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OF TWO TYPES OF ACTIVE AVOIDANCE BEHAVIOR
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EFFECT OF SEPTAL LESIONS ON THE ACQUISITION OF
TWO TYPES OF ACTIVE AVOIDANCE BEHAVIOR IN RATS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
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By

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* * * * *

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INTRODUCTION

The past ten years of limbic system research has dealt heavily with the problems of emotionality, passive avoidance, active avoidance, and motivation. Major impetus for such work was provided by the classical investigations of Papez (1937), Kluver and Bucy (1939), and Kaada (1951). Papez described the major structures and interconnecting pathways of the limbic system, and he proposed that this system might provide the neural substrate for emotion. Large temporal lobe lesions in monkeys were found by Kluver and Bucy to make normally aggressive animals tame and docile. Electrophysiological studies by Kaada revealed that stimulation in the subcallosal-septal area produced inhibition of ongoing responses, whereas stimulation of the medial and anterior cingulate gyrus resulted in response facilitation.

The next significant discovery was that of Brady and Nauta (1953) in which they reported that septal lesions in rats produced a dramatic increase in emotionality, which is generally referred to as the septal syndrome, hyper-emotionality, hyperreactivity, or septal rage. Increased emotionality in rats with septal lesions was also found by King (1958, 1959) and by King and Meyer (1958). During

this period, King (1958) was the first to discover that septal rats acquired a two-way conditioned avoidance response (CAR) more promptly than did normal animals. The two-way CAR is developed in a situation in which a long signal of several seconds duration is associated with electric shock from which the animal can escape by moving into another area of the apparatus. The animal learns to respond when the signal comes on and thus can avoid the shock entirely. King attributed the facilitated behavior of the lesioned animals to co-existing hyperemotionality.

Passive Avoidance and Two-way Active Avoidance Behavior

McCleary (1961) undertook to make a direct test of the "facilitatory" and "inhibitory" notions of Kaada (1951). Cats with lesions of the cingulate or subcallosal regions were observed in a two-way CAR problem and a passive avoidance test. The passive avoidance test was classically called an approach-avoidance conflict, where a positively-reinforced approach tendency is established followed by subsequent punishment of that same approach response. The results were compatible with Kaada's anatomical findings, i.e., lesions of the inhibitory (subcallosal) area led to difficulty with passive avoidance but not with active avoidance, while damage of the facilitatory (cingulate) area had the opposite effect. McCleary took exception to the "hyperemotionality" interpretation of King (1958), for this single factor could not at the same time account for

the deficit in passive avoidance behavior exhibited by cats with subcallosal damage and the facilitation in CAR behavior. Rather, a reduction in response inhibition was proposed to account for the behavior patterns of animals with septal area lesions.

A passive avoidance deficit has repeatedly been found for cats with bilateral septal lesions (Fox, Kimble and Lickey, 1964; Lubar, 1964; McCleary, Jones and Ursin, 1965; Zucker, 1965; Zucker and McCleary, 1964). The same result has been obtained with septal rats (Kaada, Rasmussen and Kveim, 1962; Kveim, Setekleiv and Kaada, 1964; McNew and Thompson, 1966; Schwartzbaum and Spieth, 1964; Van Hosen, MacDougall and Mitchell, 1969). When tested in a combination passive-active avoidance situation, septal rats perseverated a punished response while normal rats actively avoided (Ursin, McCleary and Linck, 1966).

Additional evidence incompatible with the "hyper-emotionality" explanation of the facilitated CAR behavior of septal animals is the almost total absence of any rage syndrome in septally damaged cats. Such animals usually exhibit only a slight increase in hissing and defensiveness. Using a specific testing procedure to elicit the rage syndrome, Moore (1964) found that only ten percent of his septal cats showed full-blown rage with hyperreactivity to tactile stimulation. Also, prompter acquisition of a two-way CAR has been reported for septal rats whether the

lesions failed to produce the septal syndrome or whether the CAR behavior was trained so late postoperatively that the hyperirritability had subsided (Krieckhaus et al., 1964).

