Retention of a geotaxic discrimination task following septal lesions in rats[1]

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Septal lesions did not impair retention of a simple discrimination task that was based on geotaxic cues, but it did disturb the ability of the animals to make fine discriminations and prolonged extinction when the animals were not preloaded with water.

Several recent studies have investigated the importance of the septal area in retention. Reports on the effects of lesions in this region range from complete loss of memory to slight or no impairment at all. Deficits in memory have been demonstrated on tasks that require active avoidance from shock (McCleary et al, 1965; Moore, 1964; Rich & Thompson, 1965), on a complex maze (Carey, 1968), by means of an extinction test (Carey, 1967), and to a lesser extent on a brightness discrimination task (Schwartzbaum et al, 1964). A number of other studies have reported that septal lesions disrupt preoperatively conditioned behavior (e.g., Burkett & Bunnell, 1966; Schwartzbaum et al, 1964). However, it is uncertain whether these effects represent a retention loss or are only secondary to some motivational and motor disinhibitory effects of septal damage. Septal lesions failed to impair retention of a thirst habit in a shuttle-box situation (Breen & Thompson, 1966), and of a black-white discrimination that was based on shock (Kleiner et al, 1967; Meyer et al, 1968). Rats were even found to improve their performance in a linear runway after destruction of the septal area (Raphelson et al, 1966).

The present experiment extends the inquiry to the effects of septal lesions on the retention of a discrimination based on geotaxic cues. An added incentive for using this task was that it presented a novel experimental procedure for tests of discrimination.

METHOD

Preoperative Tests

Twelve male Sprague-Dawley rats (250-300 g) were taught to discriminate between geotaxic cues on the basis of water reinforcement. The data of two animals had to be discarded due to illness and death during the experiment. Following 23-h water deprivation, each animal was initially trained to press a lever for 0.1 ml of water while the test chamber was in a level position. Discrimination training usually started on the third session and introduced tilting the cage 20 deg. The apparatus was adapted in such a way that the side of the cage housing the lever was free to move through various degrees of tilt, while the opposite side was fixed to a hinge. Each daily session during discrimination consisted of 18 trials, 60 sec in duration. On nine trials the cage was level and all responses were reinforced (S+). On the other nine trials the cage was tilted 20 deg and responses were never reinforced (S−). The session always started with a reinforced trial. The remaining S+ trials were distributed randomly among the S− trials, with the restriction of no more than three consecutive trials with either condition. Between trials the cage was raised and lowered a few times so as not to condition the animals to the direction of movement. Training on the discrimination continued for each S until at least four times as many responses were made during S+ as S− in two consecutive sessions. The animals required an average of six sessions to attain criterial performance. Throughout the experiment they were allowed to drink water for 30 min after each session.

Discrimination was followed by two sessions on which stimulus generalization was tested. Each generalization session consisted of 23 trials, 9 of which were reinforced. The remaining trials were made up of the following degrees of tilt: 20, 15, 10, 8, 6, 4, and 2 deg, with each level presented twice. In one session the tilted trials were interspersed between S+ trials in a descending order followed by an ascending order in the second half of the session. The order of presentation was reversed in the other session. All animals were operated on the day following the last generalization session and allowed 7-8 days to recover. They were maintained on food and water ad lib during this time.

Postoperative Tests

This phase of the experiment consisted of several stages. Tests on retention of the discrimination were followed by tests on generalization. Both procedures were carried out under exactly the same conditions as preoperatively and to the same criterion. After the tests on stimulus generalization, extinction of the discriminatory response was determined. The first of the extinction sessions consisted of 36 trials, 18 presented at 0 deg and 18 at 20 deg. After this, the animals were returned to ad lib water for a period of 12-14 days before they were again deprived 23 h before relearning the discrimination task. Only one session was required to establish criterial responding. Another extinction session, similar to the first, was then presented. However, 15 min before the start of the session the groups were preloaded with certain amounts of water. Septal animals were allowed to consume 8 ml from a dish placed in the home cage, and control animals, 4 ml (see Harvey & Hunt, 1965). The animals were returned to ad lib water for a period of 2-4 weeks before the relearning and extinction procedures were repeated for the last time. Relearning again started after 23 h of water deprivation, but none of the animals was preloaded with water before the extinction test.

