COMPARISON OF THE SEPTAL LesION EFFECTS ON VISUAL, AND SPATIAL DISCRIMINATIONS IN RATS

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Abstract. Postoperative performance in acquisition and reversal learning of septal rats was investigated and compared with control rats in three experiments. Experiment I involved a simultaneous black-white discrimination task. The number of errors in normal and septal rats was similar in acquisition and reversal learning. Both septal and normal rats manifested directional response sets. Experiment II examined a position habit discrimination. Acquisition was similar in septal and normal rats, while reversal learning was impaired in septal rats. Experiment III, which investigated a position habit discrimination with available irrelevant visual stimuli indicated that both acquisition and reversal learning were impaired in operated animals. Results suggested that septal rats utilize response produced cues to control their behavior, but the enhanced orienting response to the visual stimuli interferes with the proprioceptive stimuli.

INTRODUCTION

The role of the septal region in performance of visual and spatial tasks has been extensively investigated. As far as simultaneous visual discrimination is concerned, it has been shown that postoperative retention after septal removal was impaired in rats (10), but not in cats (13). Postoperative acquisition of the same discrimination was not impaired in septal cats in comparison with normals (25). Simultaneous brightness discrimination tested in a bar pressing situation was not significantly impaired in septal rats compared with normals, however, the septals demonstrated far more perseverative errors (14). These results, and
others involving the discrimination of two tones based upon an intermittent food reinforcement schedule, were interpreted to suggest that the removal of the septal area impaired inhibitory control over somatomotor activity (14). Postoperative reversal learning of simultaneous brightness discrimination was not impaired in both septal rats (15) and cats (25).

In spatial tasks we know that postoperative acquisition is not impaired, whereas reversal learning is retarded in septals (7, 8, 15, 18, 23, 25, 26). Further, the effect of septal stimulation on reversal learning of spatial tasks was found equivalent to removal of this region (2, 9). Spontaneous spatial alternation has been reported blocked in septal rats (1, 15, 18, 22). Both postoperative retention and acquisition of successive position reversals were impaired by septal lesions in rats (19–21), but not when the visual cue relevant to the correct response was included (21). This was the situation in which during successive reversals the positional response was changed but the response to the visual cue was left the same. So, if the rats were directed only by the visual cue, the task did not include reversals. It was suggested (21) that the severe impairment of performance in successive spatial reversals was due to the loss or impairment of utilization of response produced cues in septal rats. The visual cues included in the experimental situation help the animal to solve the problem (21). However, if the experimental situation contained relevant visual cues, but the animal was required to reverse both the response to the cue and the positional response, septal lesions retarded performance of the rats (21). This last result is not clear in light of other data (15, 25) showing a lack of impairment of septal rats in comparison with normals during acquisition and reversal learning of simultaneous visual discrimination.

Accordingly, it remains unclear whether some inhibitory functions or utilization of response produced cues are impaired by septal lesions: The purpose of the present experiments is to answer this question.

MATERIAL AND GENERAL EXPERIMENTAL PROCEDURE

Animals. 66 adult male hooded rats, about 75 days of age were used. The rats were housed in individual cages containing a constant supply of water which was available ad lib. Food pellets were given in the cages for only 1 hr following testing. The animals were randomly divided into the groups according to the treatment in three experiments.

Apparatus. All experiments were performed in a modified Thompson and Bryant (24) apparatus, consisting of a choice compartment and goal box, made of plain wood and covered by a colorless laquer. Two opaque one-way doors were situated at the front of the goal box. These doors
were painted gray or white and black. A blocking bar behind each door could be used to prevent entrance to the goal box. A vertical partition extending 10 cm was situated in the middle of the doors to separate them. In the goal box a tray was situated in which cookie reward could be obtained. A 60 w light located 1 m above the apparatus was centered on the choice compartment.

Surgery and histology. The operations were performed stereotaxically by direct current coagulation under 50 mg/kg Nembutal anesthesia. 2 ma anodal current was delivered for 20 sec through a platinum electrode 0.3 mm diameter, insulated except for the tip of approximately 0.3 mm. The coordinates were made according to Fifkova and Marsala (5). Two points (one at each side) were coagulated.

