Septal forebrain lesions and social dominance behavior in the hooded rat¹

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Septal forebrain lesions produced an increase in the social rank of hooded rats. Increases in the frequency of both aggressive and defensive behaviors were obtained so that changes in social status could not be attributed to a simple increase in aggressiveness. It appeared that the effects were due to the loss of previously acquired responses to other animals interacting with the sparing of a strong running response in the test situation.

Amygdalectomy typically produces a reduction in social rank and a loss of aggressiveness in many species (Goddard, 1964). It has been suggested that amygdaloid and septal nuclei may have reciprocal effects in the control of affective behavior (King & Meyer, 1958). It might be expected, then, that septal lesions would produce increases in aggressiveness and in social rank; however, both attack and flight reactions have been reported in septal rats (Brady & Nauta, 1953). The present study sought to examine the effects of septal lesions on social rank in the hooded rat.

Subjects

Four groups of male hooded rats, each consisting of five animals, were formed. The Ss, 110-130 days old at the start of the experiment, were individually housed, and maintained on an 18 hr. water deprivation schedule except for the 24 hr. periods immediately preceding and following surgery when water was available ad lib. Food was available at all times.

Apparatus

Dominance testing utilized a version of apparatus designed by Tsai (1953). It consisted of two boxes, 9 in. square, connected by an enclosed Plexiglas alley 18 in. long. The alley was adjustable, so that the opening could be made just large enough for one animal to pass through at a time. A guillotine door, located midway in the alley, isolated the two sides of the apparatus.

Procedure

In assessing social dominance relationships, each animal in a group was first trained to shuttle rapidly back and forth through the alley in order to obtain reinforcement (either sugar water or condensed milk) in the end boxes. Animals were matched against each other by starting one animal from each end of the alley with the panel closed, raising the panel, and scoring as the winner the animal which forced its opponent to back out of the alley. Normally, only one trial per day was given. In a trial, each animal in a group was paired against every other animal in that group, and a record kept of the number of wins, losses, and draws (defined as the elapse of five minutes without a winner). Dominance-submission relationships were defined in terms of the

consistency with which an animal won from or lost to the other animals in the group. The hierarchies were linear, transitive, and stable. Each S was given three reinforced runs in the shuttle box prior to the daily trial, but no incentive was present in either goal box during testing.

After the hierarchies were established, one animal in each group was given a septal lesion; the remainder received control operations. After allowing 24 to 48 hr. for recovery, dominance testing was resumed and continued until the hierarchy restabilized. The procedure was repeated one or more times with each group, except for Group III which had to be discontinued due to the death of two animals.

The bilateral septal lesions were produced electrolytically under pentobarbital sodium. In the control operations, the electrode was lowered only as far as the corpus callosum and no current was passed. The lesion effects were evaluated behaviorally using King's (1958) emotionality scale. A postoperative increase of 10 points or more was used as the basis for designating an animal as "septal." The emotionality ratings were begun three days before surgery and continued until the septal returned to its preoperative level. Lesion reconstructions showed massive destruction of the precommissural, and heavy damage to the supracommissural, septum. While there was damage to adjacent structures, no consistent relation between such damage and behavioral effects was detected.²

Results and Discussion

There were individual differences in the magnitude and permanence of changes produced by the lesions, but the general result was an increase in the number of wins. A Wilcoxon signed-ranks test, comparing percentage of wins made by each of 10 septals (eight from these four groups plus two from the follow-up study described below) on its last five preoperative trials with percentage of wins on its first five postoperative trials was significant ($N=10$, $t=4$, $p<.02$). Figure 1 shows the performance of eight septals from the first four groups. Five permanently increased in rank, two ("O" and "J") had temporary increases, and one ("T") remained the same.

The Ss that changed least after surgery ("O" and "T") had undergone fewer preoperative dominance trials than the other septals. This seemed strange, since it meant that the lesions were more effective in changing hierarchies whose members presumably had stronger habits of winning and losing. However, since each S had been given three shuttle runs prior to each day's

Fig. 1. Changes in social rank following septal lesions. Dashed line indicates period of septal hyperemotionality. Mean rank for last ten preoperative trials is circled. The arrow indicates the point at which the lesion was made.

dominance trial, Ss operated after many trials had considerably more shuttling experience than those operated after a few trials. It was possible that the magnitude and permanence of the social changes were the result of an interaction between the lesion and the strength of the shuttling habit.

As a follow up, weak shuttling habits were established in two new groups of animals (11 runs in one group, 36 in the other); one S from each group was given a septal lesion, and dominance testing initiated. Both septals achieved intermediate rank. Testing was then discontinued while the groups were given extensive shuttling experience, then 10 more dominance trials were run. At this point, the groups had dominance experience equivalent to Ss "O" and "T," but shuttling experience equivalent to that of "C" and "I." The subordinate S in each group was then given a septal lesion. Both Ss reached first rank, one on the second and the other on the sixth postoperative day. Preoperatively these animals had won only 17% of their bouts, postoperatively they won 87%.

Despite the results, qualitative judgment of the behavior do not allow the conclusion that increases in social rank were due to a simple increase in aggressiveness. The typical initial response of the septal was to back up a step and freeze. When an opponent advanced,

some septals reacted by slashing with their teeth and advancing with head up and incisors bared; others remained frozen in the alley, resisting attempts to force them back. The latter won by outlasting opponents which eventually backed out of the alley after which the septal advanced to the goal box. Thus, both aggressive and defensive behaviors were seen in the testing situation. The effect of the lesions was to lower the threshold for both response classes (though not in the same animal). This fits well with disinhibition theories of septal effects (e.g., Kaada et al, 1962).

Apparently, the social changes produced by septal lesions were due to a combination of the sparing of a strong shuttling habit and the loss of previously acquired adaptive responses to other animals. Septal Ss showed exaggerated reactivity which took the form of increased aggressive or defensive behaviors. Adjustment was quite rapid and after a few trials the behavior of the dominant septals came to look like that of dominant normals. It is unlikely that the results were due to increased thirst on the part of the septals (see Harvey & Hunt, 1965) since recently operated Ss defeated those which had been given lesions earlier in the series even though the latter should have been maximally thirsty according to the Harvey and Hunt data.

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Notes

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2. Copies of the lesion reconstructions for these animals may be obtained from B. N. Bunnell.