Animals with lesions of the forebrain septum have consistently been found to show facilitated acquisition of a two-way CAR to a visual or auditory stimulus preceding shock. In the rat, large or small bilateral and unilateral septal ablations produced faster learning of such behavior (Green and Schwartzbaum, 1968; Kenyon and Krieckhaus, 1965a, 1965b; King, 1958; Krieckhaus and Kenyon, 1965; Krieckhaus et al., 1964; Schwartzbaum et al., 1967; Van Hosen, MacDougall and Mitchell, 1969). Like rats, cats (Fox, Kimble and Lickey, 1964; McCleary, 1961; Zucker, 1965) and the squirrel monkey (Buddington, King and Roberts, 1967) with septal lesions acquired a two-way CAR more rapidly than did normal animals.

Other Types of Active Avoidance Behavior

Septal lesions apparently produce only facilitated learning of a two-way CAR, for it has been found that learning of a one-way CAR was attenuated following septal damage in rats (Kenyon and Krieckhaus, 1965b; Krieckhaus and Kenyon, 1965; McNew and Thompson, 1966; Vanderwolf, 1964). Also, rats trained in a one-way CAR task to onset of a photic stimulus showed no retention of the habit following bilateral damage of the septofornix area (Rich and Thompson, 1965).

Similar results have been reported for the cat. Animals with limbic cortex-septal area lesions (Lubar, 1965) and animals with septal damage (Zucker and McCleary, 1964) behaved like normal cats during acquisition of a one-way CAR. Deficits in the retention of a preoperatively learned two-way CAR (Moore, 1964) and one-way CAR (McCleary, Jones and Ursin, 1965) have been observed for septal cats.

There have been several interpretations of the different behaviors characteristic of septal animals in the two-way and one-way CAR problems. Facilitated two-way learning has been related to a hypoactive crouch reflex following septal ablations (Kenyon and Kriekhaus, 1965a, 1965b; Kriekhaus and Kenyon, 1965; Kriekhaus et al., 1964). If a septal lesion lowers the threshold for response initiation, then septal animals should show facilitation in both types of CAR tasks. These authors contend that the discrepancy is due to decreased fearfulness among septal rats. However, in all experiments using a one-way task with rats, a critical variable appears to have intervened, i.e., the animals were picked up and returned to the starting box by hand after each trial. Handling is highly aversive to septal rats, for hyperreactivity to tactile stimulation is one of the prominent features of the septal syndrome. Thus, McCleary (1966) proposed that this factor could contribute to retarded acquisition in one-way CAR studies in which the animals were picked as a consequence of

responding. Furthermore, while avoidance behavior can be radically altered in the absence of the transient rage syndrome, some degree of increased tactile sensitivity may persist and become manifest in specific experimental situations. Liss (1965) reported that septal rats showed evidence of hyperreactivity to foot shock, a type of tactile stimulation, when obvious signs of the septal syndrome had disappeared. Support for this suggestion was provided by Zucker (1965) who employed a one-way CAR procedure that did not involve handling, and he observed improved acquisition in septally damaged cats. However, cats with septal injury did not show facilitation in two other studies using the same procedure (Lubar, 1964; Zucker and McCleary, 1964). Data are not available on rats trained in a one-way CAR without handling, nor on cats returned to the starting box by hand.

Reversal, Alternation and Discrimination Behavior

Septal rats were deficient in acquiring a novel type of active avoidance habit (Nielson, McIver and Boswell, 1965) in which the animal avoided shock by selecting the correct arm in a T-maze and depressing a lever. The arm not selected on an initial non-avoidance trial was designated as the correct arm for remaining trials. Thus, the rats had to reverse an initial position preference. This may have been the critical variable, for septal lesions have been found to affect various position and

discrimination habits not limited to emotional behavior. Septal rats showed disturbance of a position reversal in a T-maze (Thompson and Langer, 1963). Cats with septal lesions required more training than did normals to reverse a learned position habit (Zucker and McCleary, 1964) in a Wisconsin General Test Apparatus (WGTA). Zucker (1965) reported that cats with lesions of the septal-limbic area were deficient on the acquisition and first reversal of a successive discrimination, but not deficient on the acquisition or reversal of a simultaneous discrimination in a WGTA. In contrast, rats with septal lesions showed no impairment of original learning of either a spatial or simultaneous brightness discrimination, and selective impairment of reversals of the spatial but not the brightness problem (Schwartzbaum and Donovanick, 1968). In a study of localized septal lesions on the behavior of rats, Donovanick (1968) found that lesions of the anteromedial region retarded acquisition of a spatial-alternation habit and reversals of a spatial discrimination task. This group of experiments concerning position, reversal and alternation habits can be viewed as supporting the "lack of response inhibition" or "response perseveration" hypothesis proposed by McCleary to account for the behavioral patterns characteristic of animals with septal ablations.

