Background stimuli as a reminder after spontaneous forgetting: Potentiation by stimulation of the mesencephalic reticular formation

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Reliable forgetting of a relatively complex maze is seen in rats when the training-to-test interval is 24 days. Forgetting is measured by longer time to run the maze and by an increase in the number of errors from the last training trials to the test trial. A contextual cue reminder alleviates forgetting when presented just prior to the test trial, but is only marginally effective when given 1 h before testing. The present experiment, using the same forgetting paradigm, was aimed at testing the hypothesis that such a marginal cuing effect can be potentiated by a stimulation of the mesencephalic reticular formation. Half of the animals were exposed for 90 sec to the experimental room (reminder condition), whereas the other half were exposed to the colony room (pseudoremind condition), 1 h before testing. These two groups were divided into two subgroups, stimulated and pseudostimulated. The results showed that there was no effect of reminder alone and no effect of the stimulation given with the pseudoremind; the stimulation given concurrently with the reminder alleviated forgetting as measured by errors. The results suggest that the stimulation acts to potentiate retrieval processes already triggered by the significant contextual cue reminder.

After a long retention interval, forgetting of a food-reinforced maze task can be alleviated by exposure to background stimuli in the experimental room immediately before testing (Deweere, Sara, & Hars, 1980). These data fit well within the theoretical framework provided by Spear (1978), who holds that any kind of stimulus noticed during initial learning *and* during cuing may facilitate memory retrieval processes. Thus, even contextual cues that do not contain any information concerning response-reinforcement contingencies can improve subsequent maze performance in rats that have "forgotten," presumably by facilitating retrieval. These data are also consistent with Tulving's view of memory retrieval, which states that "remembering is regarded as a joint product of information stored in the past and information present in the immediate cognitive environment of the rememberer" (Tulving & Thomson, 1973, p. 352).

Such a view implies that retention performance, at least after forgetting (but see also Riccio & Richardson, 1984, for memory reactivation after experimentally induced amnesia), depends not only on the amount of information stored, the current environmental demands, and the homeostatic state of the organism, but also upon the level of arousal, which might determine or at least modulate the attention to contextual stimuli during pretest cuing or

at testing (Sara, 1985). Our earlier experiments lend support to this hypothesis. Increasing the level of activation of the brain by low-intensity, long-duration stimulation of the mesencephalic reticular formation (MRF) alleviated forgetting in exactly the same paradigm in which Deweer et al. (1980) showed a contextual cue reminder effect (Sara, Deweer, & Hars, 1980). Similar results were later obtained with pretest injection of amphetamine (Sara & Deweer, 1982). The question raised by these experiments is whether the arousal-inducing properties of these treatments alone are sufficient to facilitate the retrieval processes, or whether these processes must first be primed or triggered by the contextual cue reminder. The latter possibility would imply that MRF stimulation has its effect by enhancing perceptual analysis and treatment of information in the retrieval environment. An attempt was made to address this question by administering the MRF stimulation under two conditions: in the presence of a pretest reminder (memory retrieval primed) and in the absence of a reminder (Sara et al., 1980). The prediction was that the MRF stimulation would potentiate the reminder effect, and that it would have little or no effect when given in a context unrelated to the experiment and which therefore did not predict reinforcement. In our previous experiments, all reminded animals, stimulated or not, had performed at testing as well as they had at the last training trials. This result was accounted for in terms of ceiling effect of the robust facilitation by pretest reminder alone. On the other hand, rats that were stimulated without reminders performed as well as the two reminded groups and significantly better than the non-

These results were presented at the annual meeting of the European Brain and Behaviour Society (Oxford, England, September 1985). The authors would like to thank Gérard Le Floch for technical assistance. The authors' address is Centre National de la Recherche Scientifique, Département de Psychophysiology, C.N.R.S.—L.P.N. 2, F 91190 Gif sur Yvette, France.

reminded nonstimulated rats. These results suggested that the stimulation alone was sufficient to improve performance at testing and that priming the retrieval process by a reminder was not necessary to produce the facilitative effect. However, the procedure used by Sara et al. (1980) to produce a nonreminded condition left open an alternative interpretation. The nonreminded groups were, in fact, groups that had been exposed daily to the experimental context (reminder) for the last 14 days of the retention interval so as to extinguish any association between context and reinforcement. This procedure was effective in preventing the subsequent reminder effect of pretest exposure to this context. The unexpected facilitative effect of the MRF stimulation in this nonreminded condition could have been due to a dishabituation brought about by the stimulation itself.

