Background stimuli as a reminder after spontaneous forgetting: Role of duration of cuing and cuing-test interval

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With a relatively complex maze, reliable forgetting is seen clearly when the training-to-test interval is 25 days. This forgetting is demonstrated by longer time to run the maze and by an increase in the number of errors and retracings from the last training trials to the first test trial. In this case, forgetting is a lapse, not a loss, since performance attains the last training trial level at a subsequent test. Furthermore, a reminder—a 90-sec exposure to background stimuli in the experimental room just prior to the test trial—that does not in itself contain sufficient information to facilitate performance in naive animals, significantly improves maze performance in rats that have “forgotten,” even on the first test trial. Two additional experiments were aimed at assessing the role of time and duration of pretest cuing. In the first experiment, the animals were presented the reminder (90 sec in duration) at different times before the test trial. The results show that this reminder significantly alleviates forgetting only when presented just prior to the test, and is less effective when given 1 or 24 h before the test. In the second experiment, contextual cues, which were presented just prior to testing in all experimental groups, varied in duration. The results showed that (1) animals given the reminder treatment for only 10 sec perform at the same level as controls; (2) cuing for 30 sec and especially for 90 sec alleviates forgetting; and (3) a longer exposure to background stimuli (300 sec) leads to intermediate levels of performance, probably due to a partial extinction of the cue value of these stimuli.

In recent years, an increasing amount of evidence has accumulated to demonstrate that many instances of memory deficits can be accounted for in terms of retrieval failure (Spear, 1973). A large part of this evidence is provided by experiments in which performance deficits, observed in such diverse paradigms as short-term memory assessment (Feldman & Gordon, 1979; Gordon & Feldman, 1978), experimentally induced amnesia (e.g., Quartermain, McEwen & Azmitia, 1970, 1972), proactive interference (Spear, 1971), or spontaneous forgetting after a long training-to-test interval (Deweer, Sara, & Hars, 1980; Gatti, Pais, & Weeks, 1975), can be alleviated by pretest cuing. These cuing procedures typically include one or several exposures to some elements of the training situation, prior to retention testing. Animals submitted to a source of forgetting and then given a cuing treatment generally show much better retention performance than do nontreated control animals. In most of these experiments, the presence of appropriate control conditions permits the conclusion that the improvements observed in cued animals could not be accounted for in terms of additional learning pro-

vided by pretest cuing (see Gordon, 1981, and Spear, 1978, for thorough discussions on this topic).

These facilitative effects on retention performance can be observed after a variety of cuing treatments: while the most widely used has been a noncontingent presentation of the unconditioned stimulus (UCS; typically a footshock) in a chamber quite different from the conditioning apparatus (e.g., Spear & Parsons, 1976), exposures to intra-apparatus (e.g., Hickis, Robles, & Thomas, 1977; Thomas, 1981) or to extra-apparatus stimuli (Deweer et al., 1980) influence subsequent performance as well. This functional similarity of such different cuing treatments would suggest that any kind of stimulus noticed during initial learning and represented during cuing, influences the retrieval process in a similar manner through a common mechanism (Spear, 1981). One means of testing this hypothesis consists of comparing, either in a series of experiments (e.g., Spear, Smith, Bryan, Gordon, Timmons, & Chiszar, 1980) or in the same experiment (Deweer, in press), the effects of such different cuing treatments as the reinforcer, internal cues, and intra- or extra-apparatus cues. Another means consists of systematically studying the effects of cuing treatments that vary in terms of intensity or temporal parameters, in order to uncover some general principles governing cue effectiveness.

In previous experiments (Deweer et al., 1980), we

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have shown that after a 25-day retention interval in a food-reinforced maze task, forgetting could be alleviated by a 90-sec exposure to background stimuli immediately before testing. In the experiments reported here, we tried to modulate this facilitating effect by varying either the interval between cuing and subsequent testing (Experiment 1) or the duration of contextual cuing given immediately prior to testing (Experiment 2). Some authors have used these procedures in rather different situations. Using a reinstatement paradigm, Silvestri, Rohrbaugh, and Riccio (1970) showed that the duration of repeated exposures to fear cues alone was an important factor in maintaining retention. In studies aimed at determining the characteristics necessary to restore appetitive memory in rats after ECS-induced amnesia, Miller, Ott, Berk, and Springer (1974) showed that three successive exposures to the apparatus were as effective as the presentation of the reinforcer outside the training situation. More recently, Gordon, Smith, and Katz (1979) demonstrated that either enhanced or decreased responding could be induced after the same response blocking procedure was used after avoidance training; they showed, moreover, that the effects of this treatment depended on (1) the duration of the blocking trial, and (2) the moment in the retention interval when this blocking trial occurred. Our experimental situation differed in several ways from those experiments: As in the Gordon et al. study, rats were submitted to a single cuing episode between training and testing; but in our situation the cuing treatment consisted of an exposure to extra-apparatus cues rather than the apparatus itself. As in the Miller et al. study, an appetitive memory was assessed, but the source of forgetting was a long training-to-test interval rather than ECS. Thus, the present experiments examined to what extent the temporal parameters of cuing, shown to be important in reinstating memory after ECS, determine the efficacy of cuing after spontaneous forgetting of a food-reinforced task.

