ABSTRACT

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The present study examined the effects of intermittent shock, septal lesions, and the use of a hurdle vs. doorway task on the learning of a conditioned response in rats. Septal animals were facilitated in the acquisition of the conditioned avoidance response and made more intertrial responses. The results indicated that septal animals were more fearful and differences were discussed from the standpoint of the enhanced generalization hypothesis (D'Amato, Keller, & DiCara, 1964), and the fear and discrimination hypotheses suggested by Dalby (1970).

EFFECTS OF SEPTAL LESION AND HABIT REQUIREMENT ON THE ACQUISITION OF A CAR IN RATS

by

Duane Elwood Shuttlesworth

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Approved by

David A. Dalby
Thesis Adviser

APPROVAL PAGE

This thesis has been approved by the following committee of the Faculty of the Graduate School at The University of North Carolina at Greensboro.

Thesis Adviser David A. Dalby

Oral Examination Committee Members Ernest A Lumsden

Wm K. Bates

D. R. Soderquist

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INTRODUCTION

The inordinate difficulty encountered by some investigators (Meyer, Cho, & Wesemann, 1960; D'Amato & Shiff, 1964) while attempting to establish a discriminated lever press avoidance response with rats severely limited the use of discriminated avoidance paradigms and raised several problems of a theoretical nature. The procedure involves training animals to perform a response in the presence of a stimulus (the conditioned stimulus, CS) which signals the occurrence of an aversive stimulus (the unconditioned stimulus, US), which is, generally, shock. The response, either pressing a lever in a Skinner box, or shuttling between two compartments in a shuttle box avoidance situation, terminates the signal and prevents the advent of the US. The efficacy of discontinuous (intermittent) shock as the US in facilitating the acquisition of a discriminated avoidance response (Hurwitz, 1964; D'Amato, Keller, & DiCara, 1964) served only to present additional difficulties for a theoretical explanation of discriminated avoidance behaviors (D'Amato _et al._, 1964). This study is a partial attempt to resolve the theoretical questions posed by the effects of discontinuous shock in avoidance situations.

D'Amato _et al._ (1964) have suggested that intermittent shock, as opposed to continuous shock, facilitates discriminated avoidance responding on the basis of the enhanced generalization of an escape response to the preshock period. If intermittent shock exerts its effects like continuous shock, there are two important theoretical issues that have to be resolved. First, the characteristics of intermittent shock parameters, brief on times and long off times, suggest that CS-US pairings occur more often under this procedure and may, therefore, serve to reinforce a class of responses which are antagonistic to an efficient escape response sequence. Secondly, as D'Amato et al. (1964) point out, an escape response performed during the shock-shock interval, or off-shock period, will not be reinforced as strongly as a response performed as a direct consequence of the US as in an on-shock period. The significance of these two issues in relation to the enhanced generalization hypothesis has not been fully determined.

Feldman and Bremner (1963) pointed out that discontinuous shock may function to facilitate discriminated bar press response acquisition through the effect of reducing freezing or crouching responses elicited in rats by the presentation of the CS in avoidance situations. Such responses are incompatible with efficient discriminated avoidance learning (Meyer et al., 1960; Feldman & Bremner, 1963). The application of "momentary" bursts of .1 ma. shock to rats who assumed a crouching or freezing posture, or to those who held the lever throughout the experimental session, resulted in a marked reduction in these incompatible responses and served to facilitate the acquisition of the desired response. Learning to actively avoid the onset of the US was said to occur, generally, within 50-60 trials. These results in a discriminated lever-press avoidance situation are not incompatible with the learning scores recorded by other investigators using intermittent shock in an entirely different apparatus, the two-way shuttle box (Moyer & Chapman, 1966).

There are, then, two alternative explanations for the facilitative effects of discontinuous shock on the acquisition of a discriminated operant avoidance response. The first concerns the enhanced generalization hypothesis. Briefly, this hypothesis accounts for the facilitation of avoidance learning by the efficiency of discontinuous shock in enhancing the generalization of responses made during the off-shock periods to the preshock periods (i.e., the intertrial interval (ITI) as well as the CS-US interval). The second explanation accounts for faster acquisition rates on the basis of the reduction in freezing responses found when discontinuous shock is used as the US. Discontinuous shock facilitates avoidance conditioning by breaking up the freezing responses and by reinforcing successive movements toward the goal.

