The effects of hippocampal-pyriform ablations on the acquisition and transfer of cues in successive discrimination by cats[1]

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The acquisition and transfer performance of six cats with hippocampal-pyriform ablations was compared with that of seven normal animals. All animals were trained on a successive, go/no-go, auditory-brightness discrimination (Task 1). Ss were tested for transfer to the auditory and/or brightness cues of Task 1 by training them on similar discriminations using only the brightness cue (Task 2) or the auditory cue (Task 3). The hippocampectomized Ss were inferior to the normals on acquisition of Task 1 (p < .022), but they were not significantly different from the normals on the two transfer tasks (2: p < 0.394; 3: p < 0.662). These results support the hypothesis that previous experience with the relevant cues of a successive discrimination is a crucial factor in reducing acquisition deficits on that discrimination by hippocampal animals.

Several studies indicate that lesions of the hippocampal region cause acquisition deficits on successive discriminations (Kimble, 1963; Niki, 1965; Stein & Kimble, 1966; Buerger, 1969), even though these lesions may not produce deficits on simultaneous problems (Teitelbaum, 1964; Webster & Voneida, 1964). In order to determine if hippocampal animals were also impaired in the acquisition of problems in which the cues were familiar, the present study examined the effects of transfer of cues between successive discriminations. If the amount of new information to be learned were an important variable in determining whether or not hippocampal Ss were impaired on a problem, then hippocampal animals ought to be less impaired on tasks using familiar cues. For example, if operation animals and normal animals are trained first on a discrimination, A, and second on a discrimination, B, then the more similar the cues of the two discriminations are, the less difference there will be between the learning ability of the operated and normal animals on the second discrimination (B), because the amount of new information learned will become smaller as the cues of the two discriminations become more similar. There should, of course, be a significant difference between the operated and normal animals on the first discrimination (A). This effect may explain several reports in which ablations in the hippocampal region affected postoperative learning ability on some problems more than on others (Mishkin & Pribram, 1954; Kveim, Setekleiv, & Kaada, 1964).

In the present study, the acquisition of a successive, go/no-go, auditory-brightness discrimination (Task 1) was compared in seven normal and seven operated cats; the operated animals had bilateral ablations of their hippocampal regions, including much of Ammon's horns and the pyriform cortices. These Ss' acquisition of two similar successive go/no-go discriminations was also tested. In Task 2, the brightness cue was identical to that in Task 1, but there was no auditory cue. In Task 3, the reverse was true; that is, the auditory cue was identical to that in Task 1 and there was no brightness cue.

METHODS

Fourteen naive adult cats, ranging in weight from 2.6 to 4.2 kg, were divided into two groups. The seven Ss in Group 1 received bilateral hippocampal ablations, whereas the animals in Group 2 remained intact. The surgical techniques, the chamber used in this experiment, and some of the data described below have been reported in detail elsewhere (Buerger, 1967). Briefly, all surgery was performed in one step under barbiturate anesthesia. Pyriform cortices, ventral portions of Ammon's horns, and a small part (6 to 12 mm^3) of the temporal cortex dorsolateral to the pyriform cortex, were aspirated from Group 1. Before surgery and again 1 or more weeks postoperatively, all animals were given a standard neurological examination devised by Dr. A. de Lahunta and Dr. J. F. Cummings of the Department of Anatomy, New York State College of Veterinary Medicine. There were no changes in the results of the examinations after recovery from the operation. On the basis of these examinations, all the intact animals appeared normal. Starting 10 or more days after surgery, all Ss learned a successive, go/no-go, auditory-brightness discrimination. The stimuli were a square of light (L) projected on a translucent tapping key and a 300-Hz tone (T) broadcast from a loudspeaker within the chamber. Either L or T was presented randomly for 6 sec. Ss were fed 1.5 cc of condensed milk if the key was pressed when L was presented or if it was not pressed when T was presented. Ss were shocked through a floor grid if they pressed when T was presented or did not press when L was presented. Any key press while either L or T were being presented caused a 3-sec intertrial interval. Each day, Ss were allowed 50 correct responses and as many errors as they required to reach this number of correct responses; Ss were run until they reached a criterion of six or less errors (89.4% correct) on 3 consecutive days, but no S was run more than 40 days on any task.