After postoperative training was completed, all operated animals were sacrificed, the brains were perfused in 10% neutral formaline and embedded in paraffin. Coronal sections, 10 μm thick were cut. Every 10th section in the vicinity of the lesions and every 5th in the zone of lesion was taken for verification. Every second of these sections were stained with the Nissl or Klüver–Barrera method. The reconstructions of the lesions were transferred on the standard drawings taken from stereotaxic atlas of König and Klippel (11).

Procedure. Preoperatively all animals were adapted to the apparatus. During consecutive 2 days, the rats were left for 5 min in the discrimination box with both doors opened. In the goal box the food was offered. Then 36 rats were operated and 30 rats served as controls. After the 2 weeks of postoperative recovery and free period for normal animals, all rats were subjected to preliminary training during which both doors were grey and unlocked. The animals could pass through either of the two doors and obtain the food reward in the goal box. In all experiments 10 trials a day were given and intertrial intervals were about 60 sec.

Preliminary training was terminated when each animal accomplished 5 of 10 runs under 10 sec.

After preliminary training, normal and septal animals were divided into three groups and subjected to the three different series of experiments. Training in all experiments was made by the self correction method.

The following parameters were recorded as measures of performance:

1. Errors — touch responses to the incorrect door.
2. Repetitive errors — all errors except the first one made during a single trial.
3. Vicarious responses — approach responses to the correct or incorrect doors but without contact.
4. Perseverative errors — the first response in each trial to the previously reinforced stimulus, up to the first correct response. These errors could be made only during reversal learning.

5. Directional response sets (DRS) — five or more consecutive approach responses made in the same direction (to the same door).

For statistical evaluation of the data the Mann–Whitney U test, two-tailed was used.

EXPERIMENT I

Visual discrimination (V-task). 10 normal and 13 septal rats were used to investigate acquisition and reversal learning of a simultaneous black–white discrimination task. During acquisition, the black door was the correct stimulus and the white door was incorrect and their position was randomly varied. After acquisition training, reversal learning began on the next day. All the animals have given 200 trials each of acquisition and reversal learning.

Results. Figure 1 shows the mean number of errors in acquisition and reversal learning of the V-task. The septal rats made significantly more errors than normals in the first block of acquisition ($p < 0.01$). In the remaining three blocks the mean number of errors in both groups
Fig. 2. Mean number of vicarious responses in acquisition and reversal learning in normal and septal rats in the V-task. Each block represents the mean number of vicarious responses made in 50 consecutive trials.

Fig. 3. Mean number of trials after which the normal and septal rats began to make the first DRS.
is similar and statistically not significant. Comparison of the differences in total number of errors made by septal and normal rats in original learning indicated a lack of statistical significance. Reversal learning was more difficult than original learning for both groups of rats ($p < 0.001$). However, differences in the number of errors made by normal and septal rats either in each block of in the entirely of reversal learning were not statistically significant.

Figure 2 shows the number of vicarious responses in acquisition and reversal learning in normal and septal rats. Septal rats made many more vicarious responses than normal animals over the course of original learning, as well as during each block of this learning (in each comparison $p < 0.001$). In reversal learning, septal rats also made more vicarious responses than normals, but the differences were not statistically significant, except of the first block of reversal learning ($p < 0.01$).

Directional response sets (DRS) were observed in acquisition as well as in reversal learning in both groups of animals. However, during acquisition the number of runs engaged in the DRS was smaller in normals (about 36) than in septal rats (about 49) but the difference was not statistically significant. The number of DRS was greater in septals (about 8) than in normal rats (about 4), and this difference was significant ($p < 0.05$). These findings suggest that the septal rats changed their directional responses more often with shorter bursts of responses than normals. During reversal learning the number of DRS and their length were similar in both groups of animals.

Figure 3 shows the mean number of trials until the normal and septal
rats began to make the first DRS during acquisition and reversal learning. The normal rats started to make directional responses from the second trial while the septal rats from 13th trial in original learning ($p < 0.01$). During reversal learning the normal rats initiated directional responses from the 48 trials while the septal rats from 14 trials ($p < 0.01$). So, the normal rats began to make the DRS earlier during original learning, while during reversal learning they began to make the DRS in the later phase ($p < 0.001$). In septal rats there was no difference in the number of trials after which the rats started to make the DRS either in original or reversal learning.

Figure 4 shows the length of the first and the second DRS in normal and septal animals during original and reversal learning. The length of the first DRS is longer than the length of the second DRS in original learning for normal rats ($p < 0.01$), but there was no significant difference between the length of the first and the second DRS in reversal learning for these Ss. In the septal rats, neither original nor reversal learning indicated a difference in the length of the first and the second DRS.