Another, more pragmatic purpose of these experiments was to establish the experimental procedures in which there is only a partial cuing effect. Several experiments have shown that, in our experimental conditions, spontaneous forgetting can be alleviated either by a 90-sec cuing episode or by pretest physiological manipulations, such as midbrain reticular stimulation (Sara, Deweer, & Hars, 1980) or the peripheral administration of d-amphetamine (Sara & Deweer, 1982), which are known to influence processing of both recently acquired and reinstated memories (see Bloch, Deweer, & Hennevin, 1970, DeVietti & Kirkpatrick, 1977, and Deweer, 1976, concerning reticular stimulation; see, e.g., Quartermain & Botwinick, 1975, for amphetamine). Since, in our previous work, pretest contextual cuing in-

duced almost total alleviation of forgetting when given immediately prior to testing, we tried in these experiments to establish a set of parameters leading to a moderate facilitation of retention performance, in order to test the hypothesis of a potentiation of this effect by pretest physiological manipulations in subsequent experiments.

Finally, in our previous studies (Deweer et al., 1980; Sara et al., 1980), we examined the persistence of the reactivated memory by a second test trial, 24 h after the first, but in the absence of reminder treatment. If the improvement in performance after pretest treatment is due to facilitation of memory retrieval, than a logical requirement would be that the good performance persists in the absence of pretest treatment. Furthermore, there should be a marker improvement in performance in control animals from Test 1 to Test 2, since a full test trial should be an effective memory reinstater.

EXPERIMENT 1

It is well known that the effects of cuing treatments depend on the moment when they are administered during the training-to-test interval. More precisely, it seems now established that there is a clear relationship between retrievability of memory at the time of cuing and the effects of this treatment; in a variety of situations, it has been shown that such reminders as noncontingent footshocks (see Spear, 1978), response blocking in the training situation (Gordon et al., 1979), or exposure to background stimuli (Deweer et al., 1980) have no facilitating effects on retention performance when given shortly after the end of training, that is, when the memory is assumed to be available, whereas they are effective in alleviating memory deficits when administered after the source of forgetting (see also Miller, 1982, Experiment 6). But whether the same cuing acts differentially when given at different times before testing, after the source of forgetting (i.e., when the memory can be assumed to be more or less equally unavailable) is less clear, especially when it consists of exposure to extra-apparatus cues. Although Spear's (1976) hypothesis assuming that "the effectiveness of direct reactivation should be found to decline with longer intervals between the reactivation operation and the retention test" seems widely accepted, it has not yet been submitted to extensive testing. Among the experiments cited earlier, however, Gordon et al. (1979) mentioned that facilitative effects of exposures to apparatus cues or to the reinforcer seem to be less the earlier the treatment occurs in the retention interval. The search for moderately facilitating cuing parameters in our experimental conditions gave us the opportunity to further test this hypothesis with still another treatment.

Method

Subjects

Eighty naive male Sprague-Dawley rats, obtained from Iffa Credo, Saint Germain sur l'Arbresle, France, served as subjects. They weighed 220 g on arrival in the laboratory and were housed, in pairs, in wire-mesh cages, measuring $35 \times 21 \times 18$ cm, for the duration of the experiment. Eight days after arrival, they were placed on a food-deprivation schedule in which the daily ration, given between 5 and 7 p.m., was gradually reduced to 15 g over 4 days. The animals were maintained at 15 g per day during the pre-training and training periods. Under this regime—and with some individual corrections when necessary—they continued to gain weight and weighed approximately 85% of their free-feeding weights at the end of the training period.

Apparatus

The maze, a modified Krechewsky maze, consisted of six $50 \times 40 \times 35$ cm units, with 10-cm openings between them. A $25 \times 25 \times 35$ cm startbox was separated from the first maze unit by a sliding door. The goalbox, of the same dimensions as the startbox, could also be closed by a sliding door. The choice point, or stem of the T, was located 15 cm from the entrance of each unit. The transverse of the T was 25 cm from this choice point. The barriers in each unit could be changed from one side to the other; the maze configuration was L-R-R-L-L-R or R-L-L-R-R-L.

The apparatus was located in a room (experimental room) adjacent to the room in which the animals were housed (colony room). The major difference between these two rooms was that the colony room was naturally lighted, whereas the windows in the experimental room were hidden by large black panels; during the experimental sessions, this room was illuminated by three 60-W bulbs, located 2.5 m above the maze. The air-conditioning system was common to both rooms.

Procedure

The first 5 days consisted of a pretraining period, during which the animals were habituated to the experimenter, the maze, and the experimental conditions. On Day 1, each rat was allowed to feed for one 20-min period in a box similar to the startbox and the goalbox. The food reward consisted of .2-g rat pellets. On Day 2, the rats, in gangs of six, were given 30 min of free exploration of the entire maze, with the sliding doors opened, the barriers removed, and food pellets available in the goalbox. On Day 3, using only the last maze unit, two rats at a time were trained to enter the goalbox (sliding door opened) and feed for a 10-min period. The procedure on Day 4 was the same, except that the rats ran singly and for only 5 min. On Day 5, the sliding door was closed after a rat entered the goalbox; the individual rats were then allowed to feed in the goalbox for 5 min.

Training began on Day 8. Barriers were placed at the appropriate points, and the path was changed to its mirror configuration for every other rat. Each animal was carried, in the hand of the experimenter, from the colony room to the experimental room and placed into the startbox; the sliding door was then immediately opened, and the time it took for the rat to reach the goalbox was recorded, as were the number of incorrect choices (errors) and the number of retracings (a retracing is defined as a return to the preceding maze unit or units; this behavior mostly occurred after an error, and usually disappeared after the first training trial). The animals were allowed to eat in the goalbox for 2 min, before being removed and returned to the colony room. There were five training trials, with a 24-h intertrial interval.

