Effect of septal lesions on behavioral contrast

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Rats with septal lesions and control animals were tested on a multiple schedule. When extinction was instituted in one component of the multiple schedule, septal-lesioned and control animals exhibited approximately equal amounts of positive contrast in the unaltered component. The results were discussed in terms of the situation specificity of the enhanced reaction to nonreward associated with septal damage.

The response of the septal-lesioned animal to withdrawal or omission of reinforcement has been the subject of a number of investigations (e.g., Butters & Rosvold, 1968; Caplan, 1970; Schwartzbaum, Kellicut, Spieth, & Thompson, 1964). It has generally been found that omission of reinforcement is followed by accelerated responding or increased perseveration in the septal-lesioned animal above control levels. Caplan (1970) found, for example, that when scheduled reinforcement was omitted on a DRL schedule all subjects accelerated their response rates, but the increase was greatest for septal-lesioned animals. Mabry and Peeler (1972) found, however, that animals with septal lesions and control animals did not differ in response to frustrative nonreward in a double-runway task. Both groups increased running speed and starting speed following omission of reinforcement, but there was no difference in the magnitude of alterations in running speed and starting latency for the two groups of animals.

The present study attempted to determine whether the operant nature of the task or some other factor is critical to the observation of an exaggerated response to nonreinforcement in the septal-lesioned rat. In two experiments, responses of septal-lesioned and control animals were compared during the formation of a successive discrimination in an operant situation. All animals were initially placed on a multiple schedule in which different schedules of reinforcement were in effect for successive components. Each component was associated with a distinctive cue. After response rates stabilized on a multiple VI VI (MULT VI VI), extinction was instituted in one component (MULT VI EXT). Septal-lesioned and control animals were compared on behavioral contrast—an increase in response rates in the unaltered VI component.

EXPERIMENT I

Method

Animals. Ten Long-Evans male rats served as subjects. Their

ages ranged from 120 to 150 days at the beginning of the study. During the course of the study they were housed in individual cages.

Apparatus. Training occurred in Lehigh Valley operant chambers placed in sound-attenuating cubicles. A white-noise generator minimized the extraneous sounds. Electromechanical programming and recording apparatus was located in an adjacent room. A 7-W houselight powered by 20-V ac served to differentiate multiple schedule components.

Surgery and histology. Prior to any operant training, five animals received bilateral lesions of the septal region, three served as operated controls, and two served as unoperated controls. The operated animals were anesthetized with sodium pentobarbital (60 mg/kg) and positioned in a stereotaxic with the nosebar level with the interaural line. A stainless steel electrode insulated to within 1 mm of the tip was lowered 2.25 mm anterior to bregma, .5 mm lateral to the midline, and 4.5 mm below the dura for the septal lesions and a RF current passed for 20 sec. For the operated control animals, the electrode was lowered 2.0 mm below the dura and no current was passed. The animals were given a 2-week recovery period following surgery.

At the completion of the study, the animals with lesions were perfused with physiological saline followed by 10% formalin, and the brains were removed, dehydrated, and embedded in celloidin. Sections were cut at 40 micrometers, and every fifth section was mounted and stained with cresyl violet.

Procedure. Following the 2-week recovery period, all subjects were placed on a 22-h food-deprivation schedule and shaped to leverpress for 45-mg Noyes food pellets. Subjects were given 100 reinforcers on a continuous-reinforcement schedule, following which they received 31 daily 1-h sessions on a MULT VI VI schedule. Throughout the session, 1-min components in which the houselight was illuminated were randomly alternated with 1-min components in which the houselight was off. Reinforcers were delivered according to a VI 15-sec schedule during both components for one session and according to a VI 30-sec schedule for 25 sessions. Subsequent to the MULT VI VI sessions, no reinforcement was delivered during one of the components (EXT). The reinforcement schedule remained unaltered in the other component. Extinction was introduced in the light-on component for half the subjects and in the light-off component for the remaining subjects. All subjects received 25 daily sessions lasting 1 h on the MULT VI EXT schedule. The animals were given approximately 10 g of food following each daily session.

Figure 1. Reconstruction of the smallest and largest lesions. The black area represents the smallest lesion (S-3) and the black area plus the stipled area represents the largest lesion (S-5).

