Consolidation time of hippocampectomized rats in a one-trial learning situation*

WILLIAM I. RIDDELL

State University of New York College at Brockport, Brockport, N.Y. 14420

Twenty rats with hippocampal lesions and 40 rats with control lesions were tested in a step-down passive avoidance situation. The step-down response was followed by a 35-mA ECS after 6.6 sec in one group and after 3.3 sec in another group, while a third group served as a footshock (FS) control. The results indicated that, although retention of the FS was an increasing function of the temporal interval between the FS and ECS for all groups, there were no differences between Ss with hippocampal lesions and controls at any ECS interval. The results were interpreted as suggesting that the hippocampus is not involved in the consolidation process.

The initial impetus for much of the recent work on hippocampal function was probably the striking memory deficit following hippocampal damage in human patients described by Scoville & Milner (1957) and Penfield & Milner (1958). On the basis of these observations, it has been suggested that the hippocampus is necessary for the consolidation of memory traces. Studies which have employed infrahuman species, however, have generally failed to find an analogous deficit. In contrast to previous negative results (see Douglas, 1967, for a review), Uretsky & McCleary (1969) have reported that the isolation of the hippocampus via a combined entorhinal-fornix lesion produces a significant retention deficit if performed 3 h following training. The pattern of their results led Uretsky and McCleary to suggest that the surgical interference with the hippocampal-entorhinal complex effects the consolidation process. Earlier work (Hostetter, 1968) on retrograde amnesia following electroconvulsive shock (ECS) in hippocampectomized rats, however, can be interpreted as suggesting that hippocampectomized rats consolidate at a "faster rate" than normals.

The absence of a general passive avoidance deficit in hippocampectomized rats in the Hostetter (1968) study is probably attributable to the small electrolytic lesions employed and could suggest a possible explanation of why a deficit in consolidation might not also have been observed. As suggested by Douglas (1967), the contradictions between different investigations of passive avoidance learning in rats with

hippocampal lesions may be attributable to differences in the lesion. That is, those investigations which have employed small lesions have generally failed to find a passive avoidance deficit, while those that employ larger lesions have generally found a deficit.

The present experiment tested for differences in consolidation time between control and hippocampectomized rats on a task, i.e., a step-down situation, which is known to be effective in showing ECS-produced amnesia (Chorover & Schiller, 1965) and employing lesions that result in a passive avoidance deficit (Riddell, 1968). Previous evidence (Chorover & Schiller, 1965) indicates that in the step-down situation, normal Ss will show a decline in retrograde amnesia as the interval between the footshock (FS) and ECS is increased from .5 to 10 sec. It was hypothesized that hippocampectomized Ss would show a greater retrograde amnesia than the controls for any interval within this period. This hypothesis was tested by administering ECS at 3.3 and 6.6 sec after the FS.

SUBJECTS

The Ss were 60 male hooded rats of the Long-Evans strain, 80-100 days of age at the time of surgery. Twenty Ss received bilateral hippocampal damage, 20 received bilateral cortical damage, 10 received sham lesions, and the remaining 10 Ss served as normal controls. During the time Ss were tested, they were housed individually in standard wire mesh cages.

APPARATUS

The step-down apparatus employed was identical to that used by Chorover & Schiller (1965). It consisted of a 40-cm-sq compartment, with walls 80 cm high made of Plexiglas and a grid floor constructed of 3/32-in.-diam stainless steel rods spaced 1.25 cm apart. The grid floor was connected to a source of ac voltage so that a FS of

1 mA could be delivered when the rat's feet touched the grid floor. Located in the center of the compartment was a 13-cm-square insulated platform, 5.5 cm high.

PROCEDURE

The same general procedures previously employed by Riddell (1969) were used. On the basis of the SDL on Days 1-4, the four groups were divided into three experimental conditions. The first group (FS) contained 30 Ss: 10 hippocampectomized, 10 cortical controls, and 10 normal controls. These animals received a 1-sec 1-mA FS when they made the step-down response on Day 5; they received no ECS. For the purpose of measuring the effect of drive level on this task, one-half of the rats in each group were tested under 23½ h of food deprivation. The remaining 30 Ss were divided into two groups, containing 15 Ss each, 5 from each operate group. The only difference between these groups was the interval between the offset of the FS and the onset of the ECS following the step-down response. For one group (FS/ECS 3.3), the 35-mA ECS was delayed for 3.3 sec after the offset of the FS; for the other group (FS/ECS 6.6), a 6.6-sec delay was imposed. All the Ss in these two groups were run satiated.