After training, the animals were divided into four matched groups, on the basis of their mean performance on the last two training trials (acquisition trials 4 and 5). Performance criteria were total time to run the maze, number of errors, and number of retracings. The animals were kept in their home cages with free access to food and water for the first part of the training-to-test interval. Seven days before retention testing, the gradual reduction in food was reintroduced, just as before pretraining.

On the first test day, 25 days after the last training trial, each rat was removed individually from the home cage and carried, in the hand of the experimenter, to the experimental room. The “non-manipulated” control rats (Group C) were placed directly into the startbox and the sliding door was opened. For the rats in Group R-0, the individuals were placed in a wire-mesh cage, similar to the home cages, next to the startbox of the maze and kept there for 90 sec; after this cuing period, they were removed and placed into the startbox, after which the door was immediately opened. Animals in Groups R-1 and R-24 were administered the same reminder treatment 1 and 24 h before testing, respectively. These animals were then carried back to their home cages, where they spent the reminder-testing interval. For testing, they were placed directly into the startbox of the maze.

For all groups, the exact path traced by each animal, the errors and retracings made, and the total time to run the maze were noted. Upon arrival at the goalbox, each rat was allowed to eat for 2 min and was then removed and returned to its home cage. All animals were later fed 15 g of rat chow. The animals were retested on the next day, without any pretest treatment.

This experiment was run in two replications, with 40 animals (10 in each group) in each. Statistical comparisons showed no difference between these replications, either in acquisition or in retention performance. So the data were pooled for subsequent analyses.

Results and Discussion

Acquisition Trials

As in preceding experiments (see Deweer et al., 1980), the animals showed considerable enhancement in performance throughout training. Running times dropped from about 2 min on the first trial to 25 sec at the end of training. The number of errors, which was approximately 5 on the first trial, was only 3 on the second trial (i.e., chance level in the absence of retracings) and 1.8 on acquisition trials 4 and 5. The number of retracings was important only on the first training trial (mean score = 2.8 retracings), and dropped to 0.5 on the second trial and 0.3 at the end of training.

First Test Trial

Within-group comparisons. The “nonmanipulated” control animals (Group C) ran more slowly and made more errors and more retracings on the first test trial than they did on the last two acquisition trials. Within-group comparisons showed this performance decrement to be significant for running times [$F(1,76) = 11.66$], for errors [$F(1,76) = 31.62$], and for retracings [$F(1,76) = 16.94$] (all $ps < .005$; see Figure 1). So, noncued animals showed significant forgetting on all retention measures.

Those animals which received pretest cuing immediately before testing (Group R-0) did not show such a performance decrement; the within-group comparisons showed no difference for any performance index [$F(1,76) = .79$ for running times; $F(1,76) = .69$ for errors; $F(1,76) = .03$ for retracings]. In other words, this cuing treatment alleviated forgetting.

Animals in Groups R-1 and R-24 (submitted to the reminder treatment 1 and 24 h before testing, respec-

Figure 1. Mean errors ($\pm$ SEM at Test 1) for the four groups on the last two acquisition trials, Tests 1 and 2. Note the forgetting in the control group and the high performance in Group R-0 at Test 1. See text and Table 1 for statistical comparisons.

tively) showed a significant performance decrement on this retention test, as compared with the last training trials, in terms of running times [$F(1,76)=27.49$ for Group R-1; $F(1,76)=18.67$ for Group R-24; both $ps < .005$]. However, this performance decrement was not significant, either in terms of errors [for R-1, $F(1,76)=1.68$, and for R-24, $F(1,76)=2.47$] or in terms of retracings [$F(1,76)=3.87$ and $F(1,76)=2.89$, respectively]. This suggests some alleviation of forgetting in these two groups.

Between-group comparisons. Overall analyses of variance for the four groups showed significant differences among these groups in terms of running times [$F(3,76)=4.16$, $p < .01$], number of errors [$F(3,76)=3.01$, $p < .05$], and number of retracings [$F(3,76)=3.85$, $p < .05$]. Between-group comparisons (see Table 1) showed that (1) animals in Group R-0 performed significantly better than "nonmanipulated" control animals, whatever retention index considered; (2) animals in Groups R-1 and R-24 displayed very similar performance on this first test; and (3) the level of performance in these latter groups was intermediate between the high retention scores noted in Groups R-0 and the poor performance observed in control animals.

The two groups that had a delay between cuing and testing did not differ significantly from the control

group; the difference between those groups and the R-0 group was likewise not significant. Although this suggests that there was some partial effect in Groups R-1 and R-24 to be able to suggest a temporal gradient of the efficacy of cuing would require further studies using delays between 0 and 1 h.

Second Test Trial

On the second test trial, the next day, animals in Group C showed a significant improvement in performance. Within-group comparisons yielded significant differences between Tests 1 and 2, for running times [$F(1,76)=14.71$], number of errors [$F(1,76)=11.53$], and number of retracings [$F(1,76)=18.24$; all $ps < .005$]. Animals in Groups R-1 and R-24 showed the same improvement between Tests 1 and 2 in terms of running times [respectively, $F(1,76)=21.26$ and $F(1,76)=15.80$; both $ps < .005$] and number of retracings [respectively, $F(1,76)=5.01$ and $F(1,76)=4.14$; both $ps < .05$]. The difference between Tests 1 and 2, in terms of errors, just failed to reach an acceptable level of significance [both $F(1,76)=3.84$].

Statistical comparisons showed that animals in Group R-0 maintained the same level of performance as seen on Test 1 [respectively, for running times, errors, and retracings: $F(1,76)=2.75$; $F(1,76)=1.71$; $F(1,76)=.01$].

