Posttrial REM sleep: A critical period for consolidation of shuttlebox avoidance

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Deprivation of REM sleep for 2 h immediately following shuttlebox avoidance training produced deficient retention at 24 h after initial training. REM deprivation beginning 2 h after training had no effect. REM sleep appears to be involved in consolidation of this learning.

Despite extensive research, the function of stage REM sleep remains uncertain. Most promising hypotheses have withered for lack of data (Hennevin & Leconte, 1971). The idea that stage REM is involved in consolidation of long-term memory, however, has gradually accumulated supporting evidence (Greenberg, 1970; Fishbein, McGaugh, & Swarz, 1971; Pearlman, 1971). Leconte and Bloch (1970) found that deprivation of REM sleep (REMD) for 2 days after training produced markedly deficient retention of an incompletely learned shuttlebox avoidance response. We replicated this observation using only 1 day of REMD followed by a day for recovery. The recovery period allowed subsidence of nonspecific effects of the REMD procedure (stress, fatigue, and confinement) before retention testing. In both these studies, learning following the retention test was normal. Thus, the deficit could not be ascribed to impaired learning ability. Leconte and Hennevin (1971) made EEG recordings of rats following this avoidance procedure. The animals usually fell asleep soon and showed increased stage REM during the first 3 h following training. Hennevin, Leconte, and Bloch (1971) subsequently reported that the increase in stage REM was specifically related to acquisition of the avoidance response. As performance reached a plateau after a few days of training, the posttrial increase in REM sleep no longer occurred. These findings suggested a critical period for stage REM and consolidation in this situation.

The present study was designed to investigate the effect of REMD during those first few hours following learning. Since only a brief period of REMD was involved, the animals had ample time to recover completely before retention testing. Because of the limitations of all REMD procedures, we used three different methods whose principal common element was REMD. Thus, a finding of impaired retention with REMD immediately after training would strongly implicate stage REM in the consolidation of this learning.

METHOD

The Ss were female Wistar rats, about 3 months old. The apparatus was a Lehigh Valley Electronics shuttlebox with a 5-cm barrier.

Each animal had four consecutive series of 10 training trials. Each series was preceded by 5 min of rest in the box. Training followed the conventional delayed conditioning procedure in which both CS and US are response terminated. A 5-sec sonalert as CS preceded a .3-mA shock as US. The intertrial interval was variable, with an average of 1 min. Pilot work had shown an average of about 65% avoidance on the fourth series with this procedure. Fifty animals with at least two avoidances on the fourth series were divided into five groups roughly equated for percentage avoidance on these 10 trials. Three groups had REMD immediately after the training procedure by different methods: Group 1 Ss were placed on inverted flower pots, 7 cm in diam, surrounded by water for 2 h, and then returned to their home cages. Group 2 received IP injections of imipramine, 5 mg/kg, and Group 3 received IP injections of pentobarbital, 35 mg/kg. EEG recordings of other animals showed that these REMD procedures were reasonably specific. Animals on the pots averaged 4 min of non-REM (NREM) sleep during the 2 h with no stage REM. Animals given imipramine averaged 46 min of NREM sleep during the first 2 h after injection with 0.5 min of stage REM, and animals receiving pentobarbital averaged 117 min of NREM sleep during the first 2 h with no stage REM. Baseline recordings at this time of day (between 10:00 a.m. and 4:00 p.m.) averaged 65 min of NREM sleep per 2-h period with 14 min of stage REM. The total amount of stage REM per 24 h was not significantly altered by the pot and imipramine REMD. Normal animals averaged 104 min, pot animals averaged 90 min, and imipramine animals averaged 102 min. Pentobarbital animals averaged considerably less (45 min). The remaining two groups served as controls. Group 4 Ss rested in their cages for 2 h after training, then had 2 h of REMD by the pot, and then were returned to their cages. Group 5 had normal sleep following training. Twenty-four hours after training, all animals had 10 retention trials that were identical to the initial trials.

RESULTS

A measure of percentage change in retention was calculated for each rat from the difference between avoidance on the final 10 training trials and avoidance on the retention trials divided by avoidance on the final

Table 1
Mean Avoidance on Final 10 Training Trials and 10 Retention Trials, and Mean Percentage Retention Change*

	Group 1 Immediate REM by Pot	Group 2 REM by Imipramine	Group 3 REM by Pentobarbital	Group 4 REM After 2 H	Group 5 No REM
Training Trials	6.7 (3 - 10)	6.8 (4 - 10)	7.1 (3 - 10)	6.7 (2 - 10)	6.6 (4 - 9)
Retention Trials	1.4* (0 - 4)	1.8* (0 - 8)	0.8* (0 - 3)	5.0 (2 - 9)	4.9 (3 - 7)
Mean Percentage Retention Change	-77%*† (-100 - 0)	-80%*† (-100 - -20)	-86%*† (-100 - -33)	-23%† (-70 - +50)	-23%† (-67 - 0)

*Differs from Groups 4 and 5 ($p < .01$) †- refers to poorer performance on retention trials, + refers to improved performance

training trials. Mean values for the five groups appear in the table. The U test showed that Control Groups 4 and 5 had about the same percentage retention change and both were significantly superior to the REMD Groups 1, 2, and 3 ($p < .01$).

DISCUSSION

Deprivation of REM sleep for 2 h immediately following shuttlebox avoidance training caused a marked retention deficit. The previously mentioned nonspecific effects of the pot REMD procedure seemed negligible in this situation. These factors should have influenced Group 4 more than Group 1 because the REMD occurred closer to the retention test. One might wonder if the retention deficit in Group 1 resulted from retroactive interference due to sleep loss during the critical period. This interpretation would be hard to reconcile with the fact that Group 3 slept throughout the critical period. Similarly, the retention deficit in Groups 2 and 3 might be ascribed to a nonspecific drug effect. Except for their influence on the REM mechanism, however, pentobarbital and imipramine are, in general, pharmacologic antagonists. Finally, postulation of retroactive interference due to the stress of pot confinement could not account for the results in Groups 2 and 3, which had no confinement. Thus, it seems parsimonious to conclude that REMD is the critical variable in the retention deficit.

These findings suggest that the deficient retention of shuttlebox avoidance observed at 1-2 h following training (the Kamin effect; cf. Brush, 1970) might result from disruption of the REM-consolidation mechanism by the retention test. We are investigating this possibility.

These results also have implications for other studies of consolidation. Conventional methods for producing retrograde amnesia such as ECS, barbiturate anesthesia, and spreading cortical depression disturb REM sleep during the hypothetical critical period following training (Cohen & Dement, 1966; Weiss, Roldan, Bohdanecky, & Fikova, 1964). Other amnesic agents probably have a similar effect. The influence of REMD on retention

varies widely in different species and situations. Thus, this factor could be one source of the confusing discrepancies in results of consolidation studies.

As discussed by Bolles (1970), shuttlebox avoidance, which involves return to a place associated with aversive stimuli, is difficult for the rat. Such learning requires integration of instinctive defense reactions (freezing and fleeing) with environmental feedback of the consequences of behavior. This complexity of the shuttlebox task might account for its vulnerability to REMD, whereas retention of simpler conditioned avoidance is unaffected (Joy & Prinz, 1969). In humans, habituation to repeated viewing of a frightening film is impaired by REMD (Greenberg, Pillard, & Pearlman, 1972), whereas tasks requiring no emotional adaptation are unaffected (Grieser, Greenberg, & Harrison, in press). Thus, the function of stage REM sleep may involve integration of new information into existing structures as described by Breger, Hunter, and Lane (1971).

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