A recent series of experiments (Deweert & Sara, 1984) established a procedure in which there is only a marginal cuing effect. The same 90-sec exposure to contextual cues that alleviates forgetting when presented just prior to the test proved to be only partially effective when given 1 or 24 h before testing. Thus, the ceiling effect that might have masked any potentiation of the reminder treatment by the MRF stimulation in Sara et al.'s (1980) experiment can be circumvented.

The aim of the present experiment was to further examine the question of whether it is necessary to first prime retrieval processes in order to facilitate these processes by MRF stimulation. The paradigm described above was used, but the reminded and nonreminded conditions were replaced, respectively, by a reminder treatment known to induce only a partial alleviation of forgetting and by a pseudoreminder. The reminder was a 90-sec exposure to the experimental room, which contained cues relevant to the to-be-retrieved memory; this occurred 1 h before the test. The pseudoreminder was a 90-sec exposure to the colony room, also given 1 h before testing.

METHOD

Subjects

Forty-eight 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. For the duration of the experiment, they were housed in pairs in wire-mesh cages measuring 35 × 21 × 18 cm, and were maintained under a 12-h light-dark cycle (8 a.m.–8 p.m. light). Ten days before pretraining and training, they were placed on a food-deprivation schedule in which the daily ration, given between 5 and 7 p.m., was progressively reduced until the rats' weight loss was 15%, as compared to control animals on a normal diet. The daily food intake was reduced to 15 g over 4 days and then maintained at this level until the end of the training period. Animals were weighed daily and the diet was individually adjusted in order to maintain a homogeneous weight loss.

Surgery

Two to 3 weeks before the beginning of the experiment, all the animals were implanted with bipolar coaxial stainless steel electrodes (0.3 mm in external diameter) in the MRF (according to Albe-

Fessard, Stutinski, & Libouban, 1966; anterior 1.5 mm, lateral 1.5 mm, and vertical +3.0 mm). This electrode was connected to the pins of a miniature socket, which was fixed to the skull with dental acrylic cement. The surgery was performed under general anesthesia (pentobarbital 50 mg/kg, i.p.).

Arousal Thresholds and Stimulation Intensity

After surgery, the animals were placed on the food-deprivation schedule and the behavioral arousal threshold was measured, in the colony room, for each individual rat. For two or three consecutive sessions, separated by at least a 24-h interval, the awake and completely immobile animal was subjected to mild and relatively brief reticular stimulation periods (sinusoidal current, 300 Hz, 2 sec in duration). The stimulation intensities were variable and were delivered in a random order. The behavioral arousal threshold was defined as the minimal intensity required to induce an observable and reproducible behavioral modification (which was in most cases an acceleration of the vibrissae movements associated with respiration) for the entire stimulation period. These thresholds, thus measured, varied among rats from 3 to 9 μ A.

The pretest stimulation used in this experiment had a total duration of 90 sec, and was divided into 6-sec periods of continuous stimulation separated by 3-sec intervals. The stimulation frequency was 300 Hz, the same as that used for determining arousal thresholds, and the intensity for each rat was just below the individual threshold (i.e., between 2.9 and 8.9 μ A).

Apparatus

The maze, a modified Krechevsky maze, consisted of six 50 × 40 × 35 cm units, with 10-cm openings between them. A 25 × 25 × 35 cm startbox was separated from the first maze unit by a sliding door. The goalbox, identical to 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. In each unit, the barriers could be moved from one side to the other; the maze configuration was R-L-L-R-R-L or L-R-R-L-L-R (see Sara, 1985, for a schematic diagram of the maze). The apparatus was located in a room (the experimental room) adjacent to the colony room. The air conditioning system was common to both rooms.

Procedure

All training and testing was carried out between 10 a.m. and 4 p.m. and each rat was run at approximately the same time each day. The first 5 days constituted a pretraining period, during which the animals were familiarized with the experimenter, the maze, and the experimental conditions. On Day 1, each rat was allowed to feed for a 20-min period in a box similar to the startbox and the goalbox and located along a wall of the experimental room. The food reward consisted of .2-g rat pellets. On Day 2, the rats, in gangs of 6, were given 30 min of free exploration of the entire maze, with the sliding doors open, the barriers removed, and food pellets available in the goalbox. On Day 3, using only the last maze unit, 2 rats at a time were trained to enter the goalbox (sliding door open) and feed for a 10-min period. The procedure on Day 4 was the same, but for individual rats and for only 5 min. On Day 5, the sliding door was closed after a rat entered the goalbox; the rat was then allowed to feed 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 backward moves to the preceding maze unit or units

(retracings). 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 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 access to food and water ad lib 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. Throughout the training-to-test interval, the animals were handled daily for 1 min in the colony room in order to decrease the probability that handling by itself would later serve as an effective reminder cue.