Timing and Extinction Behavior

Several operant studies have demonstrated overresponding

in septally damaged rats (Carey, 1967; Ellen and Powell, 1962a, 1962b; Ellen, Wilson and Powell, 1964; Schwartzbaum and Gay, 1966; Schwartzbaum et al., 1964). Ellen and his co-workers found that septal lesions led to increased responding in the immediate postresponse period of a DRL-20-second schedule of reinforcement, and higher than normal responding during the last ten seconds of a FI-1-minute schedule. However, increased responding on DRL schedules has since been shown to be a function of lesion placement and training procedure. Carey (1968) placed discrete lesions throughout the septal area and found increased responding on a DRL-22-second schedule only if damage occurred to the dorsal fornix or diagonal band region. Septal rats suppressed responding to meet a DRL contingency if the acquisition phase proceeded slowly or if the DRL requirement was low (Caplan and Stamm, 1967). Similarly, rats with septal lesions demonstrated superior response inhibition relative to control animals in a Sidman-avoidance task by accepting fewer shocks and by having a lower response rate (Morgan and Mitchell, 1969).

Schwartzbaum et al. (1964) used a discriminated operant response and observed that septally lesioned rats responded at significantly increased rates during the non-reinforced stimulus, but did not show increased responding when food was available. There was also a transient postoperative increase in response rate during stimulus-free-blackout

periods between trials. A third indicant of perseveration was that lesioned subjects were more resistant to extinction.

LaVaque (1965) reported that septal rats did not differ from normal animals in the acquisition of a two-way CAR but did show more resistance to extinction of the habit. Zucker and McCleary (1964) trained septal cats in a one-way CAR task and then tested for extinction in the usual manner (all shock withheld) and found that lesioned animals did not show prolonged responding. However, after being retrained the same lesioned cats did exhibit overresponding when tested in a punished-extinction situation. But Zucker (1965) reported that septal cats did not require more shocks than normals to extinguish an avoidance response during two consecutive punished-extinction tests. Septals did require more shocks in a third test. The absence of prolonged responding in the typical extinction test has been related to a possible concomitant decrease of the underlying motivational-fear state as extinction trials continued, in which case the termination of responding might have occurred without a suppressor mechanism operating. In the punished-extinction situation, the presence of shock could have served to keep the fear-drive elevated. The same argument has been applied to extinction of a food reinforced habit in which prolonged extinction was found (Schwartzbaum et al., 1964). In this instance, the hunger-drive remained at a constant level or increased as the

extinction trials continued. As the incentive value of the non-reinforced operant dropped, the normal animal but not the septal animal possibly learned something new about the situation and/or was capable of response inhibition. Butters and Rosvold (1968) found that monkeys sustaining septal injury were more resistant to extinction of a bar press response on a VI-1-minute schedule.

Zucker (1965) did not find prolonged responding of a food reinforced habit in septal cats that were trained to displace a single object in a WGTA on a VR-2 schedule of reinforcement. This result has been attributed to extensive postoperative practice that might have elevated lesioned and normal animals to a common ceiling of habit strength. This argument was based on observations that perseverative deficits disappeared during postoperative experience with a particular behavioral test.

Motivation, Stimulation and Drugs

Septal lesions in rats have increased consummatory behavior for water (Boyce and Schaefer, 1968; Carey, 1967; Donovick and Burrigh, 1968; Donovick, Burrigh and Gittelson, 1968; Harvey and Hunt, 1965; Harvey et al., 1965; Singh and Meyer, 1968), for saline (Grace, 1968), for sucrose (Beatty and Schwartzbaum, 1968), and for food (Singh and Meyer, 1968). Zucker (1965) failed to find increased food intake in cats that had effective septal lesions according to other behavioral indices. Harvey

et al. (1965) observed increased drinking behavior in septal rats and were able to modify the operant response by preloading with water and manipulation of deprivation time. The conclusion was that the thirst drive as well as the consummatory drinking response were increased by septal injury. Increased appetitive motivation was suggested to account for the inability of lesioned animals to overcome the suppressing effect of punishment when it is superimposed on a thirst motivated or food motivated response as in the case of passive avoidance tests. An appetitive-drive mechanism fails to account for the entire septal deficit because overresponding has occurred in the acquisition and forced-extinction of an active avoidance habit not involving appetitive reinforcement (Zucker and McCleary, 1964).