Table 1
Mean Responses Per Minute Averaged Over
Blocks of Five Sessions

Schedule	Septal Lesioned Animals		Control Animals	
	Component 1	Component 2	Component 1	Component 2
VI VI	87.6	90.9	72.7	71.4
VI EXT	85.5	81.0	68.1	62.8
VI EXT	74.0	54.3	77.2	45.6
VI EXT	98.8	42.3	81.1	28.2
VI EXT	106.9	38.04	85.48	24.3
VI EXT	111.92	30.88	78.6	17.7

Figure 2. Response change ratios for the septal-lesioned and control animals.

Results

Anatomical data. Reconstruction of the smallest and largest septal lesions are shown in Figure 1. Lesions were confined to the region anterior to the crossing of the anterior commissure with the exception of the lesion in Subject S-3. The anterior boundary of all lesions was at or near the level of the genu of the corpus callosum. The lateral and medial nuclei were completely or partially destroyed in all subjects. Nucleus accumbens was damaged in four of the five subjects. The columns of the fornix were damaged in Subjects S-4 and S-5 and completely interrupted in Subjects S-3. In Subjects S-2 and S-1, the columns of the fornix were intact.

Behavioral data. The average response rates for lesioned and control animals during each component of the multiple-schedule average over the last five sessions of MULT VI VI and for each 5-day block of MULT VI EXT sessions are presented in Table 1. The mean response rates during the last five MULT VI VI sessions averaged over both components were 89.1 for the septal-lesioned animals and 72.1 for the control animals. The lesioned and control animals did not differ with respect to response rates during the last five sessions of MULT VI VI in either component.

The performance for both groups during the MULT VI EXT session is summarized in Figure 2. In order to compare the experimental and control animals with respect to changes in response rates during MULT VI EXT, the data were normalized in the following fashion. Block 1, scored as unity for all groups, represents the mean response rates in each component of both the septal lesion and the control groups during the last five sessions of MULT VI VI. Blocks 2-6 represent response-rate changes during successive blocks of five sessions of MULT VI EXT, expressed as the mean ratio of response rates in Blocks 2-6 to the mean response rate in Block 1 for each group. The response-change ratios were computed by dividing the mean response rate of each animal in each component during Blocks 2-6 by the mean response rate of that animal during the corresponding component of the last five sessions of MULT VI VI. A positive contrast effect is indicated by a response-change ratio greater than one.

Both the animals with lesions and the control animals showed behavioral contrast as groups, but the amount of response change was highly variable in each group, ranging from peak increase of 68% to 19% in the control group and 73% to 32% among the animals with septal lesions. One lesion (S-4) and one control (C-5) animal failed to show a positive contrast effect. Both of these animals showed a decrease in response rate during the VI portion of the MULT VI EXT schedule, with the highest response rate during this period representing a decrease of 14% for the septal-lesioned animal and 24% for the control animal from the baseline rate. During the extinction component of the MULT VI EXT, both groups showed a gradual decline in response rates over Blocks 2-6. Animals with septal lesions and control

animals did not differ with respect to response-change ratios in the VI or extinction components.

EXPERIMENT II

The brain-damaged and control animals did not differ either in incidence or magnitude of behavioral contrast in Experiment I, suggesting that the operant situation per se does not accentuate the effect of septal lesions on response to nonreward. Experiment II employed a VI 60-sec schedule in the VI component to investigate the effects of frequency of reinforcement and baseline response rates.

Method

Animals. Subjects were 12 male albino rats between 90 and 120 days of age at the beginning of the experiment.

Apparatus. The apparatus for Experiment II was identical to that employed in Experiment I except that reinforcement was provided by a water dipper which delivered .01 cc of tap water.

Surgery and histology. Prior to any operant training, six animals received bilateral lesions of the septal region in a procedure identical to that described for Experiment I. Three animals served as operated controls and the remaining three served as unoperated animals. Histological procedures at the termination of the experiment have also been described in Experiment I.