Twenty-four days after the last training trial, and 1 h before testing, each rat was individually removed from the home cage and placed for 90 sec in a wire-mesh cage similar to the home cages. For half of the animals, this cage was located in the experimental room, next to the startbox of the maze; this served as a reminder treatment. For the other half, the wire-mesh cage was located on a table in the colony room (pseudore minder treatment). Each of these two groups was divided into two subgroups, stimulated and pseudostimulated (0 intensity). Thus, there were four independent groups (12 animals in each group): stimulated and reminded (SR), stimulated and pseudore minded (S psR), pseudostimulated and reminded (psS R), and pseudostimulated and pseudore minded (psS psR). Immediately after the treatment, each animal was carried to the home cage, where it spent the 1-h treatment-to-test interval. For the test trial, as during training, each individual rat was placed directly into the startbox of the maze. The exact path traced by each rat, its errors and retracings, and its total time to run the maze were noted.

Figure 1. Mean number of errors for combined groups during acquisition and for individual groups at retention test ($\pm$ SEM) 24 days later. R = reminder (exposure to the experimental room); S = mesencephalic reticular formation stimulation; psR = pseudore minder (exposure to the colony room); psS = pseudostimulation. Treatment-test interval was 1 h in the four experimental conditions. Note that only animals in Group SR performed in test as well as they did at the end of training. See text for statistical analysis.

Figure 2. Mean time (log sec) to run the maze for combined groups during acquisition and for individual groups at retention test ($\pm$ SEM) 24 days later. Note that there was no effect of stimulation. See text for statistical comparisons.

Histology

After the experiment, the animals were perfused under deep anesthesia with a 10% formalin solution (intracardiac perfusion) and the brains were frozen, sliced to a thickness of 50 μ m, and colored with cresyl violet.

RESULTS

Acquisition Trials

The animals showed good learning over the five training trials, in terms of run time, errors, and retracings (see left side of Figures 1 and 2 for errors and run times). The number of errors was at chance level (in the absence of retracings) by Acquisition Trial 3 and dropped to 1.9 on Acquisition Trials 4 and 5. Retracings, in general, were seen only on the first training trial (mean score = 2.3) and rarely occurred at the end of training. Run times dropped from 90 sec on the first trial to 13 sec at the fifth trial.

Test Trial

Mean number of errors and mean log time to run the maze for each group at testing are shown in Figures 1 and 2. In terms of errors, only animals both stimulated and reminded (SR) performed as well at testing as they did at the end of training. The three other groups showed forgetting, that is, a decrement in performance over time.

A $2 \times 2 \times 2$ analysis of variance was performed for number of errors, with stimulation and reminder as between-groups factors and repetition (mean of the last two training trials and test trial) as the within-groups factor. This analysis showed a significant stimulation $\times$ reminder $\times$ trials interaction [$F(1,44) = 6.36, p = .015$], a significant main effect of repetition [$F(1,44) = 19.05, p < .001$], and a significant stimulation $\times$ reminder interaction [$F(1,44) = 5.51, p = .022$]. The signifi-

cant main effect of repetition indicates that there was global forgetting. The significant interaction between repetition and the two treatment factors suggests that the amount of forgetting was dependent upon the pretest treatment.

As can be seen from Figure 1, forgetting seemed more pronounced for animals only stimulated or only reminded (Groups S psR and psS R) than for animals pseudostimulated and pseudoreminded (Group psS psR). However, comparisons between Group psS psR and Group psS R or Group S psR over trials did not reveal a significant treatment $\times$ trials interaction [for Group psS psR vs. Group psS R, $F(1,22) = 2.03$; for Group psS psR vs. Group S psR, $F(1,22) = 1.75$]. This indicates that animals only stimulated or only reminded did not show more forgetting than did pseudostimulated, pseudoreminded animals. As Figure 1 shows, the within-group variance in the test trial was quite high in Groups psS R and S psR. For both of these groups, the elevated means were due to one or two high scores.