These data confirm the conclusions of several previous experiments in the same conditions (e.g., Deweer et al., 1980; Sara & Deweer, 1982): after a long training-to-test interval, significant forgetting occurs in a relatively complex maze (Group C, Test 1). This forgetting appears to be a memory "lapse" (Sara, Deweer, & Hars, 1976; Spear, Gordon, & Martin, 1973) or retrieval failure rather than a decay of memory, since one trial and/or cuing are sufficient to reinstate on the next day (Test 2) the same level of performance as that observed at the end of training. Moreover, such a performance decrement on Test 1 can be alleviated by pretest cuing,

Table 1
Between-Group Comparisons on Test 1

	Group R-0	Group R-1	Group R-24
Group C	10.61	0.22	1.09
	8.99	1.83	1.83
	11.58	2.90	3.85
Group R-0		7.77	4.90
		2.70	2.70
		2.90	2.07
Group R-1			0.33
			0.01
			0.07

Note—In each cell, F values for times are on the first line, F values for errors on the second line, F values for retracings on the third line. Critical values for $F(1,76)$ are 3.98 ($p < .05$) and 7.02 ($p < .01$).

consisting of a 90-sec exposure to background stimuli (Group R-0, Test 1).

However, the delay interpolated between cuing and testing seems to be an important determinant of this alleviation: pretest exposure to contextual stimuli significantly facilitates retention performance only when given immediately prior to testing. The same treatment administered 1 or 24 h before testing has only marginal effects. It appears (see Figure 1) that, in terms of retracings and especially errors (which could be considered as reflecting the most "cognitive" aspects of performance in this kind of task), the animals in Groups R-1 and R-24 showed intermediate levels of performance, indicating some partial alleviation of forgetting.

This lack of a robust effect of cuing after a cuing-to-test interval contrasts with some other data reported in the literature in this field. For instance, using a "hurdle jumping, escape from fear task," Spear and Parsons (1976) obtained a reactivation effect after a single exposure to the UCS (footshock), 24 h before testing, with a 28-day training-to-test interval, very similar to the retention interval used in our experiments. Studying appetitive memory restoration after electroconvulsive shock, Miller et al. (1974) also showed that access to the reinforcer used during training (sucrose) improved retention performance 24 h later. In a second experiment in this series, they demonstrated that exposures to apparatus cues alone could also act as effective reminders. It should be noted, however, that this latter effect could be detected only with a particular set of parameters: the exposures to the apparatus had to be repeated (see below, introduction to Experiment 2), and the last one took place only 2 h before testing. These data suggest that, at least in their conditions, different cuing treatments can induce memory reactivations that differ in duration. It cannot be excluded that, after a long retention interval in a positively reinforced task, a single exposure to extra-apparatus cues can only induce a short-lasting reactivation of memory; further experiments are planned on this topic.

EXPERIMENT 2

The aim of this experiment was to assess the importance of the duration of pretest contextual cuing in the facilitation of retention performance in the spontaneous forgetting paradigm. This question has been addressed in more general terms by several authors, especially in the context of ontogeny of memory. Using a reinstatement paradigm (see Campbell & Jaynes, 1966, and Shubat & Whitehouse, 1968), in which early learned fear in rats can be enhanced by periodic exposures to some abbreviated forms of the training situation, Silvestri

et al., (1970) showed that repeated presentations of the fear cues alone were sufficient to improve retention performance 28 days after initial learning. They demonstrated, moreover, that the duration of these exposures was a critical determinant of performance after a retention interval of 14 days: repeated brief exposures to the conditioned fear cues were an effective means of maintaining retention, whereas prolonged exposures to the same cues did not produce the reinstatement effect.

In their extensive studies of recovery of memory after electroconvulsive shock (ECS) induced amnesia (see, e.g., Miller & Springer, 1972, 1973), Miller et al. (1974) showed that the memory for a one-trial appetitive task could be restored after a single 60-sec exposure to the reinforcer outside of the training situation. They also reported that a similar recovery could be obtained by means of three 135-sec exposures to the training apparatus, in the absence of the reinforcer. They merely mentioned (Experiment 2) that, in the course of their pilot work, they found that (a) "three reminder trials were more effective than one or two trials; (b) moreover, less than 120 sec per trial were too brief a period for effective restoration of memory, and 180 or more seconds tended to be less effective, perhaps due to extinction after recovery from amnesia."

However, repeated cuing do not seem to be, in our view, the most appropriate procedure to address the question of the role of duration of cuing in facilitating subsequent test performance. First, inconsistent results have been reported in the literature: although Miller et al. (1974) found that three reminder trials were more effective than one or two, Spear and Parsons (1976) reported that two UCS presentations, separated by a 5-min interval, were as efficient in alleviating forgetting as several distributed presentations given in the reinstatement paradigm. They found, moreover, that one presentation of the UCS had no less effect on later performance than two. Second, in the field of experimentally induced amnesia, there are several examples (e.g., Sara, 1973; Zinkin & Miller, 1967) of progressive development of avoidance responses after training, ECS, and repeated testing, in the absence of footshock at testing; these repeated exposures to the training environment presumably provided cues that facilitated retrieval of the "forgotten" target memory. But, in any of these paradigms—repeated cuing or repeated testing—it is very difficult to conclude whether those treatments enhance retention performance because repetition results in more exposure to the UCS or to apparatus cues, or if this effect results from repetition per se. In this experiment, we tested the effects of single presentations of extra-apparatus cues on subsequent retention performance, and tried to assess the role of duration of these presentations.