Procedures. Two weeks following surgery, all subjects were placed on a 22-h 45-min water-deprivation schedule and shaped to leverpress for water reinforcers. They were given 100 reinforcers on a continuous-reinforcement schedule, following which they received 30 daily 1-h sessions on a multiple VI VI schedule. Reinforcement was delivered according to a VI 30-sec schedule for one session and according to a VI 60-sec schedule for the following 29 sessions. One-minute components associated with either illumination of the houselight or no illumination alternated randomly throughout the session. Following the 30 MULT VI VI sessions, extinction was instituted in one component. For half the animals, extinction was associated with illumination of the houselight, and for the remaining animals extinction was associated with nonillumination of the houselight. All subjects received 25 sessions of MULT VI EXT training. The animals were allowed access to water for 15 min following each daily session.

Results

Anatomical data. The lesions in the subjects of Experiment II were quite similar in extent and location to those of Experiment I. In all subjects, lesions extended from the genu of the corpus callosum to the region of the crossing of the anterior commissure. The lateral septal nucleus was damaged in all animals, as was the accumbens. The medial septal nucleus was partially or totally destroyed in five of the six animals, being spared in Subject S-5. Damage to the columns of the fornix was seen in four of the six animals.

Behavioral data. The mean response rates during the last five sessions of MULT VI VI averaged over both components were 11.3 for the septal-lesioned animals and 12.2 for the control animals. Table 2 presents the response rates, averaged over five sessions, for lesioned and control animals during the last five sessions of

Table 2
Mean Responses Per Minute Averaged Over
Blocks of Five Sessions

Schedule	Septal Lesioned Animals		Control Animals	
	Component 1	Component 2	Component 1	Component 2
VI VI	11.13	11.58	11.70	12.07
VI EXT	10.47	5.63	9.87	7.82
VI EXT	11.70	2.60	13.15	4.4
VI EXT	12.93	2.73	11.08	1.83
VI EXT	15.67	3.1	13.18	2.58
VI EXT	13.38	1.77	14.63	1.85

MULT VI VI and throughout all sessions of the MULT VI EXT. All subjects reached highly similar baseline rates during the last five sessions of MULT VI VI.

The performance of the brain-damaged and control groups in both components of the MULT VI EXT is summarized in Figure 3. The data were treated in a manner identical to that of Experiment I. As in Experiment I, the group data for both the lesioned and control groups gave evidence of behavioral contrast, although behavioral contrast was not consistently in evidence in the control group. One animal with septal lesion (S-3) and one control animal (C-2) exhibited negative induction during the MULT VI EXT schedule. Two control animals (C-1 and C-5) and one septal-lesioned animal (S-4) showed only minimal

Figure 3. Response change ratios for septal-lesioned and control animals.

positive contrast. There was no overall difference in the amount of behavioral contrast shown by septal-lesioned and control animals. Peak increases ranged from 20% to 216% among septal-lesioned animals and from 2% to 85% for control animals. One septal-lesioned and one control animal showed decreases from baseline rates of 21% and 58%, respectively, as the highest rate of responding during the VI component of the MULT VI EXT schedule. Both groups showed reduction from baseline levels of responding during the extinction component of MULT VI EXT, reductions which did not differ for the two groups.

DISCUSSION

The results of the present experiments demonstrate that septal-lesioned animals do not invariably show an enhanced frustration response to nonreward. Although the effect of septal lesions on responsiveness to nonreward is situation specific, the "structural difference" between an operant situation and a runway does not appear to be a critical factor. It is also unlikely that reinforcement density or baseline response rates affect the appearance of the enhanced frustration effect in septal-lesioned animals, since brain-damaged and control animals did not differ in behavioral contrast in either Experiment I or Experiment II. A factor that might account for the disparity between the results of Caplan (1970) and those of Mabry and Peeler (1972)

and the present experiment is the temporal relationship between omission of reinforcement and the response measure. In the Caplan study, measures of response output occurred immediately after nonreinforcement. In contrast, Mabry and Peeler delayed measures of start latency and running speed by a 10-sec confinement in the goalbox following omission of reinforcement, and, in the present investigation, response measures were delayed until the beginning of the next reinforced schedule component. Enhanced frustrative responding in the septal-lesioned animal might dissipate very quickly following nonreinforcement. The behavioral contrast paradigm would not be sensitive to such a short duration effect.

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