Owing to long latencies of some of the Ss during the habituation phase, the criterion for successful avoidance on Day 6 had to account for individual differences. Therefore, the criterion was 10 times S's mean SDL on Trials 3-5.

OPERATIONS AND HISTOLOGY

All operations were performed in one stage under pentobarbital anesthesia, at a dosage rate of 50 mg/kg. In the cortical control group, the cortex was removed by suction until approximately 80% of the hippocampus was exposed. The lesion was then slightly expanded anteriorly. For the hippocampectomy, the cortex overlying the hippocampus was removed and the hippocampus proper was ablated by aspiration.

After training, all animals were given a lethal dose of sodium pentobarbital. They were then perfused intracardially with 0.9% saline followed by 10% Formalin. The brains were embedded in celloidin and sectioned at 50 microns. Every 10th section through the lesions was retained and stained with thionin.

Tracings of representative cross-sections through the lesion are shown in Fig. 1. Visual inspection of photographic enlargements of the lesions indicated that, although two of the hippocampal lesions were only about 60% complete, the majority of hippocampal lesions were at least 90%

*This investigation was supported by Research Grant No. 10972 from the National Institute of Mental Health to William A. Wilson, Jr., and State University of New York Research Grant No. 022-7107A to the author.

Fig. 1. Tracings depicting the extent of the lesion in representative rats with hippocampal (left) and neocortical control lesions (right).

complete. Any specific thalamic damage was unilateral. Although the cortical control lesions did not involve as great a volume of tissue, they included more cortex than that removed for hippocampal lesions. The extent of hippocampal or cortical damage was not correlated with SDL.

RESULTS

It first should be noted that the deprivation variable had no effect on performance in the FS control group; rats within each operate group were therefore combined before further analysis. The dependent measure used was the ratio of the SDL on Day 6 to the mean SDL on the last three habituation trials. Due to the criterion, the limiting value this ratio could achieve is 10. Figure 2 summarizes the performance of the various groups, at each of the FS/ECS intervals, on Day 6.

A 3 by 3 analysis of variance was performed on the ratio of SDLs on Day 6 to mean SDL on Days 3-5. For this analysis, the sham-operated and normal Ss were grouped together. The analysis indicated that, although there

was the expected difference between treatments ($F = 3.61$, $df = 2/51$, $p < .05$), the main effect due to the lesion was not significant. The Treatment by Lesion interaction was also nonsignificant.

DISCUSSION

The results of this investigation clearly support the consolidation hypothesis, in that the retention of the FS for all groups was an increasing function of the temporal interval between the FS and ECS. Since the performance of normal Ss was consistent with results previously reported using the same procedure (Chorover & Schiller, 1965), the negative results in regard to operate differences are not readily attributable to methodological error. Since there were no differences between Ss with hippocampal lesions and controls on a task which has been found to be a sensitive measure of consolidation time and with a lesion size known to be sufficient for the production of some behavioral deficits, it is suggested that on this and similar tasks, the hippocampus is not involved in the consolidation of memory traces.

The results of both this experiment and previous work (Hostetter, 1968) therefore indicate that hippocampal lesions do not result in the impairment of the consolidation process as delimited by ECS.

REFERENCES

- CHOROVER, S. L., & SCHILLER, P. H.
Short-term retrograde amnesia in rats.

Fig. 2. Mean SDL ratio at each FS/ECS interval for each group.

- Journal of Comparative & Physiological Psychology, 1965, 59, 73-78.
- DOUGLAS, R. J. The hippocampus and behavior. Psychological Bulletin, 1967, 67, 416-442.
- HOSTETTER, G. Hippocampal lesions in rats weaken the retrograde amnesic effect of ECS. Journal of Comparative & Physiological Psychology, 1968, 66, 349-353.
- PENFIELD, W., & MILNER, B. Memory deficit produced by bilateral lesions in the hippocampal zone. A.M.A. Archives of Neurology & Psychiatry, 1958, 79, 475-497.
- RIDDELL, W. I. An examination of the task and trial parameters in passive avoidance learning by hippocampectomized rats. Physiology & Behavior, 1968, 3, 883-886.
- RIDDELL, W. I. Effect of electroconvulsive shock: Permanent or temporary retrograde amnesia. Journal of Comparative & Physiological Psychology, 1969, 67, 140-144.
- SCOVILLE, W. B., & MILNER, B. Loss of recent memory after bilateral hippocampal lesions. Journal of Neurosurgery & Psychiatry, 1957, 20, 11-21.
- URETSKY, E., & McCLEARY, R. A. Effect of hippocampal isolation on retention. Journal of Comparative & Physiological Psychology, 1969, 68, 1-8.