SURGERY

One-half of the animals received bilateral septal ablations. The lesions were made with a Grass LM 3 radio frequency lesion maker, using the following stereotaxic coordinates: 1.0 mm anterior to the bregma, 3.0 mm lateral to the midline, 5.0 mm below the surface of the dura mater and at an angle of 25 deg towards the midline. The five control animals were subjected to the same operative procedure except that the electrode was not lowered into the brain. All lesions were verified histologically. Damage to the anterior septal area was fairly uniform among animals. The amount of damage to the posterior septal area was somewhat more variable.

RESULTS

Destroying the septal area did not impair the memory of the discrimination task as measured by the relearning test. Nearly all septal and control animals reached criterion within the minimum number of two sessions. The S+/S− ratio of responses actually improved slightly after the lesion was made. Septal lesions did, however, affect the performance of the animals on tests of generalization. Not only did the brain-damaged animals require more sessions to reach criterion ($p = .056$, two-tailed Mann-Whitney U test), but their rate of responding to both S+ and S− increased after the lesion (see Table 1). The increased responding was especially noticeable to the degrees of tilt closest to S+. This pattern of response was verified in an analysis of variance of pre- and postoperative response output of the groups to the nonreinforced ($F = 2.34$, $df = 6/48$, $p < .05$ for the Group by Pre-Post by Tilt interaction), as well as to the reinforced condition ($F = 12.79$, $df = 1/8$, $p < .01$ for the Group by Pre-Post interaction).

Septal animals also extinguished more slowly than control Ss on the discrimination task (Table 2). Not only did they have a higher response output during the first half of the session ($p = .048$, one-tailed Mann-Whitney U test), but the difference between the groups became even more noticeable

Table 1
Mean response rate per trial during the two preoperative and first two postoperative generalization sessions.

	Degrees of tilt							
	0	2	4	6	8	10	15	20
Control								
Preoperative	6.8	4.8	4.3	2.6	2.5	2.2	2.7	0.8
Postoperative	5.6	1.6	2.1	2.2	2.1	1.1	1.7	0.4
Septal								
Preoperative	5.7	3.5	2.6	2.7	1.1	1.3	1.6	1.2
Postoperative	7.1	6.0	6.5	5.2	2.6	2.7	1.7	0.2

towards the latter half of the session ($p = .004$, one-tailed Mann-Whitney U test). All animals exhibited a similar pattern of decreased responding during the extinction period when they were preloaded with water. The septal Ss, however, seemed to be more sensitive to preloading, for this was the only occasion when their response rate during extinction dropped below that of the control animals (see Table 2).

DISCUSSION

The excellent performance of septal animals on relearning the simple discrimination task suggests that the lesion did not disrupt the memory of the thirst habit that was based on geotaxic cues. These findings are in agreement with results of some of the studies on retention (Breen & Thompson, 1966; Kleiner et al, 1967; Meyer et al, 1968; Raphelson et al, 1966). However, the generalization tests indicated that the ability to make fine discriminations were impaired after destruction of the septal area. These results cannot be easily explained by loss of response inhibition, although some of the extinction data would seem to favor such an interpretation. The septal animals were able to inhibit quite adequately their responses to larger degrees of tilt and to S− during the simple discrimination task. They were often observed during nonreinforced trials to approach and place their feet on the bar without actually pressing it. Thus it seems as if the impairment on generalization does reflect an inability on the part of the brain-damaged animals to make fine discriminations. Similarly, it is quite likely that differences in the degree of difficulty of the task that has to be remembered, can account for some of the discrepant findings in the literature. For instance, retention deficits did not show up on a straight runway (Raphelson et al, 1966), but it did in a complex maze (Carey, 1968). It may also explain why septal animals were more impaired postoperatively on a tone than on a brightness discrimination (Schwartzbaum et al, 1964). We are at present investigating whether the retention of a task involving fine discrimination of geotaxic cues would be more susceptible to disruption by septal ablation than the discrimination of 0 from 20 deg.

However, the poor performance of septal animals on geotaxic generalization may also reflect increased thirst motivation, for the greater resistance to extinction exhibited by septal animals was abolished after allowing them to drink 8 ml of water before the start of extinction. This finding does suggest that thirst motivation is a factor of considerable importance and that it has to be taken into account in tests determining the importance of the septal area in retention.

Table 2
Median number of responses made to S^+ during the different extinction sessions.

	Extinction 1 Without Preload Blocks of 9 Trials		Extinction 2 With Preload Blocks of 9 Trials		Extinction 3 Without Preload Blocks of 9 Trials	
	1	2	1	2	1	2
Control	43	17	30	8	34	11
Septal	76	37	18	5	35	31

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NOTE

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