$F(60,560) = 1.36$]. There was no significant effect of groups [$F(3,28) = 0.6$] or groups by blocks interaction [$F(15,140) = 0.99$].

Subsequent analyses revealed a significant effect of fifths in every block [$F_s(4,356) > 24.9$], except in Block 1, and in every group [$F_s(3,356) > 6.5$], except for Group 50 in Block 2. Analyses also revealed a significant effect of the blocks in every fifth [$F_s(5,317) > 3.34$] except for the last one. This means that, as training progressed, there was a decrease in the suppression to the first four fifths of the CS duration. A reliable discrimination of CS duration was evident after Block 1, except for Group 50, which appeared to be slightly slower in acquiring the discrimination.

A 4 (groups) by fifths (5) analysis of data from Block 6 was conducted to test the superposition effect at the end of the training. It revealed a significant effect of fifths [$F(4,356) = 107$] but not of groups [$F(3,44) = 2.7$]. Most important, there was no fifths by groups interaction [$F(12,356) = 1.5$], suggesting that the pattern of suppression over fifths was independent of the CS duration. Thus, the results confirm and extend the superposition effect found with operant (e.g., Gibbon & Church, 1992) and temporal (e.g., LaBarbera & Church, 1974) conditioning. Superposition appears to be a general phenomenon.

Finally, the mean baseline lever-press response rates (rpm) for groups 50, 100, 150, and 200 were, respectively: Block 1: 25, 22, 26, and 21; Block 2: 36, 47, 42, and 37; Block 3: 40, 54, 52, and 49; Block 4: 41, 58, 57, and 53; Block 5: 40, 55, 53, and 44; and Block 6: 38, 53, and 46. There were no significant differences among groups in any of the blocks [$F_s(3,28) < 1$].

As expected, rats ultimately displayed a higher CER to the CS the closer it was to the shock occurrence. This suggests that rats discriminated the CS duration after training. Furthermore, temporal discrimination seemed to be independent of the particular duration employed as it was found to a CS duration of 50, 100, 150, or 200 s. However, the discrimination was acquired most slowly with a CS duration of 50 s.

EXPERIMENT 2

Once a reliable temporal discrimination was obtained, we ran an experiment in which we tested whether the temporal information was lost with the passage of time. Following Experiment 1, every subject was tested after retention intervals of 3, 7, and 20 days. Increasing the retention interval might produce an increase of forgetting of the temporal discrimination. We were especially interested in whether such forgetting was independent of the CS duration, and whether forgetting of temporal information was accompanied by a loss (Hammond & Masser, 1970), or retention of the CR (e.g., Gleitman & Berheim, 1963; Lejeune, 1989).

Method

Subjects and Apparatus

The same subjects and apparatus were used.

Procedure

Rats received tests session 3, 7, and 20 days after the end of the training of Experiment 1. Each test session was identical to a conditioning session of Experiment 1. During the retention interval, rats rested in their home cages, except for one recovery session of the lever press response (VI 60-s training) that was given the day before each test session. These recovery sessions were identical to the previous ones. The 80% food deprivation procedure was in effect throughout the experiment.

Suppression ratios were calculated and analyzed the same as in Experiment 1, but only data of the first trial of each test were considered. Data from the last conditioning trial of the Experiment 1 were also included as a baseline estimate of the temporal discrimination.

Results

Figure 2 shows the suppression ratios plotted across the fifths of the CS duration during the last trial of training (upper left panel) and the first trial of the tests after 3 (upper right panel), 7 (bottom left panel), and 20 (bottom right panel) days. The use of single-trial data instead of blocks of sessions as used previously introduced greater variability. Nonetheless, the results suggest a loss of the temporal discrimination after 20 days but not after 3 or 7 days, independently of the CS duration. The CER itself was retained with the passage of time.

A 4 (groups) \times 5 (fifths) \times 4 (tests, including the last trial of training) ANOVA was conducted. It found a significant main effect of groups [$F(3,28) = 3.02$], fifths [$F(4,112) = 19.18$] and tests [$F(3,84) = 5.73$]. The fifths by tests interaction was significant [$F(12,336) = 19$], but the groups by fifths [$F(12,112) < 1$] and the groups by test [$F(9,84) = 1.37$] interactions were not. The groups by fifths by test interaction was significant [$F(36,336) = 1.59$].