**EXPERIMENT II**

*Spatial discrimination (S-task).* 10 normal and 12 septal rats were used in this experiment, in which acquisition and reversal learning of position discrimination was investigated. Both doors were grey, and during acquisition the right door choice was incorrect, while the choice of the left door was correct. In reversal learning the right door choice was correct. The required criterion consisted of one error or one vicarious response permitted in 20 consecutive trials.

*Results.* Figure 5 shows the mean number of errors made by normal and septal rats in original and reversal learning of the S-task. Both groups of animals made similar numbers of errors to obtain criterion in acquisition. In reversal learning of this task, septal rats made more errors than normals and the difference was statistically significant ($p < 0.01$). When the vicarious responses were taken into account (Fig. 6), similar results were obtained. The same number of vicarious responses were made by both groups of rats in original learning, while in reversal learning, animals of the septal group made more of these responses than normal rats ($p < 0.05$).

**EXPERIMENT III**

*Spatial discrimination with application of irrelevant visual cues,* which may be called spatial with visual distractors discrimination (S-with-Vd
Ten normal and 11 septal rats were used for this experiment to investigate acquisition and reversal learning of a position discrimination. The animals were required to go to the left door during acquisition training and the right door in reversal learning. Black and white doors were used but their positions were varied randomly, so that the visual cue was never consistently associated with either reinforcement or nonreinforcement. Thus the visual cues were irrelevant with correct responses. Ten daily trials were given until 200 acquisition trials and 200 trials of reversal learning were obtained.

Results. Figure 7 shows the number of errors made by normal and septal rats during acquisition and reversal learning of the S-with-Vd task. 

Fig. 5. Mean number of errors made by normal and septal rats during acquisition and reversal learning of the S-task.

Fig. 6. Mean number of vicarious responses made by normal and septal rats during acquisition and reversal learning of the S-task.
Fig. 7. Mean number of errors made by normal and septal rats during acquisition and reversal learning of the S-with-Vd task. Each block represents the mean number of errors made in 50 consecutive trials.

Fig. 8. Mean number of vicarious responses made by normal and septal rats during acquisition and reversal learning of the S-with-Vd task. Each block represents mean number of vicarious responses made in 50 consecutive trials.

task. The trials were combined in blocks of 50 consecutive trials. All errors were made by both groups of rats only in the first block of both original and reversal learning. Rats with septal lesions made more errors than control rats, and this difference was significant for both original ($p < 0.001$) and reversal learning ($p < 0.01$).

Figure 8 shows the number of vicarious responses made by both groups of rats during acquisition and reversal learning. Rats with septal lesions made more of these responses than normal animals in both acquisition and reversal learning during each block of training. The differences between the total number of vicarious responses made by normal and septal rats during acquisition ($p < 0.50$) as well as reversal learning ($p < 0.001$) was significant.

**Comparison of the Results of Three Experiments**

Figure 9 indicates the comparison between normal and septal rats in performance of the three experimental tasks. It appeared that in original learning normal rats made the most errors in the V-task, less errors in the S-task and least in the S-with-Vd task. Significant differences of similar magnitude ($p < 0.001$) were found between the V- and S-tasks and between the V-task and S-with-Vd task, while the difference between the S-task and S-with-Vd task attained a significance level of
p < 0.01. The animals with septal lesions made a greater number of errors (p < 0.001) in acquisition of the V-task than in both spatial discrimination tasks. The difference between the S-task and S-with-Vd task was not statistically significant within the septal animals. Comparison of the number of errors made by normal and septal rats in acquisition of the three tasks showed that, although the septal rats made slightly greater number of errors than normals in the V-task and S-task, the differences were not statistically significant. A significant difference between normal and septal rats was found only in the S-with-Vd task (p < 0.001).

Reversal learning of these three tasks in comparison with their acquisition was more difficult for both normal and septal rats. The most difficult task to reverse for normal and operated rats was the V-task, while the easiest was the S-task. There were no statistically significant differences between the S-task and S-with-Vd task in either normal or septal rats. Accordingly, the differences between the V- and S-tasks and between the V-task and S-with-Vd task for both normal and septal rats was found significant at p < 0.001. Normal and septal rats did not differ
in performance of the V-task reversal learning, while in the S-task the difference attained a level of $p < 0.01$, and in the S-with-Vd task the difference was also found significant at $p < 0.01$.