D'Amato *et al*. (1964) suggested that the effect of discontinuous shock may operate to reduce CS-elicited response suppression in the rat, but rejected this notion in favor of the enhanced generalization hypothesis in the light of additional evidence obtained in a later study (Biederman, D'Amato, & Keller, 1964). In this study intermittent shock was used as the US while the location of the CS (illumination of lights on the front and back walls of a Skinner box) were manipulated so as to dissociate the CS and the manipulandum (a lever). Although facilitative effects were found when the CS and the lever were dissociated, the effect of discontinuous shock was more striking. The results favored an interpretation which was in line with the enhanced generalization hypothesis. With continuous shock the escape response is made in the presence of shock which is probably "constituting the most salient stimulus component acting at the time the instrumental response is executed" (Biederman, *et al*., 1964). With intermittent shock, however, a substantial number of escape responses may occur during the off-shock periods. The shock component in the intermittent shock situation is supposedly removed from the stimulus complex associated with the escape response. This notion suggests that a response made during the off-shock period is generalized to the preshock period since both stimulus situations are relatively similar. It also suggests that the response may generalize to the ITI if, and only if, the shock factor alone accounts for responding in this situation (i.e., the CS presentation is non-functional).

Variables affecting the occurrence of conditioned response suppression have been suggested. D'Amato and Fazzaro (1966) have pointed out that strong shock reduced the occurrence of avoidance responses and increased the occurrences of conditioned response suppression. D'Amato et al. (1964) noted that the nature of the US employed in the avoidance situation may be a factor influencing the occurrence of conditioned response suppression. Meyer et al. (1960) have suggested that the effects of the CS may contribute, particularly during early trials, to conditioned response suppression occurrence.

The enhanced generalization hypothesis explains the inability to learn an avoidance response on the basis of the inadequate generalization of the escape response to the preshock periods. If this conceptualization is valid then it can be suggested that there should exist a close relation between the avoidance acquisition scores and the percentage of escape responses made during off-shock periods or responses made during the ITIs. D'Amato, Keller, and Biederman (1965) did find that such a correlation existed between acquisition scores and responses made during off-shock periods. The facilitating effect of discontinuous shock, on the basis of these results, was concluded to be due to the enhanced generalization of off-shock period responses to the preshock interval. Measures of the relationship between the number of intertrial responses (ITRs) and learning scores were not obtained.

Two explanatory mechanisms were suggested to account for these results. Intermittent shock may either function to shape-up the escape response (i.e., as in successive approximations to the goal), or it may serve to reduce the aversiveness of shock presentations. In the first case discontinuous shock may function to develop the escape response into an efficient, well-organized response sequence which closely resembles the desired avoidance response and can, therefore, adequately generalize to the preshock periods. Continuous shock, as was pointed out earlier, leads to a state of response suppression (D'Amato _et al._, 1964; D'Amato _et al._, 1965) which represents an antagonistic response pattern to an efficient avoidance response. This accounts for the difficulties encountered by earlier investigators (Meyer _et al._, 1960; D'Amato & Shiff, 1964) in establishing discriminated operant avoidance responses (D'Amato _et al._, 1965). Secondly, intermittent shock may be less aversive than continuous shock (Biederman _et al._, 1964). Continuous shock leads to a state of response suppression in this case on the matter of aversiveness, not on the basis of freezing or crouching behaviors, although the two may be analogous to each other in the final analysis.

The parameters of intermittent shock shed additional light on the nature of the facilitative effects of discontinuous shock. In two studies directed toward the quantification of the most effective and efficient discontinuous shock parameters (D'Amato _et al._, 1965; D'Amato & Fazzaro, 1966) it was found that both the duration and the intensity of discontinuous shock were involved in the facilitation of avoidance conditioning. The most effective temporal parameters were found to be .2 sec. on time with a 2.0 sec. off time (D'Amato et al., 1965). D'Amato and Fazzaro (1966) found that US avoidance conditioning was inversely related to shock intensity with continuous shock, but with intermittent shock the facilitation was found to hold over a wide range of shock intensities (i.e., from .16 to 1.0 ma.).