Electrophysiological evidence indicates that increased appetitive drive is not a necessary ingredient of the perseverative deficit even when response suppression is required in the presence of appetitive reinforcement. Kasper (1964, 1965) found that mild continuous electrical stimulation of the septum duplicated the effects of a lesion during behavioral testing using water reinforcement. Stimulated rats showed increased perseverative errors on a passive avoidance test and on the reversal of a position habit. The same duration of stimulation failed to produce increased water intake when measured following a few days

of deprivation or over several 24-hour periods. Keesey and Powley (1968) reported that septal lesions reduced the current threshold of lateral hypothalamic self-stimulation reward in rats, and they concluded that the septal area exerts an inhibitory influence over lateral hypothalamic processes.

Pharmacological studies also support the suggestion that increased thirst and a decreased ability to suppress responding may be separate manifestations of septal dysfunction. Grossman (1964) reported that stimulation of the septum with atropine, a cholinergic blocking agent, improved active avoidance behavior relative to controls, and, at the same time, reduced water consumption of the experimental animals. Cholinergic stimulation with carbachol had reciprocal effects on both types of behavior. The possibility that response inhibition by the septum involved a cholinergic system received support from a study by Meyers (1965) in which injection of scopolamine, another cholinergic blocking agent, produced a passive avoidance deficit in rats. Similarly, the administration of atropine to the septal area in cats produced a passive avoidance deficit, increased resistance to extinction of a generalized avoidance response, but did not affect food intake, acquisition of a one-way CAR, or reversals of a position habit (Hamilton, McCleary and Grossman, 1968). It may be that the septal area contains a cholinergic system

or systems capable of influencing both avoidance and drinking behavior. Also, localized surgical damage to these systems might improve active avoidance behavior without also increasing drinking behavior.

Spontaneous Activity and Septal Lesions

At the most simple level of consideration, the activity of septal animals as compared to normal subjects when measured in open-field situations has been found to not differ (Zucker, 1965), to decrease (Corman, Meyer and Meyer, 1967; Schwartzbaum and Gay, 1966), and to increase (Donovick and Wakeman, 1969; Nielson et al., 1965). It was also reported that septal rats became "hyperactive" in an open-field only after the introduction of small compartments with connecting doorways and the elimination of high illumination (nielson et al., 1965). However, Donovanick and Wakeman (1969) found that rats with septal ablations had higher levels of activity in bright and dim light conditions. Control subjects were more active only in red light, and both control and lesioned animals were suppressed by heat.

Present Experiment

The present experiment investigated the behavior of normal and septal rats which were trained in two types of active avoidance problems. One problem was a typical two-way CAR habit in which the animals learned to avoid punishment by shuttling between two compartments. The

other task was a free-choice CAR situation in which the animals could move into either of two available compartments to avoid shock. In this problem, the subjects could perform by adopting a one-way pattern of responding, a two-way pattern of responding, or a combination of these strategies.

METHOD

Subjects

The Ss were 80 male albino rats 90-120 days of age at the beginning of the experiment. The Ss were first randomly assigned to a control group or to an experimental group. The control group consisted of normal rats, and the experimental group of rats which sustained bilateral lesions of the septal region of the forebrain. All Ss were housed in individual cages and given constant access to food and water.

Surgery

Surgery was performed under pentobarbital sodium anesthesia injected intraperitoneally. The septal lesions were produced by intracerebral insertion of an electrode insulated except for .5 mm. at the tip. A direct current of 2.0 ma. was passed for 15 sec. through this electrode, with an anal electrode completing the circuit. The stereotaxic coordinates for the septal ablations were anterior-posterior +8.3, lateral ± 0.5 , dorsal-ventral +1.0. The above coordinates were computed from the stereotaxic atlas by deGroot (1959). Following surgery, Ss were allowed a two-day recovery period before the start of training.