Method

Subjects

One hundred and five rats, with the same characteristics and obtained from the same supplier as in Experiment 1, served as subjects. They were housed, handled, and food deprived as in the preceding experiment.

Apparatus

The experimental conditions, the maze, and the "reminder cage" were the same as in Experiment 1.

Experimental Design and Procedure

All animals were given pretraining and training as in Experiment 1. At the end of training, they were divided into five matched groups, on the basis of their performance on the last two training trials: 21 rats were assigned to a "nonmanipulated" control group (Group C), in which the animals were placed directly into the start-box of the maze for testing, 25 days after the end of training; the animals in the four other groups (21 animals in each) were submitted, immediately before testing, to the pretest treatment used in Experiment 1 (exposure to the background stimuli, in a wire-mesh cage, next to the startbox of the maze). The duration of this treatment was varied among these groups from 10 sec (Group R-10) to 300 sec (Group R-300); the intermediate durations were 30 sec (Group R-30) and 90 sec (Group R-90).

The experiment was run in two replications, with, respectively, 10 and 11 animals in each group. Statistical comparisons showed no difference between these replications, either in acquisition or in

retention performance, and the data were pooled for subsequent analyses.

Since the results of Experiment 1 totally confirmed the conclusions of previous work, in that one test trial was sufficient in our experimental conditions to reinstate a maximal level of performance on a subsequent test, the second test was deleted in this experiment.

Results and Discussion

Acquisition Trials

As in Experiment 1, the animals showed considerable improvement in performance during training (see Figure 2 for errors).

Within-Group Comparisons

As in the preceding experiment, animals in Group C took more time to run the maze and made more errors and more retracings on retention test than they did at the end of acquisition. Within-group comparisons yielded significant differences for all retention indices [$F(1,100) = 54.04$ for running times; $F(1,100) = 10.67$ for errors; and $F(1,100) = 12.53$ for retracings; all $ps < .005$], indicating forgetting 25 days after learning (see Figure 2 for error scores).

Figure 2. Mean errors for combined groups during acquisition (Trials 2, 3, 4, and 5) and at retention test ($\pm$ SEM) 25 days later. Note the forgetting in control animals and in animals cued for 10 sec, and the total alleviation of this forgetting in Group R 90. See text for statistical comparisons.

The same picture emerged in Group R-10, indicating that a 10-sec pretest exposure to background stimuli was not sufficient to elicit an efficient retrieval of the target memory. Within-group comparisons showed significant deficits in test performance in terms of running times [$F(1,100)=49.98$], number of errors [$F(1,100)=11.44$], and number of retracings [$F(1,100)=19.91$; all $ps < .005$; see Figure 2].

As in Experiment 1, those animals that were submitted to pretest cuing for 90 sec did not show such a performance decrement [respectively, for running times, errors, and retracings: $F(1,100)=3.36$, $F(1,100)=.01$; $F(1,100)=.02$]. This absence of a significant deficit was also observed in animals given pretest cuing for only 30 sec [respectively, for times, errors, and retracings: $F(1,100)=2.38$, $F(1,100)=1.10$; $F(1,100)=.59$; see Figure 2].

This facilitative effect of pretest cuing was much less apparent in animals presented with background stimuli for 300 sec immediately before testing. In fact, even though those animals did not show forgetting in terms of retracings [$F(1,100)=.21$], they exhibited significant deficits in terms of either running times [$F(1,100)=12.12$; $p < .005$] or errors [$F(1,100)=3.98$; $p < .05$].

Between-Group Comparisons

Overall analyses of variance showed significant differences among groups for all retention indices [running times, $F(4,100)=7.27$, $p < .005$; errors, $F(4,100)=2.61$, $p < .05$; retracings, $F(4,100)=3.20$, $p < .025$]. Planned comparisons confirmed that test performances did not differ between Groups C and R-10 [for times, errors, and retracings, respectively: $F(1,100)=.18$, $F(1,100)=.11$, and $F(1,100)=.40$]. Animals in Group R-300 performed better than controls in terms of running times [$F(1,100)=6.05$, $p < .025$], but these two groups did not significantly differ in terms of number of errors [$F(1,100)=.86$] or number of retracings [$F(1,100)=2.81$] [note that another between-group comparison, the Dunnett statistic, did not show any significant difference between Group R-300 and control animals; for times, errors, and retracings, ts were, respectively, 2.04, .83, and 1.69 (critical value of $t=2.18$)].

The facilitative effect of pretest cuing on test performance was significant in both Group R-30 and Group R-90. Animals in Group R-90 performed significantly better than controls for all retention indices [for running times, errors, and retracings, respectively: $F(1,100)=11.35$, $p < .005$; $F(1,100)=5.57$, $p < .025$; $F(1,100)=4.40$, $p < .05$]. The animals in Group R-30 were also better than controls in terms of running times [$F(1,100)=13.42$, $p < .005$] and retracings [$F(1,100)=13.42$, $p < .005$], but the difference between these two groups failed to reach an acceptable level of significance in terms of errors [$F(1,100)=3.13$] (see Figure 2).