One of the theoretical issues raised by the use of intermittent shock concerns the generalization of the results from discriminated operant avoidance situations to other avoidance situations. Moyer and Chapman (1966) attempted to determine whether or not discontinuous shock was effective as the US in a two-way shuttle box situation as it was in the operant situations described previously. The results demonstrated that superior acquisition of a two-way shuttle avoidance response can be accomplished by using intermittent shock as the US. In addition, the authors point out that they observed fewer instances of freezing and perseveration of responding when discontinuous shock groups were compared to continuous shock groups. Moyer and Chapman failed to measure the number of off-period escape responses in relation to the acquisition of the avoidance response. Their results, therefore, do not serve to test the validity of the enhanced generalization hypothesis. Furthermore, the number of ITRs were not recorded for either group. The authors did conclude, however, that their results were due to the efficacy of discontinuous shock in moving the required locomotor response higher on the subject's response hierarchy. This explanation is similar to the one offered by Bolles (1970) in his discussion of species-specific defense mechanisms in relation to avoidance conditioning.

Studies conducted on the role of anticipatory (avoidance) responses (D'Amato, 1967; D'Amato, Etkin, & Fazzaro, 1968; D'Amato, Fazzaro, & Etkin, 1968) suggest the importance of yet another variable within the intermittent shock-avoidance conditioning paradigm. The role of the anticipatory response is that of an avoidance response which occurs in the absence of an avoidance contingency. Avoidance and anticipatory responses are actually similar in that they both occur during the CS-US interval, but they are dissimilar in that only the avoidance response terminates the CS and eliminates the possibility that the US will occur. The anticipatory response does not terminate the CS nor eliminate the US. Typically, anticipatory responses are thought to be due to the avoidance contingency rather than to other factors. The results of a study by D'Amato (1967) suggest, however, that initial anticipatory responses are generated by factors other than the avoidance contingency. D'Amato observed that substantial numbers of anticipatory responses were maintained even in the absence of an avoidance contingency. He suggested that, theoretically, if an independent variable facilitates the acquisition of the avoidance response, as does intermittent shock, while at the same time increasing the occurrence of another response, the anticipatory response, then it can be concluded that some of the conditioning of the avoidance response is through the conditioning of the anticipatory response. This argument is in line with the concept of enhanced generalization which suggests that intermittent shock, by facilitating avoidance response acquisition, should also serve to increase the occurrence of anticipatory responses.

D'Amato *et al*. (1968a) tested this hypothesis by manipulating both shock intensity and type (continuous vs. discontinuous) in the absence of an avoidance contingency. On anticipatory response trials, the CS and US termination did not occur simultaneously with the response, and the US was delivered at the end of the five second CS-US interval. The animals had to respond again in order to escape the shock. Controls consisted of a group in which the anticipatory response terminated the CS and eliminated the US (typical avoidance situation), and another group in which the CS was terminated independently of the conditioned response. Higher shock intensities significantly reduced the frequency of anticipatory responses, but the type of shock did not differentially affect occurrences of these responses. These results questioned the validity of the enhanced generalization hypothesis of D'Amato *et al*. (1964).

In a later study, D'Amato *et al*. (1968b) re-examined the classic notion of Mowrer (1951) that CS termination on anticipatory response trials may serve to reinforce avoidance acquisition by acting as a discriminative cue for US avoidance by terminating fear generated by the CS. They tested this concept by manipulating the discriminability of the stimulus complex operating at the time when an avoidance response occurred. The significance of the discriminative cue could only be learned on trials when an anticipatory response was made. They found, as was expected, that the addition of extra discriminative cues contingent on the occurrence of anticipatory responses facilitated avoidance conditioning, which supported the notion that the major function of prompt CS termination is that of a discriminative cue for US avoidance.

They concluded that facilitated acquisition of an avoidance response is due to the effects of discriminative cues rather than to the generalization of responding during the off-shock period to the CS-US interval, the basic concept of the enhanced generalization hypothesis.

The fear hypothesis offered by Biederman et al. (1964) argues that the subject's fear response to the type of shock is the most significant factor which influences the acquisition of an avoidance response. Increasing the length of time between successive presentations of the CS-US contingency should allow the fear generated by previous CS-US pairings to dissipate. Biederman (1967), using discontinuous shock as the US, found that longer ITIs did facilitate the acquisition of a discriminated lever press avoidance response with rats. Strain (Wistar and Sprague-Dawley) and ITI duration interaction effects were significant. They were, however, confounded by experiment order as Wistars preceded Sprague-Dawleys in the experiment. The results suggest that a mean ITI duration of approximately 30 sec. or less serves to facilitate response acquisition with Sprague-Dawleys and a mean ITI of 60 sec. for Wistars. Biederman failed to replicate the results of an earlier study (D'Amato & Fazzaro, 1966) in which high levels of avoidance behavior were found with ITI durations ranging from 22.5 sec. to 90 sec. The main conclusion that one may draw from the results is that ITI duration may have an effect on avoidance acquisition through a fear reduction mechanism which operates over time.