Apparatus

Training was conducted in an apparatus patterned after one described by Meyer, Isaac and Maher (1958). The walls and ceiling of the experimental room were covered with acoustical tile which served to reduce extraneous auditory stimuli. The apparatus, as shown in Figure 1, consisted of a black plastic box 21 in. X 21 in. X 12 in. high divided into quadrants by hurdles 4 in. high. The box rested on a grid floor, and white paper was placed below the grid. The grid and the tops of the hurdles were electrifiable. A center post 8 in. high, which functioned to eliminate diagonal responses, extended from the junction of the hurdles to the top of the apparatus.

The box was covered by 4 removable clear lucite panels placed 12 in. above the grid. The walls and post were grooved in such a manner that two of the quadrants could be blocked off by the insertion of black plastic panels onto the tops of the hurdles. A 150-w light bulb in a standard porcelain reflector was suspended 12 in. above the lucite covers and provided constant illumination of 65 ft. candles at the outer edge of the grid floor. A door buzzer was mounted at the base of the bulb, and when activated it provided an auditory stimulus of 65 db S.P.L. as measured at the junction of the hurdles.

Procedure

The quadrants of the apparatus were numbered 1-2-3-4

Figure 1. Schematic diagram of the apparatus.

in a clockwise fashion, and the initial starting position of each S was determined on a random basis such that all positions were employed equally. In the two-way problem, only two quadrants were utilized, while in the free-choice task, four quadrants were used. Thus, in the two-way condition S was placed in the first compartment of combination quadrants 1-2, 2-3, 3-4, 4-1; and in the free-choice situation S was started in quadrant 1, 2, 3, or 4.

Equal numbers of control and experimental Ss were trained in the two-way and free-choice problems, i.e., 20 animals per group. On day 1 S was placed in the apparatus and allowed to explore for 5 min. The S was then given 25 habituation trials to a 5-sec. CS (onset of the buzzer) followed by an intertrial interval (ITI) of 30 sec. If S made more than 5 hurdle-crossings during the CS presentations, it was given additional 25 habituation trials/day until 5 or fewer crossings occurred in a single day.

Avoidance training was begun on the day following the completion of habituation trials. Animals trained in the two-way situation were started in the same combination of quadrants that had been used for them during habituation trials. The Ss trained in the free-choice situation were started in the quadrants that they occupied during their last habituation trials. Avoidance-training trials were

presented every 30 sec. The required response was movement of S from the quadrant which it occupied at the time of CS onset into another quadrant. The CS was onset of the buzzer, and shock ensued after 5 sec. unless S made the required response within this interval. Brief intermittent shock (0.6-0.8 ma.) from a scrambler source was administered at the rate of 1 shock/2 sec. When either an escape or an avoidance response was made, all stimuli were terminated. The stimulus sequence was started and terminated by manual switches operated by E. The frequency of the intermittent shock was controlled automatically. The rat was not shocked for responses during the ITI. Training was continued for 25 trials/day until S made 9 avoidance responses out of any 10 successive trials.

Histology

After reaching criterion, operated Ss were given a lethal dose of pentobarbital sodium anesthesia and perfused intracardially with 0.9% saline followed by 10% formalin. The brains were removed from the skull, placed in formalin for several days, embedded in celloidin, and serially sectioned at 30 micra. Every 10th section through the septum was saved, mounted, and stained with cresyl violet. Sections were examined microscopically to determine the placement and extent of the lesions.

The septal lesions were generally bilateral and symmetrical in placement. The damage typically started

anterior to the genu of the corpus callosum, and extended dorsally to the corpus callosum, ventrally to the level of the anterior commissure, laterally to the nucleus caudatus, and posteriorly to the descending columns of the fornix. There was slight damage to the nucleus caudatus in 32 of the animals. There was some postcommisural sparing in eleven Ss, injury to the cingulate cortex in three animals, and damage to the corpus callosum in two Ss.

The following structures were damaged in all septal rats: fornix precommisuralis, fornix superior, hippocampus pars anterior, nucleus accumbens, nucleus caudatus, nucleus septi lateralis, nucleus septi medialis, nucleus tractus diagonalis (Broca), stria longitudinalis lateralis, stria terminalis pars commisuralis, tractus diagonalis (Broca), tractus hippocampocorticalis, tractus septocorticalis, and tractus septohypothalamicus. All septal Ss showed some degree of Brady-Nauta "hyperreactivity" when handled on the first postoperative day of training.