Subsequent one-way analyses of variance revealed significant effects of the fifths at the last trial of training for every group except Group 50, and at the 3-day and 7-day tests for every group except Group 100 [$F_s(4,394) > 2.6$]. The effect of fifths was not significant at the 20-day tests for any group, suggesting a loss of the temporal discrimination. Moreover, the effect of tests was significant in the first and the second fifth for every group and in the third fifth for groups 100 and 200 [$F_s(3,415) > 2.7$]. In general, the suppression level to the early portions of the CS was increased for every group at the 20-day test.

A significant effect of the groups was only obtained in the second fifth at the end of the training and at the 3-day test [$F_s(2,124) = 3.02$]. In both cases, the suppression level for Group 200 was lower than for 50 and 150 groups. Applying

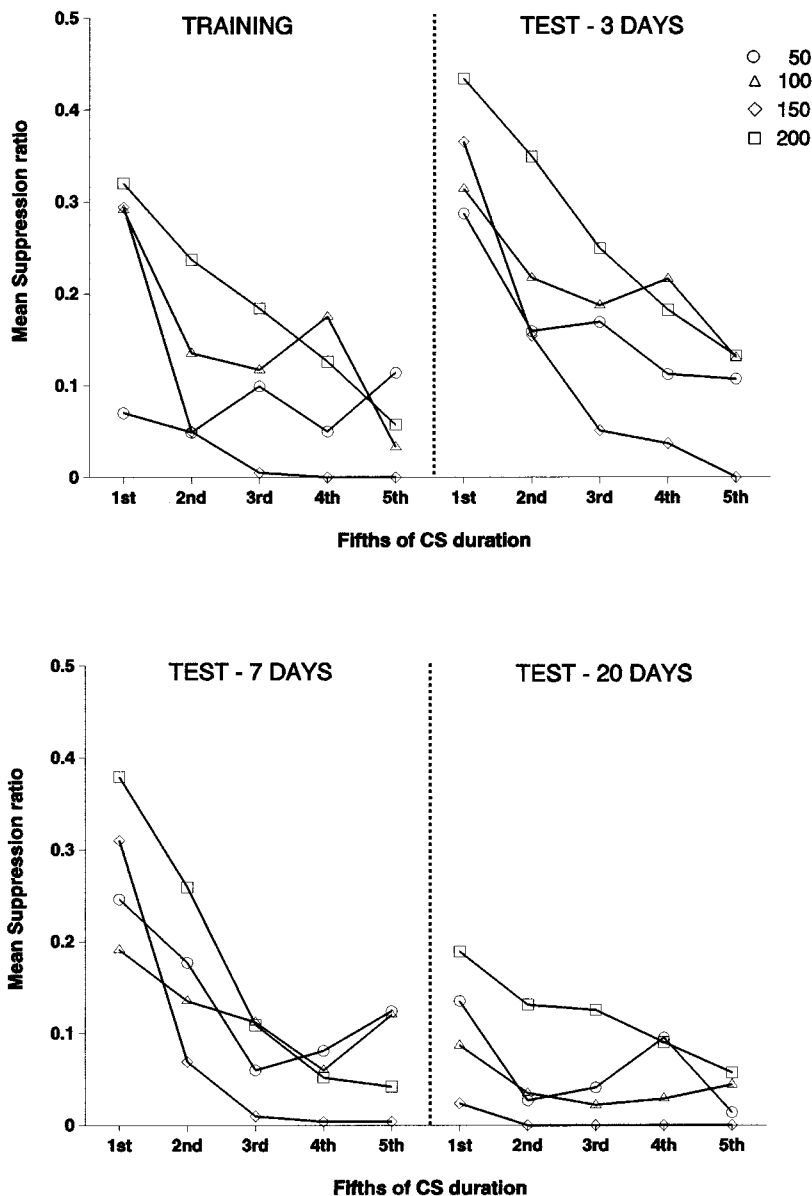


FIG. 2. Mean conditioned suppression ratios plotted across fifths of the CS duration during the last trial of training (upper left panel) and the first trial of the tests after 3 (upper right panel), 7 (bottom left panel), and 20 (bottom right panel) days for Groups 50, 100, 150, and 200.

the Bonferroni criterion ($p < .002$), however, these differences were not significant.