Further criticism of the enhanced generalization hypothesis arose from studies conducted by Hess and Shafer (1968a, 1968b). Noting that the crucial factor underlying this hypothesis was the generalization of escape responses to the preshock periods, Hess and Shafer (1968a) suggested that the presentation of shock in a normally off-shock period should inhibit avoidance responding. The results failed to support the hypothesis since the subjects under the additional shock requirement performed as well as the control group which was tested under standard intermittent shock avoidance procedures. Two interpretations of the data were suggested. First, the subjects may be pacing their responses during escape responses so as to receive a minimal number of shocks. Secondly, the subjects may be responding to discrete bursts of shock. In this case the subjects would often approach the bar and place their paws above it, waiting until the US was presented before responding. Such behavior occurred when continuous shock was used. Discontinuous shock increased the number of off-shock period escape responses and decreased the association between the to-be-learned response and shock intensity, which suggests that the subjects were responding to discrete presentations of the US rather than pacing their responses.

In a subsequent study, Hess and Shafer (1968b) concluded that, at least in the discriminated bar press avoidance situation, the effect of discontinuous shock was exerted on the acquisition of the avoidance response through a systematic shaping procedure in which intermittent shock has the dual function of breaking up freezing behaviors while simultaneously reinforcing successive movements by the subject toward the completion of the escape response. Escape responding is best acquired, as they point out, when the US is terminated by the response as in a continuous shock condition, rather than before the completion of the response as in a discontinuous shock situation. Arguing that intermittent shock allows the response to occur during the off-shock period where shock termination and escape responses are not simultaneous, Hess and Shafer point out that discontinuous shock exerts its effects by systematically shaping the desired response in relation to presentations of discrete bursts of the US.

In order to re-evaluate the enhanced generalization hypothesis Biederman (1969) manipulated the CS present in the off-shock period contingent upon the subject's failure to make the appropriate avoidance response. If the CS is a relevant variable (Meyer et al., 1960) in the avoidance situation then avoidance conditioning should not benefit when the CS was omitted during the escape phase of each trial when discontinuous shock was used as the US. By terminating the CS at the conclusion of the avoidance period (the CS-US interval) Biederman provided an off-shock period stimulus complex which was different from the CS-US interval stimulus situation, but was, in fact, similar to the ITI stimulus complex. The results showed that intermittent shock facilitated the production of conditioned responses whether or not the CS was present during escape. This finding was consistent with the results obtained by Hess and Shafer (1968b). Discontinuous shock exerts its effects then, not through the generalization of escape responses, but by the accidental elimination of incompatible responses (i.e., freezing and crouching). Subjects in discontinuous shock groups were observed to be more likely to vary their positions during off-shock periods than were subjects in continuous shock groups. The results of this study are interestingly compatible with an explanation of the facilitative effects of intermittent shock in terms of the systematic shaping of the response and the reduction in freezing and similar behaviors which are incompatible with efficient response acquisition.

Shafer and Hess (1969) demonstrated that avoidance performance was definitely unrelated to the subject's opportunity to make escape responses during off-shock periods (i.e., the CS-US interval and the ITI), thus eliminating another possible variable from the discriminated operant avoidance response situation. Utilizing an avoidance paradigm suggested earlier (Hess & Shafer, 1968b) in which continuous and intermittent shock trials were combined in an alternating fashion, they noted that subjects trained under this condition were significantly better in acquiring the response than were subjects trained under standard intermittent shock conditions. The results of this study point out the importance of escape response latency as well as subsequent avoidance response latencies in efficient avoidance behavior. In an analysis of the conditions producing superior avoidance performance in the experimental group Hess and Shafer suggested that the use of intermittent shock tends to eliminate freezing responses which are incompatible with efficient escape responding and that continuous shock produced shorter escape latencies which provided a more favorable reinforcement situation when the US was terminated by the response. The combined effect of both types of US facilitated avoidance responding.