RESULTS

Table 1 presents the mean trials, standard errors of the mean trials, and median trials for learning at the 9/10 criterion for all groups.

TABLE 1
Mean and Median Trials to Criterion

Group	N	Mean $\pm\sigma_M$ /Median
Normal Two-Way	20	23.0 $\pm$ 4.1/14.5
Normal Free-Choice	20	19.8 $\pm$ 2.6/15.0
Septal Two-Way	20	38.2 $\pm$ 5.3/31.5
Septal Free-Choice	20	18.5 $\pm$ 3.2/15.0

The learning functions for all groups are presented in Figure 2. The curves are Meltonized (1936) and of the type used by Horel et al. (1966). These functions give the group mean trials required to reach 1 correct response out of 10 trials, 2 correct responses out of 10 trials, and so on to the final 9/10 criterion. Thus, if all Ss were to reach a criterion of 9/10 in the initial 10 trials of training, the learning score in such a plot would be 0. If the mean trials to reach the criterion, or any lower

Figure 2. Mean trials to reach each of nine successive criteria.

criterion, were 15, the score would be 5. Each mean score is based upon all Ss, for every S met each of the nine successively more stringent criteria of performance.

An analysis of variance was conducted on individual trials required to reach the 9/10 criterion of the four groups. The over-all analysis of variance revealed a significant lesion X habit interaction ($F = 10.24$, $df = 1/19$, $p < .01$). A posteriori tests of mean differences between the four groups were made with the Tukey (a) procedure.

In the two-way problem, the septal group was impaired relative to the normal group, and the difference between the mean scores at the 9/10 criterion for septal Ss (38.2) and normal Ss (23.0) was significant ($p < .01$).

In the free-choice problem, the normal and septal groups did not differ in their rates of learning ($p > .05$), and both groups reached criterion faster in this habit than in the two-way task. The small difference between the 9/10 mean scores for normal free-choice Ss (19.8) and normal two-way Ss (23.0) was not significant ($p > .05$). However, the large difference between the 9/10 mean scores for septal free-choice Ss (18.5) and septal two-way Ss (38.2) was significant ($p < .01$).

Various types of responses that occurred during the 5-min. exploration period, habituation trials, and avoidance training were also tested by separate analyses of variance. During the exploration period, all groups made very few

hurdle-crossings ($\bar{X} = .9$), and there were no significant intergroup differences. Similarly, few hurdle-crossings were emitted by any group during the habituation trials in the presence of the CS ($\bar{X} = .8$), and 79/80 animals reached the criterion on the first day. There were no reliable differences on this measure. The same general finding was also obtained when the frequencies of intertrial responses (ITRs) were compared; again, there were no intergroup differences, and all groups made very few ITRs per trial ($\bar{X} = .1$). Thus, during exploration and habituation, there were no noticeable differences between the behavior of the normal and septal Ss in either training situation.

During avoidance training, operated animals made more mean ITRs/trial than did normal rats (.4 vs. .0), and the difference was significant ($F = 10.18$, $df = 1/19$, $p < .01$). However, there was no reliable difference between groups trained in the two problems, i.e., the lesion X habit interaction was not significant ($F = 2.45$, $df = 1/19$, $p > .10$).

The final analysis compared the frequencies of one-way responses of normal and septal Ss trained in the free-choice task. In this analysis, the score was each S's one-way responses/total responses (one-way and shuttle). Both the normal Ss and the septal Ss made more one-way than shuttle responses in the free-choice habit. However, the mean proportion of one-way responses by septal animals (.75)

was higher than that by normal rats (.62), and the difference was significant ($F = 16.16$, $df = 1/19$, $p < .01$).

DISCUSSION

The outcomes of this study are, at first glance, surprising on two counts. First, with one exception (LaVaque, 1965), prior experimenters (Green and Schwartzbaum, 1968; Kenyon and Krieckhaus, 1965a, 1965b; King, 1958; Krieckhaus and Kenyon, 1965; Krieckhaus et al., 1964; Schwartzbaum et al., 1967; Van Hosen, MacDougall and Mitchell, 1969) have found that septal rats in two-way CAR problems learn somewhat faster than normal control animals. Second, prior experiments concerned with one-way CAR habits have generally resulted in septal rats being inferior to normal control animals (Kenyon and Krieckhaus, 1965b; Krieckhaus and Kenyon, 1965; McNew and Thompson, 1966; Vanderwolf, 1964). In contrast to these data, the present study shows that septal rats are slower in the two-way situation, and are equal to the normal rats in the free-choice task (in which one-way learning is allowed).