Taken together, these data confirm that the duration of a cuing treatment, administered after a source of forgetting, is an important determinant in alleviating performance deficits. They corroborate earlier conclusions, drawn from studies in the field of avoidance learning (Gordon et al., 1979; Silvestri et al., 1970) or restoration of memory after induced amnesia (Miller et al., 1974), and extend them to another cuing treatment, that is, exposure to extra-apparatus cues. While direct comparisons must be made with caution, it could nevertheless be hypothesized, from these data and some other ones in the literature, that the optimal parameters to induce restoration of a memory depend on the reinforcement (namely, appetitive vs. aversive tasks). After avoidance learning, it seems that brief exposures to the UCS, or relatively brief exposures to the apparatus cues (Gordon et al., 1979), are sufficient to enhance subsequent retention performance when given after the source of forgetting. On the other hand, reactivation of appetitive memories seems to require longer exposures, either to the reinforcer (Miller et al., 1974) or to training or contextual cues. Additional experiments are required in order to further test this hypothesis, although the lack of effect of 10-sec cuing in this experiment lends it some support.

It seems difficult to account for these data in terms of the nonspecific arousing effects of our treatments. In each experimental group, the animals were submitted to the same manipulations (i.e., the carrying from the home cage to the experimental room, the exposure to background stimuli in a wire-mesh cage, and placement into the startbox of the maze) immediately prior to testing. It could be argued that two manipulations within 10 sec (Group R-10) are less likely to be discriminated by the animals, and thus are much less arousing than two more spaced manipulations; however, while such a hypothesis could account for the lack of effect in Group R-10, it would imply at the same time that facilitative arousing effects must have been maximal in Group R-300, which is clearly not the case. In fact, alleviation of forgetting is maximal after moderate (i.e., 30 sec, and especially 90 sec) durations of exposure to contextual stimuli. This last result is very similar to observations mentioned earlier, in experimental situations involving different retention intervals (e.g., Gordon et al., 1979), different cuing treatments (apparatus cues; e.g., Silvestri et al., 1970), and different sources of forgetting (e.g., Miller et al., 1974), and attests to the generality of the phenomenon. Just as with other cuing treatments, pretest presentation of extra-apparatus cues results in alleviation of forgetting when given for intermediate durations, and has a much less facilitating effect when given for longer periods. It is likely that a long exposure to the reminder treatment leads to extinction of the cue value of background stimuli and, more generally, that the

two functions of cuing (reactivation of a stored memory, and learning of new information at the time of cuing) occur sequentially, as convincingly argued by Gordon et al. (1979; see also Gordon, 1981). Indeed, we have shown that, with repeated exposures (90 sec in duration) to the extra-maze cues during the retention interval, these cues presented just before the retention test no longer facilitate performance; this is most likely an extinction effect (see Deweer et al., 1980).

GENERAL DISCUSSION

These results confirm the role of context in retrieval of memory which has been "forgotten" after a long retention interval. Furthermore, they underline the fact that the duration of the pretest exposure to background stimuli and the interval between this exposure and subsequent testing are important in determining the strength of the facilitative effect. While this contextual cue reminder effect has proved to be quite robust and reliable, and even susceptible to "dose-response" studies, its mechanisms of action remain unknown.

A general hypothesis that would imply that the cuing treatment induces modifications of the internal context, that is, a general arousal reaction, could be maintained in order to account for these data (including results of Experiment 2, if it is assumed that the "extinction effect" is an extinction of arousal reactions). There is no doubt that any learning episode must be considered as an exceptional event in the rather uneventful everyday life of laboratory rats, and thus that the corresponding memory includes some attributes related to arousal. Some data, such as those of Springer and Miller (1972), which show that the memory of avoidance learning reinforced by immersion in ice water can be restored, after ECS, by a noncontingent footshock outside the training apparatus, lend support to this hypothesis. It is worth noting, however, that the generality of this phenomenon is limited: attempts to restore appetitive memory, after ECS, using as a recovery agent a noncontingent footshock in another apparatus have proved unsuccessful (Miller et al., 1974). These data suggest that arousal can act as an effective reminder, inasmuch as arousing treatment corresponds to specific "arousal attributes" of memory.

Some manipulations of the general level of arousal influence memory retrieval in our experimental conditions as well: As mentioned earlier, spontaneous forgetting can be alleviated by pretest mild reticular stimulation (Sara et al., 1980) or by peripheral administration of d-amphetamine (Sara & Deweer, 1982). The problem is to know whether a nonspecific arousal is sufficient per se to induce enhanced retention performance, or if test performance results from integration of the weak memory with informa-

tion in the test environment. We have several reasons to prefer the latter hypothesis. First, the task was selected in order to allow for the assessment of several aspects of performance, including speed and accuracy; although a pretest manipulation of the level of arousal is likely to improve subsequent performance in terms of speed, an improvement in terms of accuracy of choices in the maze would be much less expected unless the main effect consisted of facilitating the processing of available contextual information. Second, there is no direct relationship between the arousing properties of the pretest physiological treatment and its facilitative effects. In fact, pretest amphetamine administration enhances retention performance only at low doses (.25 or .50 mg/kg); it is ineffective at higher doses, and this result could be interpreted in the same way as the Miller et al. (1974) data. Third, the same reticular stimulation which has been shown to facilitate retention performance when given immediately prior to testing in the experimental context (Sara et al., 1980) has opposite effects when administered in the colony room, presumably because it triggers the processing of irrelevant information, which interferes with the retrieval of the target memory (Sara & Deweer, unpublished data). Finally, in a recent experiment (Deweer, 1982), we found retention performance to be highly sensitive to subtle modifications in the cuing treatment: contextual cuing was much more effective in alleviating forgetting when given in a familiar and relevant location in the experimental room (close to the startbox) than when given in another location in the same experimental room. These data suggest that retention performance is not only controlled in a general way by available contextual information, but also that there is high level of specificity of this information contained in context.