Within-group comparisons showed that animals in Group psS psR made significantly more errors at testing than at the end of training [$F(1,11) = 7.19$, $p = .020$]. Thus, animals in this control group exhibited forgetting similar to that shown by nonmanipulated control groups in our previous experiments (Deweert & Sara, 1984; Deweert et al., 1980; Sara & Deweert, 1982); a 90-sec pretest exposure to the colony room, whatever the treatment-to-test interval, was ineffective in alleviating spontaneous forgetting. The same picture emerged for Groups S psR and psS R, indicating that neither a 90-sec MRF stimulation in the colony room nor a 90-sec contextual cuing episode, given 1 h before testing, was sufficient by itself to alleviate spontaneous forgetting. Within-group comparisons proved these performance deficits to be significant [for Group S psR, $F(1,11) = 7.16$, $p = .021$; for Group psS R, $F(1,11) = 8.03$, $p = .016$]. On the other hand, within-group comparisons for animals submitted to both MRF stimulation and exposure to background stimuli in the experimental room (Group SR) showed no significant performance decrement over time in terms of errors [$F(1,11) = 0.16$]. Direct comparisons between Group SR and the two control groups over trials showed a significant group $\times$ repetition interaction [for Group SR vs. Group psS R, $F(1,22) = 4.99$, $p = .034$; for Group SR vs. Group S psR, $F(1,22) = 4.49$, $p = .043$]. This, again, indicates that reminder alone and stimulation alone were ineffective treatments compared to stimulation and reminder given together. This potentiation of a reminder effect by stimulation is further supported by the significant interaction, mentioned above, between stimulation and reminder. This also confirms that the effect on performance of the MRF stimulation depends upon the place where stimulation was delivered.

A $2 \times 2 \times 2$ analysis of variance, with stimulation, reminder, and repetition as the factors, was performed on log time to run the maze. This analysis showed a significant main effect only of repetition [$F(1,44) = 79.91$,

Figure 3. Left: Typical electrode placement in the mesencephalic reticular formation. Right: location of the electrode, in 12 randomly chosen stimulated animals. CG = central gray; DpMe = deep mesencephalic nucleus; IP = interpeduncular nucleus; MGD = medial geniculate nucleus; RMC = red nucleus, magnocellular; SN = substantia nigra.

$p < .001$], and no significant interactions [for stimulation $\times$ reminder $\times$ repetition, $F(1,44) = 1.31$; all other F s < 1]. This indicates that the animals took longer to run the maze at testing than at the end of training, whatever the pretest treatment.

Histology

The location of the electrode in the vicinity of the MRF was confirmed in all stimulated animals (see Figure 3). There was no correlation between exact electrode placement and maze-retention performance.

DISCUSSION

The principal results of this experiment were as follows: (1) Animals exposed to the experimental room and animals exposed to the colony room performed at approximately the same level 1 h later, both showing significant forgetting of the initial training. (2) A 90-sec reticular stimulation had facilitative effects on test performance only when administered concurrently with exposure to the training (and testing) context. (3) When stimulation was delivered in a neutral, irrelevant context, there was no effect. Two major points can be drawn from these results. First, the existence of an interaction between stimulation and the place where it is delivered argues strongly against any interpretation of the effects of MRF stimulation in terms of nonspecific motivational or locomotor modifications. In the same way, it is important to emphasize the fact that these facilitative effects were limited to errors—which can be considered to reflect the most cognitive aspects of performance in this kind of task—and did not apply to run times (see Figure 2). It should be noted that MRF stimulation had no effect on run time in our previous experiments, nor did pretest injections of yohimbine (Sara, 1985). Both of these treatments facilitated perfor-

mance in terms of errors only. Therefore, although treated animals took just as long to make choices as did nontreated control animals, their more effective memory retrieval was reflected by their more accurate discriminations.

The second point to be drawn from the present results is that this experiment answers the question raised by Sara et al. (1980) as to whether a nonspecific arousal *per se* is sufficient to facilitate subsequent test performance, or whether a simultaneous reactivation of the memory of initial training is a necessary condition for the action of MRF stimulation in alleviating spontaneous forgetting. The first of these alternatives implies that facilitative effects of pretest MRF stimulation should be totally independent of the context within which it is given. In the present experiment, pretest MRF stimulation was effective in alleviating forgetting only when given in the presence of background stimuli associated with the experimental situation, that is, in a "significant" context. There was apparently no effect when the stimulation was administered in a neutral context, that is, in the colony room. In fact, the performance of the stimulated pseudoremined group was actually worse than that of its nonstimulated control group (although not significantly). Therefore, it is possible that enhancing misinformation or irrelevant information by MRF stimulation could have a negative effect on some animals on the subsequent test trial.