The free-choice findings show that the septal rats' impairments in the present two-way situation are not due to non-specific surgical effects, but rather are completely task-specific. The fact that the present group of septal rats show no impairment in the free-choice condition is also consistent with McCleary's (1966) contention that

septal rats' performances in other one-way tasks were poor because the Es picked up the rats between successive one-way training trials. However, it is not quite so easy to discern the reason for the two-way deficit, and hence, this discussion will be largely limited to a consideration of that problem.

The deficit is certainly related to the fact that insertion of the panels which enforced two-way learning interfered with septal rats' stronger-than-normal tendencies to avoid returning to the quadrant in which they had been shocked on the immediately-preceding trial. That is, in the free-choice situation, septal rats exhibited a 3:1 preference for a new quadrant over a quadrant-just-escaped-from, while normal rats showed a significantly less (.62) preference for "progressing" over "shuttling." Hence, it appears that septal lesions in rats produce an increased fear of returning to a spatial location where shock has been experienced.

But, if this is true, why do septal rats usually do better than normal animals when trained in ordinary shuttle boxes? While no final answer can be given to this question, it seems highly likely that most shuttle boxes train rats to "run" when the CS comes on, but do not train rats to "run away." That is, we can doubt that the usual shuttle box, which consists of two compartments with a door in between them, presents a situation that is readily

discriminable by rats from a large single box. The present apparatus, with its high hurdle between any two adjacent quadrants, is much more clearly partitioned for the S than, say, a Miller-Mowrer box. Such a conjecture is supported by the fact that present learning rates for both normal groups ($\bar{X} = 21.2$ trials) was many times faster than the typical learning rate of 100 trials in other shuttle boxes (Bolles, 1969).

Septal animals respond more than normals in the two-way situation insofar as ITRs are concerned. Why do septal rats, if they are "fearful" of the other box, move into it so often during the ITI? Since Liss (1965) found that septal rats were hyperreactive to foot shock, it seems reasonable to conclude that the increased ITRs by septal Ss reflect a heightened fear of shock. Thus, a possible explanation is that septal rats, after having been shocked, are sensitized to make more responses than normal rats, and the tendency to respond due to fear of being shocked is slightly stronger than the tendency to avoid a specific location due to fear of being shocked in that location.

The notion of sensitization permits us to believe that, if the rat does not discriminate between the two compartments of most shuttle boxes, it should be "faster" in active avoidance learning because it is simply being shocked in conjunction with a light, is running in response to that pairing, and is not discriminating running away vs.

running into a compartment. When such a discrimination is possible, as it is in the present apparatus, the septal rat, when constrained to avoid by returning to a place where it has just been shocked, easily discriminates the place where it has just been shocked and is slower to learn the CAR than normal animals.

Finally, the finding that septal rats avoid a punishing location more actively than normal rats suggests that classically response perseveration, as measured in McCleary's passive avoidance situation, is neither due to a "lack of sensitivity to shock" delivered through the mouth while the animal eats food nor to a "decreased fearfulness of being shocked" in that test situation (Krieckhaus and associates). Whatever the reasons for the passive avoidance effect, it is not, on the basis of the present results, a perseveration stemming from an ineffectiveness of punishment of septal animals.

APPENDIX

Trials to reach the 9/10 criterion

Normal Subjects		Septal Subjects	
Two-Way CAR	Free-Choice CAR	Two-Way CAR	Free-Choice CAR
5	4	6	5
8	8	9	5
10	8	15	7
10	9	26	8
11	10	28	9
12	11	28	9
12	13	30	9
13	13	30	10
13	13	30	10
14	15	31	15
15	15	32	15
25	15	32	16
28	27	36	17
29	28	38	22
30	31	39	23
31	32	51	31
34	33	62	31
34	34	64	32
38	36	66	32
39	40	111	64
Mean $\pm$ σ_M /Median	23.0 $\pm$ 4.1/14.5	38.2 $\pm$ 5.3/31.5	18.5 $\pm$ 3.2/15.0

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