The mean baseline lever press rates (rpm) for groups 50, 100, 150, and 200 were, respectively, 39, 57, 51, and 46 during the last training session; 41, 61, 46, and 44 during the 3-day test; 37, 51, 51, and 38 during the 7-day test; 29, 44, 35, and 35 during the 20-day test. The differences among groups were not significant [$F_s(3,28) < 1.5$].

In general, the results suggest that there was little forgetting of temporal discrimination 3 and 7 days after training. However, forgetting was clearly obtained 20 days after training. This forgetting took the form of an increase in the CER to the initial part of the CS that yielded a flattening of the temporal discrimination gradient. On the other hand, no forgetting of the CER itself was found.

The time-course of forgetting may have varied to some extent as function of the CS duration. For instance, the discrimination was not reliable for Group 50 on the last trial of training, although this was presumably attributable to the variability introduced by one trial data, since it was evident 3 and 7 days later. Still, there was also no discrimination of the 100-sec duration 3 and 7 days after training, while the temporal discrimination seems to have actually improved with durations of 50 and 200 at the same time. Therefore, although the forgetting of temporal discrimination 20 days after training was clearly independent of the CS duration, the time-course of forgetting may have depended on it to some extent.

GENERAL DISCUSSION

The presentation of a long CS immediately followed by an aversive US initially produced a strong CER throughout the whole CS, but as training progressed, the strength of the CER decreased during the early parts of the CS, so that the CER increased as a function of CS duration. The maximum CER occurred near the US, which we take as an index of the expected time of the US. Learning of the temporal discrimination took the form of the animals showing decreased CER to the early parts of the CS. In general terms, this result was found regardless of whether the CS duration was 50, 100, 150, or 200 s. Rats are clearly able to discriminate CS duration in the conditioned suppression paradigm.

The change in the temporal pattern of the CR after training looks similar to that described previously in the literature (e.g., Millenson & Hendry, 1967). It suggests that rats associated the aversive consequence first with the general features of the CS, and ultimately with the end of the CS. Obviously, this change in the association requires a discrimination between the beginning and the end of the CS. One explanation was first proposed by Pavlov (1927). A temporal discrimination may be a consequence of changes in the CS perception while CS is on. Since the US only coincides with the last perception of the CS, but not with the first one, the first part of the CS should acquire inhibitory properties, resulting in a CR to the first part of the CS that is weaker than that to the last part.

This account of time discrimination does not handle all aspects of the present results. Most important, it does not make a priori predictions about the effect of different CS durations on the temporal discrimination; it does not predict the present superposition. Nowadays, the most general theory of time discrimination is the internal clock theory (see Church, 1989; Gibbon, 1977), which assumes an internal clock with properties analogous to a standard stopwatch (e.g., Church, 1984; Roberts, 1983). The clock also involves memory and comparator mechanisms. In the situation described here, CS duration would be stored in reference memory. While the CS is on, its current duration value would be contrasted with the stored duration value. As the difference between these two values decreases, the strength of the CR would increase. The theory assumes that the comparison rule in the comparator is proportional. Thus the CR would not vary with the real time spent in the CS, but instead, with proportional units of it. One consequence of this assumption is the prediction of superposition.

However, even after accepting internal clock theory, it is still possible to consider Pavlov's idea about the acquisition of inhibition to the first part of the CS. Internal clock theory explains how the rat might recognize the stimulus duration, and suggests that the CR to the CS onset would be smaller because its current duration value is still far from the stored one. Pavlov's theory would add the idea that this smaller response at CS onset is caused by the influence of inhibition. There is evidence that the first part of a CS acquires inhibitory properties (Pavlov, 1927; Rescorla, 1967), although there was no test for inhibition in our work.