After being run on Task 1, animals were run on Task 2 and/or Task 3. The order in which each animal learned these tasks is indicated in the first column of Table 1. Task 2 was identical to Task 1 except that there was no 300-Hz tone (T) during trials in which Ss had to not press in order to

Table 1
Number of Days to a Criterion of 50 Correct Responses and Six or Less Incorrect Responses on Three Consecutive Days for Each of Three Tasks

Animal Number	Task Order	Task 1 Auditory-Brightness Discrimination	Task 2 Brightness Discrimination	Task 3 Auditory Discrimination
		Hippocampal Pyriform Group		
1	1,2,3	18	40+	3
2	1,3,2	40+	40+	10
3	1,2,3	29	13	34
4	1,3,2	14	6	27
6	1,3,2	23	4	18
7	1,2,3	19	18	8
		Normal Group		
8	1,2,3	11	11	34
9	1,2	21	6	--
10	1,3	17	--	17
11	1,2	12	4	--
12	1,2,3	15	8	18
13	1,2,3	12	7	4
14	1,3,2	5	19	28
Results of two-tailed Mann-Whitney Test		p < 0.002	p < 0.394	p < 0.662

receive condensed milk; that is, there was no tone during "no-go" trials. Task 3 was the same as Task 1 except that L was not presented during "go" trials. In short, Tasks 2 and 3 were identical to Task 1 except that the auditory cue was removed in Task 2 and the brightness cue was eliminated from Task 3. Therefore, both Tasks 2 and 3 were go/no-go successive discriminations, but Task 2 was a brightness problem and Task 3 was an auditory discrimination. The training criteria were the same on all three tasks.

During training, all Ss were kept at 80% to 85% of their ad lib weights with canned cat food and/or vitamin pills. The Mann-Whitney test (Siegel, 1956) was used to evaluate the behavioral data. Animals were sacrificed with pentobarbital and perfused with 0.85% saline and then 10% formalin. Brains were cut into 3- to 5-mm blocks, photographed, and sectioned. Representative sections were stained with cresyl violet, Luxol fast blue, and hematoxylin and eosin.[3]

RESULTS

The Ss of Group 1 had large portions of the pyriform cortex and Ammon's horn ablated. Except in Animal 5, there were no lesions in structures adjacent to the hippocampal region, such as the optic radiation and thalamus. Animal 5 was dropped from the experiment because of these lesions. Some of the dorsal parts of Ammon's horn remained from all of Group 1; three Ss also had small portions of the anterior ventral tips of Ammon's horn remaining, but this remnant was always isolated from the dorsal parts. The pyriform cortices were also virtually completely ablated from Group 1.

Table 1 compares the days required to reach criterion on each of the three tasks; criterion was 50 correct responses and six or less errors for 3 consecutive days. The two-tailed probabilities of these results are also indicated, according to a Mann-Whitney test (Siegel, 1956). The cats with hippocampal and pyriform ablations were inferior ($p < 0.022$) to the normal animals on the auditory-brightness discrimination (Task 1), but they were not significantly different from normal on the problems with familiar cues ($p < 0.394$ on Task 2, and $p < 0.662$ on Task 3).

The animals in Group 1 were ranked by an independent O (Dr. V. Molony of the Department of Anatomy, N.Y.S. Veterinary College) in two separate orders: according to extent of ablation of Ammon's horn, and according to extent of removal of the pyriform cortex. It is theoretically possible to differentiate the effects of ablation of Ammon's horn from those of the pyriform cortex by computing Spearman rank correlation coefficients

(Siegel, 1956) between a measure of each cat's ability to acquire Task 1 and each cat's rank in amount of Ammon's horn or pyriform cortex removed. However, neither of these coefficients approached significance, perhaps because of the small number of Ss involved. The operated animals in Table 1 are numbered in order of increasing damage to Ammon's horn.

DISCUSSION

The results on Task 1 confirm the author's previous report (Buerger, 1969) that, in the cat, lesions of the central hippocampus (Ammon's horn) and/or the pyriform cortex impair acquisition of successive go/no-go discriminations. In the previous report, the task was a visual pattern discrimination, whereas the present problem is an auditory-brightness discrimination. As in previous reports (Buerger, 1967, 1969), it is not clear why acquisition deficits were found on these two problems following hippocampal lesions, especially because earlier investigators have not reported acquisition deficits by hippocampal animals (Hunt & Diamond, 1954; Isaacson, Douglas, & Moore, 1961; Teitelbaum, 1964; Webster & Voneida, 1964). Either anatomical or behavioral explanations are possible. It may be that ablation of both Ammon's horn and the pyriform cortex is essential to acquisition deficits, because it is combined lesions of these two areas that are reported to reduce the ability of neurosurgical patients to learn new information (Barbizet, 1963). However, it is more probable that the behavioral task used in this experiment is a more important determinant of the deficit. Kimble (1963) found that rats with hippocampal lesions primarily in the dorsal portions of Ammon's horn showed acquisition deficits on successive, but not on simultaneous, brightness discriminations. The other evidence cited in the introduction also indicates that bilateral ablations of the hippocampal region disrupt acquisition of successive discriminations more than similar simultaneous problems. Hence, the bulk of the evidence suggests that hippocampal ablations impair the acquisition of successive discriminations.