How the animal actually uses this specific extra-maze information to achieve more accurate performance still remains an open question. We see two possibilities: the extramaze cues might actually be discriminative stimuli for the rat; providing a specific reminder such as "turn right at the ceiling lamp" would set the rat off on the right track in running the R-L-L-R-R-L sequence. This seems unlikely, since the behavior of the rats in the maze does not suggest that they extensively use extramaze cues in finding the correct path. Early in acquisition, some rats do tend to rear and look at ceiling features, but this kind of exploratory behavior tends to disappear and is rarely seen at the end of training or at retention testing. This possible explanation for the contextual cue reminder effect could be easily tested by training animals in a closed maze, while at the same time providing the same amount of exposure to the experimental room. If the contextual cue reminder effect was still observed under these conditions, then an explanation in terms of extramaze cues acting as dis-

criminative stimuli would be untenable. Automation of the maze will make this experiment feasible.

The mechanism of action of the contextual cue reminder effect might involve a conditioned response to the specific stimuli found in the environment immediately surrounding the startbox. The stimuli become associated with the reinforcement during pre-training and training, and thus are capable of eliciting a response—a truncated conditioned reflex, in Pavlovian terms (see Kupalov, 1961). This conditioned response, elicited during the reminder period, may include an increase in norepinephrine activity (such a conditioned NE response to environmental cues previously associated with footshock has recently been demonstrated by Cassens, Roffman, Kurac, Orsulak, & Schildkraut, 1980). Several lines of research have suggested that the noradrenergic fore-brain projections are intimately involved in the regulation of attentional mechanisms (Robbins & Everitt, 1982; Segal & Bloom, 1976; Waterhouse & Woodward, 1980). Conditioned increase in this activity could result in better attention to intramaze discriminative cues during the subsequent test, thereby resulting in better performance in terms of the errors seen in reminded animals. The duration of the exposure would be important in that the animals must have sufficient time to notice the specific CS associated with the reinforcement. The decrease in efficacy of the 300-sec reminder might then be due to a partial dissipation of those physiological aspects of the response which facilitate attention to intramaze cues. This dissipation would likewise account for the lack of effect of the reminder treatment given 1 or 24 h before testing.

These two alternatives are highly speculative, and we do not as yet have any evidence to support either view. However, while proposed mechanisms of action remain speculative, our behavioral experiments have provided concrete information concerning the properties of the contextual reminder. The effectiveness of the contextual cues as a memory reinstater can be extinguished by repeated nonreinforced presentations of these cues during the retention interval (Deweere et al., 1980), or by a relatively long presentation immediately prior to testing. But this reminder effect is robust and reliable when the context is presented for intermediate durations before testing. Finally, even though this treatment elicits the activation of "arousal attributes" of memory, its efficacy seems to be highly dependent on the contextual similarity between training and testing (Deweere, 1982).

REFERENCES

- BLOCH, V., DEWEER, B., & HENNEVIN, E. (1970). Suppression de l'amnésie rétrograde et consolidation d'un apprentissage à essai unique par stimulation réticulaire. *Physiology & Behavior*, **5**, 1235-1241.
- CAMPBELL, B. A., & JAYNES, J. (1966). Reinstatement. *Psychological Review*, **73**, 478-480.
- CASSENS, G., ROFFMAN, M., KURAC, A., ORSULAK, P., & SCHILDKRAUT, J. (1980). Alterations in brain norepinephrine induced by environmental stimuli previously paired with inescapable shock. *Science*, **209**, 1138-1140.
- DEVIETTI, T., & KIRKPATRICK, B. (1977). Stimulation of specific regions of brain in rats modifies retention for newly acquired and new habits. *Journal of Comparative and Physiological Psychology*, **91**, 662-673.
- DEWEER, B. (1976). Selective facilitative effect of post-trial reticular stimulation in discriminative learning in the rat. *Behavioral Processes*, **1**, 243-257.
- DEWEER, B. (1982). Memory retrieval in rats: Critical role of contextual similarity between training and testing. *Behavioural Brain Research*, **5**, 97-98. (Abstract)
- DEWEER, B. (in press). An attribute-analysis of memory retrieval in rats: Additivity of different cueing treatments in alleviating "spontaneous forgetting" after a long interval. *Behavioural Brain Research*. (Abstract)
- DEWEER, B., SARA, S. J., & HARS, B. (1980). Contextual cues and memory retrieval in rats: Alleviation of forgetting by a pre-test exposure to background stimuli. *Animal Learning & Behavior*, **8**, 265-272.
- FELDMAN, D. T., & GORDON, W. C. (1979). The alleviation of short-term retention decrements with reactivation. *Learning and Motivation*, **10**, 198-210.
- GATTI, S. V., PAIS, N., & WEEKS, J. R. (1975). Effect of reinstatement procedure on retention of differential appetitive responding. *Bulletin of the Psychonomic Society*, **6**, 57-60.
- GORDON, W. C. (1981). Mechanisms of cue-induced retention enhancement. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals, memory mechanisms*. Hillsdale, NJ: Erlbaum.
- GORDON, W. C., & FELDMAN, D. T. (1978). Reactivation induced interference in a short-term retention paradigm. *Learning and Motivation*, **9**, 164-178.
- GORDON, W. C., SMITH, G. J., & KATZ, D. S. (1979). Dual effects of response blocking following avoidance learning. *Behaviour Research and Therapy*, **17**, 479-487.
- HICKIS, C. F., ROBLES, L., & THOMAS, D. R. (1977). Contextual stimuli and memory retrieval in pigeons. *Animal Learning & Behavior*, **5**, 161-168.
- KUPALOV, P. S. (1961). Some normal and pathological properties of nervous processes in the brain. *Annals of the New York Academy of Sciences*, **92**, 1046-1053.
- MILLER, R. R. (1982). Effects of intertrial reinstatement of training stimuli on complex maze-learning in rats: Evidence that "acquisition" curves reflect more than acquisition. *Journal of Experimental Psychology: Animal Behavior Processes*, **8**, 86-109.
- MILLER, R. R., & SPRINGER, D. A. (1972). Induced recovery of memory in rats following electroconvulsive shock. *Physiology & Behavior*, **8**, 645-651.
- MILLER, R. R., & SPRINGER, D. A. (1973). Amnesia, consolidation and retrieval. *Psychological Review*, **80**, 69-79.
- MILLER, R. R., OTT, C. A., BERK, A. H., & SPRINGER, D. A. (1974). Appetitive memory restoration after electroconvulsive shock in the rat. *Journal of Comparative and Physiological Psychology*, **87**, 717-723.
- QUARTERMAIN, D., & BOTWINICK, C. (1975). Role of biogenic amines in the reversal of cycloheximide-induced amnesia. *Journal of Comparative and Physiological Psychology*, **88**, 386-401.
- QUARTERMAIN, D., McEWEN, B. S., & AZMITIA, E. (1970). Amnesia produced by electroconvulsive shock or cycloheximide: Conditions for recovery. *Science*, **169**, 683-686.
- QUARTERMAIN, D., McEWEN, B. S., & AZMITIA, E. C. (1972). Recovery of memory following amnesia in the rat and mouse. *Journal of Comparative and Physiological Psychology*, **79**, 360-370.
- ROBBINS, T. W., & EVERITT, B. J. (1982). Functional studies of the central catecholamines. *International Review of Neurobiology*, **23**, 303-365.