Even though the temporal discrimination seemed to occur in the direction of superposition prediction, it was not entirely consistent with it. The performance to the 50-s CS was not completely consistent with the others. The acquisition of the temporal discrimination was apparently slower, and the final temporal discrimination, although good when the last block of 5 sessions was considered, was not evident when the last trial of training was regarded alone. This result was not likely due to the rat's inability to discriminate durations shorter than 50 seconds. The timing literature shows that rats can discriminate event durations even as short as 2 or 8 s (see Church & Gibbon, 1982). Since timing of such short durations was found using tasks quite different to that used here, it could still be argued that in this specific procedure the use of a CS longer than 50 s is necessary to support the discrimination. However, this argument seems unlikely as Davis *et al.* (1969) found a reliable temporal discrimination of a 30-s duration CS using a procedure similar to the one we used. Moreover, the slower acquisition rate of the discrimination observed when the CS duration was 50 s is unlikely due to a slower conditioning rate. Excitatory conditioning occurred at the same rate with the different CS durations. In addition, one could expect the opposite result: shorter CS would be conditioned quicker with the same inter-trial interval (e.g., Gibbon & Balsam, 1982; Stein, Sidman & Brady, 1958).

The weaker temporal discrimination obtained here with the 50-s CS may reflect the influence of the combined effect of the mean VI duration (to obtain

food) and the CS duration (to US occurrence). Given that animals may discriminate the mean interval duration between reinforcers (Kacelnik, Brunner, & Gibbon, 1990), and given that the mean VI duration (60 s) was greater than the CS duration (50 s), that discrimination may interfere, in some unknown way, with the CS duration discrimination. Indeed, the only conditioned suppression study we know reporting a temporal discrimination with a CS shorter than 50 s (Davis *et al.*, 1969) used a mean VI duration equal to the CS duration (30 s in both cases).

With respect to the effect of the retention interval, we did not find memory deficits 3 and 7 days after training. However, 20 days later we found a loss of the temporal discrimination. Flattening of the temporal gradient was observed as a consequence of an increase of the CER during the first part of the CS. It seems that rats forgot the CS duration, but not the "meaning" of the CS; they did not forget that the CS is followed by the US. That was in general true regardless of what the CS duration was. It should be noted that in the present design, rats tested after 3, 7, and 20 days were actually tested 3, 4, and 13 days since their most recent conditioning session. Therefore, our results may provide conservative estimates of forgetting at our nominal retention intervals.

Our forgetting results are essentially in agreement with those of Hammond and Masser (1970). These authors found a loss of temporal discrimination after a retention interval of 25 days. However, they also found that the average level of conditioned suppression across intervals of the CS was the same at the end of training and at the test, whereas our results showed that it was higher at the 20-day test, particularly during early parts of the CS. In this respect, our results are different from these obtained by Hammond and Masser, but consistent with those who have shown strong retention of conditioned suppression after intervals even longer than 90 days (e.g., Gleitman & Holmes, 1967). Furthermore, they are also consistent with the results of some experiments using a fixed interval schedule (e.g., Gleitman & Berheim, 1963) and a differential low-rate reinforcement schedule (Lejeune, 1989). In both cases, the temporal discrimination was forgotten but the conditioned response was retained.

The differential forgetting obtained in this study may be consistent with modern theories of the interference and retrieval that have emphasized the rapid forgetting of inhibition (e.g., Bouton, 1993, 1994). However, it would be necessary to assume that, in this situation, the first part of the CS had acquired inhibitory properties, which competed with the excitatory properties initially acquired by the CS, as Pavlov (1927) had proposed. Pavlov also considered that conditioned inhibition is weaker than conditioned excitation and, in turn, easier to dissipate with the passage of time. This idea has been taken up again by Bouton, who suggests that conditioned inhibition would be more easily disrupted by retention interval or changes in the context. Bouton also suggests that the information learned second would be forgotten sooner. Therefore, according to this theory, temporal discrimination (learned in the second place) and/or conditioned inhibition (weaker and learned in the second place) would be more easily

affected than conditioned excitation by the implicit changes in the context produced by the passage of time. At any rate, the excitatory properties (the CR) to the whole CS would be displayed after time elapsed, as occurred here.

The results are also consistent with the differential forgetting of the stimulus features hypothesis (Riccio, Rabinowitz & Alxerod, 1994; Riccio, Richardson, & Ebner, 1984). That hypothesis implies that animals will forget the specific characteristics of the conditioning situation, but remember other more general features with the passage of time. Thus, as retention interval increases, rats might remember that the CS is followed by the US, but they might generalize the CR across multiple CS durations.

In summary, these results suggest that rats are able to discriminate the CS duration with enough training, that this discrimination is scalar, and that the temporal information about the CS is forgotten with the passage of time. Precisely what aspect of the discrimination was forgotten, however, is not yet clear.