The absence of acquisition deficits on the problems with familiar cues (Tasks 2 and 3) suggests that the amount of new information to be acquired is an important variable in producing acquisition deficits in hippocampal cats. All Ss had learned a problem (Task 1) in which L (a square of light projected on the tapping key) and T (a 300-Hz tone) were relevant cues. One of these same cues was the discriminative stimulus in Tasks 2 and 3, L in Task 2 and T in Task 3. Hence, the total amount of information required to learn Tasks 2 and

3 was less than that required in Task 1. If the hippocampal regions were instrumental in the acquisition of new information, then one would expect that hippocampal animals would be less impaired in acquiring tasks with familiar cues (e.g., Tasks 2 and 3) than in acquiring tasks in which the cues had never before been relevant (Task 1). The data indicate that hippocampal cats show acquisition deficits on successive problems with unfamiliar cues, but do not show deficits on similar problems with familiar cues. These results therefore suggest that the acquisition of new information is an important variable in determining whether or not hippocampal animals are impaired on successive discriminations.

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NOTES

The redefinition of extinction applied to Sidman free-operant avoidance responding

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Extinction in a free-operant avoidance situation was defined as removing the effectiveness of the response in delaying shocks rather than the removal of shocks. This was identified as a procedure more consistent with those used in appetitive reward studies involving extinction. In the present study, orderly extinction was found in four out of five albino rats where the R-S interval and S-S interval were both equal to 15 sec.

In recent years, more emphasis has been placed on escape and avoidance conditioning with electric shock as the aversive stimulus. Assuming that performance in the aversive shock situation should fit some general unified picture of behavior theory, comparable experimental operations in food-reward and aversive-conditioning studies would appear desirable.

The extinction procedure utilized in the food-reward situation is to disconnect the feeder and observe the resulting decrease in response rate when the response no longer produces food. An apparently analogous operation has been performed in both free-operant avoidance studies (Sidman, 1966) and discriminated avoidance (Kimble, 1961), where the shocker is disconnected and a response decline (sometimes quite slowly, other times very rapidly) is observed when shock is no longer presented. A functional analysis of the relationship between response and reinforcement indicates that these

"extinction" procedures are not operationally comparable (Davenport & Olson, 1968). The reinforcing event in the food-reward situation is the presentation of food, and the response is being extinguished when food is withheld, that is, when the response is no longer effective in producing reinforcement.

The reinforcing events for the instrumental response in the avoidance situation is apparently the omission, delay, or reduction in frequency of the scheduled shocks or warning signals accompanying shock (Sidman, 1966; Kimble, 1961). Thus, the disconnection of the shocker in the traditional extinction procedure is, at best, ambiguous to the S, because the previously utilized "reinforcement" is now applied following any response that may

occur, including the response that was effective during avoidance training. That is, all responding is followed by shock omission, a consequence previously restricted to a specified avoidance response. The new definition suggested by Davenport & Olson (1968) for extinction of avoidance responding involved making the instrumental avoidance response ineffective in terminating the warning signal and in avoiding the shock, thus withholding the reinforcement provided earlier. Davenport & Olson (1968) demonstrated that when extinction, redefined in this way, was applied to responses established in a discriminated avoidance procedure, the response decreased in probability in a quick and orderly manner and did not show the extended responding obtained in earlier studies following the shock removal type of extinction.

The present study was designed to determine whether or not this redefinition of extinction could be effectively applied to the Sidman free-operant avoidance procedure, which does not involve a warning signal. In the free-operant avoidance procedure, brief shocks are periodically presented, with the interval between shocks known as the S-S interval. Each specified response made by the S delays the occurrence of shock for a given time period known as the R-S interval. There typically is no warning signal prior to the shock, and the animal is allowed to respond freely throughout the training with each response delaying the next shock by the time represented by the R-S

Fig. 1. Acquisition and extinction responding with percentage avoidance in acquisition identified.