It should be noted that DeVietti, Conger, and Kirkpatrick (1977) found that MRF stimulation was effective only when administered after a reactivation of a single-trial conditioned fear response. In their experiments, the stimulation alone or the conditioned stimulus alone did not facilitate performance 24 h after the reinstatement-stimulation procedure. Thus, in two very different paradigms, using two very different tasks, it has been shown that both reminder and MRF stimulation are necessary to enhance retention performance.

Despite the fact that, in the present experiment, a 90-sec exposure to background stimuli in the experimental room had no detectable effect on test performance 1 h later, it is likely that it actually reactivated the memory of training at the time of its administration, inasmuch as this treatment has consistently been demonstrated to alleviate forgetting when given immediately prior to testing (see, e.g., Deweer & Sara, 1984; Deweer et al., 1980). We tentatively propose that MRF stimulation results in a more elaborate perceptual analysis or a deeper processing (see Craik & Lockhart, 1972) of the current information in the environment, and in its better integration with previously acquired information. This would result in a reorganized and more resilient memory trace, leading to a consequent facilitation of test performance.

The interaction between the effects of MRF stimulation and the significance of the context in which it is delivered has also been recently demonstrated (Alexinsky, Legal, & Donguy, 1986) in a working-memory paradigm, using a delayed matching-to-sample task (see Alexinsky & Chapouthier, 1978, for detailed description of the task). MRF stimulation, identical to that used in this experiment,

was given either during sampling or at the beginning of the retention interval. Matching performance improved on trials in which animals were stimulated during sampling. Performance also improved when animals were stimulated during the retention interval in the presence of a cue relevant to the to-be-remembered sample. However, the same treatment given during the retention interval either in the absence of the relevant cue or in the presence of an irrelevant cue had disrupting effects. Thus, the effects of MRF stimulation depend upon the significance of the current available information during a sampling episode or during the retention interval in a working-memory paradigm. The present experiment showed the same interaction of stimulation with the concurrent information during contextual cuing in a long-term forgetting paradigm. All of these data fit well with the suggestion made above that MRF stimulation can enhance perceptual analysis and processing of the stimuli present at the time of the stimulation. Moreover, after learning of tasks with different response contingencies in the same context, the typical interference between the conflicting memories (see Spear, 1971) should be alleviated by pretest MRF stimulation if this treatment is given concurrently with a specific cue related to one or the other of the to-be-retrieved memories. Studies testing this hypothesis are presently being carried out in our laboratory.

Regarding the histological data (see Figure 3), it should be noted that the placement of the electrode was in or near the noradrenergic dorsal ascending bundle (Hokfelt, Johansson, & Goldstein, 1984). We do not know to what extent stimulation of these fibers may have contributed to the facilitation seen in this and in our previous experiments. Pharmacological agents known to enhance noradrenergic function produce similar effects on memory retrieval (Sara, 1985; Sara & Deweer, 1982), again suggesting that this system may play a role in mediating effects of MRF stimulation. Note that the role of the noradrenergic system in mediating context-dependent effects has been demonstrated in recent studies of lesions to the dorsal noradrenergic bundle. When forebrain noradrenaline was depleted by these lesions, rats in a latent inhibition paradigm no longer attended to the context in which the to-be-conditioned stimulus was preexposed (Mohammed et al., 1986). On the other hand, recent experiments using direct stimulation of the noradrenergic nucleus locus coeruleus (LC) in the same paradigm suggest that there is a difference between this and MRF stimulation concerning the conditions under which facilitation occurs: a 10-sec LC stimulation outside of the experimental context alleviated forgetting (Sara, Devauges, & Segal, 1986). In the present experiment, the clear interaction between the MRF stimulation and the context suggests that the mediating mechanism of action of this stimulation may be more complex than the mediating mechanism of LC stimulation. Indeed, there are other fiber systems in the MRF region, and the area also contains cholinergic and other cell bodies projecting to many regions of the brain. Neuroanatomical studies us-

ing horseradish peroxidase to determine afferent projections from this region are currently under way and should generate other hypotheses concerning the mediating mechanisms of action of the MRF stimulation.

Whatever the neuroanatomical pathways implicated may be, the synergistic action of contextual cue reminder and electrical stimulation of the MRF supports our view (Deweer et al., 1980; Sara, 1985) that memory retrieval is a dynamic process involving integration of previously acquired information represented in the nervous system (memory trace) with current information (coming from the environment, or endogenous information relative to homeostasis). Treatments that enhance perceptual analysis and attention, such as MRF stimulation, will facilitate these processes and result in better memory retrieval as expressed in organized adaptative behavior—in this case, fewer errors in the maze.

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(Manuscript received June 11, 1986;
revision accepted for publication February 17, 1987.)