REFERENCES

- Annau, Z., & Kamin, L. J. (1961). The conditioned emotional response as a function of intensity of the US. *Journal of Comparative and Physiological Psychology*, **54**, 428–432.
- Boneau, C. A. (1958). The interstimulus interval and the latency of the conditioned eyelid response. *Journal of Experimental Psychology*, **56**, 464–471.
- Bouton, M. E. (1993). Context, time, and memory retrieval in the interference paradigms of pavlovian learning. *Psychological Bulletin*, **114**, 80–99.
- Bouton, M. E. (1994). Conditioning, remembering and forgetting. *Journal Experimental Psychology: Animal Behavior Processes*, **20**, 219–231.
- Campbell, B. A., Krauter, E. E., & Wallace, J. E. (1980). Animal models of aging: sensory motor and cognitive function in the aged rat. In D. G. Steing (Ed.), *Psychobiology of aging: Problems and perspectives* (pp. 201–226). North Holland: Elsevier Press.
- Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: a study of some temporal properties of behavior. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1–42). New York: Appleton-Century-Crofts.
- Church, R. M. (1980). Short-term memory for time intervals. *Learning and Motivation*, **11**, 208–219.
- Church, R. M. (1984). Properties of the internal clock. In J. Gibbon & L. G. Allan (Eds.), *Timing and time perception* (pp. 566–582). New York: Annals of the New York Academy of Sciences.
- Church, R. M. (1989). Theories of timing behavior. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 41–71). Hillsdale, NJ: Erlbaum.
- Church, R. M., & Deluty, M. Z. (1977). Bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behavior Processes*, **3**, 216–228.
- Church, R. M., & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes*, **8**, 165–186.
- Crouse, M. S., & Cohen, S. L. (1987). Memory for patterning under a fixed-interval schedule of reinforcement. *Bulletin of the Psychonomic Society*, **25**, 5–8.
- Davis, H., McIntire, R. W., & Cohen, S. I. (1969). Fixed and variable duration warning stimuli and conditioned suppression. *The Journal of Psychology*, **73**, 19–25.
- Fernandez, Serra, F. (1990). *Inhibición de demora en automoldeamiento*. Unpublished doctoral dissertation, Universidad de Sevilla.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. New York: Appleton Century Crofts.