- SARA, S. J. (1973). Progressive development of avoidance response after training, ECS, and repeated testing. *Bulletin of the Psychonomic Society*, 2, 134-136.
- SARA, S. J., & DEWEER, B. (1982). Memory retrieval enhanced by amphetamine after a long retention interval. *Behavioral and Neural Biology*, 36, 146-160.
- SARA, S. J., DEWEER, B., & HARS, B. (1976). Forgetting as a lapse, not a loss: Facilitation of retrieval by a reminder. *Bulletin de la Société Belge de Psychologie*, 2, 23.
- SARA, S. J., DEWEER, B., & HARS, B. (1980). Reticular stimulation facilitates retrieval of a 'forgotten' maze habit. *Neuroscience Letters*, 18, 211-217.
- SEGAL, M., & BLOOM, F. (1976). Norepinephrine in the rat hippocampus. III. Stimulation of nucleus locus coeruleus in the awake rat. *Brain Research*, 107, 499-511.
- SHUBAT, E. E., & WHITEHOUSE, J. M. (1968). Reinstatement: An attempt at replication. *Psychonomic Science*, 12, 215-216.
- SILVESTRI, R., ROHRBAUGH, M. J., & RICCIO, D. C. (1970). Conditions influencing the retention of learned fear in young rats. *Developmental Psychology*, 2, 380-395.
- SPEAR, N. E. (1971). Forgetting as retrieval failure. In W. K. Honig & P. H. R. James (Eds.), *Animal memory*. New York: Academic Press.
- SPEAR, N. E. (1973). Retrieval of memory in animals. *Psychological Review*, 80, 163-194.
- SPEAR, N. E. (1976). Retrieval of memories. In W. K. Estes (Ed.), *Handbook of learning and cognitive processes: (Vol. 4). Attention and memory*. Hillsdale, NJ: Erlbaum.
- SPEAR, N. E. (1978). *The processing of memories: Forgetting and retention*. Hillsdale, NJ: Erlbaum.
- SPEAR, N. E. (1981). Extending the domain of memory retrieval. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals, memory mechanisms*. Hillsdale, NJ: Erlbaum.
- SPEAR, N. E., GORDON, W. C., & MARTIN, P. A. (1973). Warm-up decrement as failure in memory retrieval in the rat. *Journal of Comparative and Physiological Psychology*, 85, 601-614.
- SPEAR, N. E., & PARSONS, P. (1976). Analysis of a reactivation treatment: Ontogeny and alleviated forgetting. In D. Medin, R. Davis, & W. Roberts (Eds.), *Coding processes in animal memory*. Hillsdale, NJ: Erlbaum.
- SPEAR, N. E., SMITH, G. J., BRYAN, R., GORDON, W. C., TIMMONS, R., & CHISZAR, D. (1980). Contextual influences on the interaction between conflicting memories. *Animal Learning & Behavior*, 8, 273-281.
- SPRINGER, A. D., & MILLER, R. R. (1972). Retrieval failure induced by electroconvulsive shock: reversal with dissimilar training and recovery agents. *Science*, 177, 628-630.
- THOMAS, D. R. (1981). Studies of long-term memory in the pigeon. In N. E. Spear & R. R. Miller (Eds.), *Information processing in animals, memory mechanisms*. Hillsdale, NJ: Erlbaum.
- WATERHOUSE, B. D., & WOODWARD, D. J. (1980). Interaction of norepinephrine with cerebrocortical activity evoked by stimulation of somatosensory afferent pathways in the rat. *Experimental Neurology*, 67, 11-34.
- ZINKIN, S., & MILLER, A. J. (1967). Recovery of memory after amnesia induced by electroconvulsive shock. *Science*, 155, 102-104.

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