Figure 10 shows the mean number of consecutive trials in which the first response was erroneous up to the trial in which the first response was correct. This index was determined for reversal learning, since the measure might show how quickly the animals inhibited a previously correct response. In all three tasks there were no significant differences between normal and septal rats.

Figure 11 shows the mean number of repetitive errors made by normal and septal rats during acquisition and reversal learning of the three tasks.
tasks. Animals with septal lesions made more of these errors than normal rats in the V-task \((p < 0.01)\) and the S-with-Vd task \((p < 0.001)\), whereas no difference was found in S-task. During reversal learning normal and septal rats made more repetitive errors in the three tasks than in original learning. In spite of the greater number of repetitive responses made by septal than normal rats in all tasks, only the V-task difference was found significant \((p < 0.01)\).

**Histological verification.** Figures 12–14 show reconstructions of the lesions in the rats from Experiments I, II and III respectively. In all animals the ablations of the septal areas were not total and located mostly in the medio-ventral region. Generally, the lesions made in animals used in experiment II were smaller than in experiments I and III. In almost all animals the lesions were partial and ventromedial. Slight damages of anterior commissure were made in rats 104, 105, 113, 114 and 85. We could not find any relation between the size and location of the lesion within-group variability in the amount of impairment in performance.

**DISCUSSION**

Our results confirmed previous data by demonstrating that original and reversal learning of simultaneous black-white discrimination is not impaired in septal rats when compared to normals, regarding the number of errors \((2, 6, 14, 15, 25)\). We also found that the number of errors made by normals and rats with septal lesions in position habit acquisition is similar, but reversal learning of this task is retarded in operated rats. This is in agreement with previous data \((7, 8, 18, 23, 25, 26)\). Similar findings have been interpreted by other authors \((3, 21)\) to suggest that septal lesions impaired utilization of response produced cues. However, if this is accepted, the question arises concerning why acquisition of spatial discrimination is mastered by normal and septal rats similarly. Or, if, the operated rats utilized other cues in original learning which permitted them to solve this task as quickly as normal rats, why were such cues not as easily utilized in reversal learning?

As performance of the simultaneous visual discrimination indicate, this task has to be learned through inhibition of the tendency to solve the task on the basis of directional cues. Accordingly, the rats made the set of many responses to one door only, after they reversed their responses to the second door. Since, the construction of these sets does not help solving the problem, the rats began to discriminate the visual cues. If septal lesions impair response produced cues, operated rats should not perform the DRS. However, normal and septal animals solved this
Fig. 12. Reconstructions of the lesions made in rats subjected to Experiment I.
Fig. 13. Reconstruction of the septal lesions in rats from Experiment II.
Fig. 14. Reconstruction of the septal lesions in rats subjected to Experiment III.
task in similar way. The only difference between these groups during original learning was that the septals changed their DRS more often than normals, and they later began to make the first DRS. During reversal learning when the response to the previously correct cue had to be inhibited, both groups of rats returned to the previous strategy to make the DRS, which were similar in length and number for both groups. These results suggest that the process of inhibiting previously correct response is similar in both groups, and inhibition of the DRS natural strategy during solving of the visual discrimination task is similar in both groups of animals. Our data also showed that septal lesions did not impair utilization of response produced cues, but it seems that there are other factors which interfere with the septal animal's reversal learning when the spatial discrimination task was used. Since, it is very difficult to exclude all visual cues in position habit discrimination, let us suppose that this task may be solved using not only response produced cues but also some weak visual cues located in space (e.g., comparison of the distance between the correct door and left or right walls of the apparatus). So, in order to solve the spatial discrimination task, the animal may use response produced cues, some weak visual cues or both. Because of short lasting process of acquisition in the S-task, compared to the longer lasting process in the V-task, it may be supposed that animals use response produced cues in the S-task. The results received in Experiment I showed that septal animals extinguished the DRS similarly to, or even better than, the normal rats. So, if the septal rats used only response produced cues in the S-task, the reversal learning in these rats should be as rapid as in normal rats. However, it has been found that reversal learning in the S-task is longer in septal than in normal rats. To explain this phenomenon we suppose that septal rats may solve this task using not only kinaesthetic, but also some visual cues, but these visual cues only supported kinesthetically elaborated responses. During reversal learning, when previously kinesthetically elaborated responses hat to be inhibited, visual cues began to be more important, as it was shown with response produced cues during reversal learning of the V-task. Since, the response to the visual cue also appeared to be inhibited, both processes retarded solution of new task.