- Gibbon, J. (1977). Scalar expectancy theory and weber's law in animal timing. *Psychological Review*, **84**, 279–325.
- Gibbon, J., & Balsam, P. (1981). Spreading association in time. In C. M. Locurto, H. S. Terrace, & J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 219–253), San Diego: Academic Press.
- Gibbon, J., & Church, R. M. (1990). Representation of time. *Cognition*, **37**, 23–54.
- Gleitman, H., & Bernheim, J. W. (1963). Retention of fixed-interval performance in rats. *Journal of Comparative and Physiological Psychology*, **56**, 839–841.
- Gleitman, H., & Holmes, P. (1967). Retention of incompletely learned CER in rats. *Psychonomic Science*, **7**, 19–20.
- Gleitman, H., Steinman, F., & Bernheim, J. W. (1965). Effect of prior interference upon retention of fixed-interval performance in rats. *Journal of Comparative and Physiological Psychology*, **59**, 461–462.
- Hamm, R. J., Dixon, C. E., & Knisely, J. S. (1984). Long-term memory of a drl task in mature and aged rats. *Experimental Aging Research*, **10**, 39–42.
- Hammond, L. J., & Maser, J. (1970). Forgetting and conditioned suppression: role of a temporal discrimination. *Journal of the Experimental Analysis of Behavior*, **13**, 333–338.
- Hendersen, R. W. (1978). Forgetting of conditioned fear inhibition. *Learning and Motivation*, **9**, 16–30.
- Hendry, D. P., & Van-Toller, C. (1965). Alleviation of conditioned suppression. *Journal of Comparative and Physiological Psychology*, **59**, 458–460.
- Hoffman, H. S., Selekman, W., & Fleshler, M. (1966). Stimulus aspects of aversive controls: long term effects of suppression procedures. *Journal of the Experimental Analysis of Behavior*, **9**, 659–662.
- Holmes, P. A., Jackson, D. E., & Byrum, R. P. (1971). Acquisition and extinction of conditioned suppression under two training procedures. *Learning and Motivation*, **2**, 334–340.
- Kacelnick, A., Brunner, D., & Gibbon, J. (1990). Timing mechanisms in optimal foraging: some applications of scalar expectancy theory. In R. N. Hughes (Ed.), *Behavioral mechanisms of food selection* (pp. 61–82). Berlin: Springer Verlag.
- Killeen, P. (1975). On the temporal control of behavior. *Psychological Review*, **82**, 89–115.
- LaBarbera, J. D., & Church, R. M. (1974). Magnitude of fear as a function of expected time to an aversive event. *Animal Learning and Behavior*, **2**, 199–202.
- Lejeune, H. (1989). Long-term memory for DRL: a comparison between weanling adult and senescent rats. *Physiology and Behavior*, **45**, 321–329.
- Lejeune, H., & Wearden, J. H. (1991). The comparative psychology of fixed-interval responding: some quantitative analyses. *Learning and Motivation*, **22**, 84–111.
- Libby, M. E., & Church, R. M. (1975). Fear gradients as a function of the temporal interval between signal and aversive event in the rat. *Journal of Comparative and Physiological Psychology*, **88**, 911–916.
- Lynch, J. J. (1973). Pavlovian inhibition of delay in cardiac and somatic responses in dogs: Schizokinesis. *Psychological Reports*, **32**, 1339–1346.
- Meck, W. H., Church, R. M., & Olton, D. S. (1984). Hippocampus time and memory. *Behavioral Neuroscience*, **101**, 465–475.
- Millenson, J. R., & Hendry, D. P. (1967). Quantification of response suppression in conditioned anxiety training. *Canadian Journal of Psychology*, **21**, 242–252.
- Pavlov, I. (1927). *Conditioned reflexes*. Oxford: Oxford Univ. Press.
- Rescorla, R. A. (1967). Inhibition of delay in Pavlovian fear conditioning. *Journal of Comparative and Physiological Psychology*, **64**, 114–120.
- Riccio, D. C., Rabinowitz, V. Z., & Alxerod, S. (1994). Memory: When less is more. *American Psychologist*, **49**, 917–926.
- Riccio, D. C., Richardson, R., & Ebner, D. L. (1984). Memory retrieval deficits based upon altered contextual cues: a paradox. *Psychological Bulletin*, **96**, 152–165.

- Richelle, M., & Lejeune, H. (1980). *Time in Animal Behavior*. Oxford: Pergamon Press.
- Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology*, **7**, 242–268.
- Roberts, S. (1983). Properties and function of an internal clock. In R. L. Mellgren (Ed.), *Animal cognition and behavior* (pp. 345–397). New York: North-Holland.
- Rodnick, E. H. (1937). Characteristics of delayed and trace conditioned responses. *Journal of Experimental Psychology*, **20**, 409–425.
- Schachtman, T. R., Channell, S., & Hall, G. (1987). Effects of CS preexposure on inhibition of delay. *Animal Learning and Behavior*, **51**, 301–311.
- Schneiderman, N., & Gormezano, I. (1964). Conditioning of the nictitating membrane of the rabbit as a function of CS-US interval. *Journal of Comparative and Physiological Psychology*, **57**, 188–195.
- Spetch, M. L. (1987). Systematic errors in pigeons' memory for event duration: interaction between training and test delay. *Animal Learning and Behavior*, **15**, 1–5.
- Stein, L., Sidman, M., & Brady, J. V. (1958). Some effects of two temporal variables on conditioned suppression. *Journal of the Experimental Analysis of Behavior*, **1**, 153–162.
- Wearden, J. H. (1992). Temporal generalization in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, **18**, 134–144.
- Williams, D. A., Frame, K. A., & Lolordo, V. M. (1992). Discrete signals for the unconditioned stimulus fail to overshadow contextual or temporal conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, **18**, 41–55.
- Zielinski, K. (1966). "Inhibition of delay" as a mechanism of the gradual weakening of the conditioned emotional response. *Acta Biologiae Experimentalis*, **26**, 407–418.
- Zielinski, K., & Grazyna, W. (1977). Stimulus intensity and conditioned suppression magnitude: Dependence upon the type of comparison and stage of training. *Acta Neurobiologiae Experimentalis*, **37**, 299–309.

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