If our contention is correct, and the septal rats in this task utilized both types of cues, while the normal rats prefered to use response produced cues only, we would predict that the septal rats may learn, but they have to be retarded in comparison to normal animals in those tasks which require use of response produced cues to solve the problem when strong irrelevant visual stimuli were employed. Results of Experiment III supported our prediction. The process of acquisition and reversal
learning in the S-with-Vd task in rats with septal lesions was retarded compared to such process in normal animals. On the basis of the present results, it may be suggested that lesions of the septal area change the balance between utilization of kinesthetic and visual cues existing in normal animals. Rats with septal lesions are probably more sensitive to the visual cues than normals.

Another proposal which may be suggested is that perhaps extinction of the visual cues was slower in septal rats than in normals. In order to answer this question, let us consider other parameters used in the present experiments. Repetitive errors may be regarded as a measure of the acute extinction process of erroneous responses during one trial, whereas perseverative errors, showing how quickly the animal inhibits previously elaborated correct response, may be considered as measure of the chronic extinction during many consecutive trials of reversal learning. The results showed that the process of chronic extinction is similar in normal and operated animals during reversal learning of all three tasks. However, the process of acute extinction was retarded in septal rats compared to normals during acquisition of the V-task and the S-with-Vd task, and also during reversal learning of the V-task only. Since acute extinction is a general process which must function in most learning tasks, it seems that either the repetitive error measure is not optimal for this process or there are some more specific factors which interfere with this process. To solve this problem let us consider another measure of performance.

Vicarious responses may be regarded as an indicator of the difficulty in utilizing the correct cue when more than one cue may be used in the experimental situation. During acquisition of the V-task, when animals utilize response produced cues and visual cues, the number of vicarious responses in both groups of rats was great, but more so in septals than normals. During the early period of reversal learning, when the response to the previously correct visual cue had to be inhibited, the previous strategy to use response produced cues was disinhibited in both groups of animals especially in the septals, but only in the first block of reversal learning. So, if the conflict exists in utilizing two different cues to solve the task, the performance of septal rats was worse than the normals. When some of the weak visual and kinaesthetic cues were not in conflict, the number of vicarious responses was small and similar in both groups of animals, as it was observed during acquisition of the S-task. During reversal learning of this task, when kinesthetically elaborated responses to the same visual cue had to be inhibited and the animal elaborated new responses when the previously correct visual cue remained in the same place, septal rats make more vicarious responses.
than normals. During acquisition and reversal learning of the S-with-Vd task when a conflict in utilization of both kinesthetic and visual cues was strong due to application of irrelevant visual cues which had to be inhibited, performance of the septal rats was strongly retarded when compared to the normal rats. Therefore, it may be seen that the two measures of repetitive errors and vicarious responses complement each other. If the conflict in choice to use the correct cue is strong in the experimental situation, both of these measures show the impairment in septal rat performance. If this conflict is suppressed during acquisition, it again appears during reversal learning. It is interesting that if the utilization of kinesthetic cues was an incorrect strategy that interfered with utilization of the correct visual cues, the conflict was revealed during reversal learning by repetitive errors (V-task). However, if utilization of visual cues was a wrong strategy, the conflict was revealed by vicarious responses, and the level of interference was proportional to the strength of visual cues (S-task, the statistical difference between normal and septal rats was significant at $p < 0.05$, in the S-with-Vd task, $p < 0.001$).

These results suggest that the septal rats may utilize the response produced cues to control their behavior, but orienting responses to the visual cues interfere with them. The interference was probably due to the sensitivity to visual stimuli which may have been manifested in enhanced reactivity to them. It has been shown recently (4) that rats with septal lesions “responded in exaggerated fashion” to response-contingent light presentation. Electrophysiological data (12) has shown that stimulation of the septal area attenuated photically evoked cortical potentials. It may be suggested that ablation of this area should potentiate these reactions. Detailed analysis of separate components in visual evoked responses recorded at the cortex in septal rats and compared with normal rats showed that behavioral reactivity to flashes is exaggerated and development of the VER is facilitated (16, 17).

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