Intermittent shock has been demonstrated to clearly facilitate the acquisition of avoidance responding although the exact mechanism through which it exerts its effects has not been demonstrated. It can be suggested that discontinuous shock has the dual effect of breaking up freezing behaviors while simultaneously reinforcing successive movements toward the completion of the escape response (Hess & Shafer, 1968b; Shafer & Hess, 1969). Interestingly, discontinuous shock avoidance paradigms have only been applied once (Dalby, 1970) to shuttle box avoidance situations with septally lesioned rats as subjects. The facilitatory effects of septal lesions on the learning of a shuttle conditioned avoidance response (CAR) have been well documented, and there have been various interpretations of the nature of this effect. Explanations have included a lack of response inhibition (McCleary, 1961, 1966); reduced freezing (Kenyon & Krieckhaus, 1965a; Krieckhaus, Simmons, Thomas, & Kenyon, 1964; Schwartzbaum, Green, Beatty, & Thompson, 1967); and reduced fear (Kenyon & Krieckhaus, 1965b). All these studies employed a continuous shock US.

Since Moyer and Chapman (1966) demonstrated facilitated learning of a CAR in a two-way shuttle box situation by normal rats with discontinuous shock as the US, it seems reasonable to expect that animals sustaining septal lesions should also learn a shuttle CAR faster than normals when a discontinuous shock US is utilized. Such results, however, were not obtained by Dalby (1970) who used an intermittent shock US in a shuttle avoidance task with rats. Subjects sustaining septal lesions were slower than normals in acquiring the two-way CAR. Dalby suggested that, while continuous shock facilitates the acquisition of a CAR with subjects having septal lesions, and retards learning by normal animals, the opposite may well be true with discontinuous shock. This statement is supported by the fact that learning rates were significantly faster for normal subjects than the typical learning rates reported by other investigators using the shuttle box (Bolles, 1970). The two-way deficit of the operated subjects was also related to the fact that a four inch hurdle was placed between the two compartments of the apparatus. The hurdle may have effectively separated the compartments of the apparatus and therefore increased the subject's fear of shuttling back to the location where he was previously shocked.

Another aspect of this study was that septal animals made more ITRs than did normals in the two-way situation. The question was raised that if septal animals are more fearful, why does this behavior occur? A possible explanation was that septal subjects are more sensitive to tactile stimulation and that the tendency to respond due to the fear of being shocked is slightly stronger than the fear of being shocked in a location where the US was delivered previously. Since operated subjects were slower to learn it can be suggested, in line with an earlier report (Meyer, Johnson, & Vaughn, 1970), that facilitated learning by animals with septal ablations was not dependent upon increased responding during the ITI. This supports the findings of Hess and Shafer (1968a, 1968b), Biederman (1969), and Shafer and Hess (1969) that responding during the ITI was not responsible for the acquisition of a discriminated bar press avoidance response.

In a later study, Dalby and Shuttlesworth (1971), the effects of septal lesions on the learning of a two-way CAR involving a hurdle or a doorway task with continuous shock were studied. It was found that normal and operated subjects in the hurdle condition learned significantly faster than did normal and operated subjects in the doorway situation. Animals with septal lesions reached criterion faster than their respective normal control groups, but there were no differences between the operated groups. This latter finding supports the discrimination hypothesis set forth by Dalby (1970) concerning the significance of the hurdle in a CAR apparatus. Since septal animals trained on the hurdle task were not significantly different from septal animals trained on the doorway task one may hypothesize that the presence of the hurdle effectively separates the apparatus and therefore makes the CAR more defined for normal subjects but not for septal subjects. If this assumption is correct one may further suggest that septal animals fail to discriminate between the two compartments and that this accounts for the relatively equal acquisition rates between doorway and hurdle animals. An alternative explanation lies in the fear hypothesis mentioned by Dalby (1970) which states that septal animals are more fearful of being shocked than they are of returning to the location in which they had just been shocked. As a result of this fear they make more shuttle responses and reach criterion faster than normal animals.

In view of the findings of the previous studies which have shown that intermittent shock facilitates the learning of a two-way CAR by normal rats but possibly retards learning by animals with septal lesions, the present study examined the effect of intermittent shock on the behavior of normal and septal rats which were trained in two types of two-way CAR problems. In one problem the two boxes were separated by a doorway and in the other task the compartments were separated by a hurdle.

METHOD

Subjects

Eighty naive, male Holtzman rats weighing 250-300 grams served as subjects. Subjects were randomly assigned to either a control group or an experimental group. The control group consisted of normal rats and the experimental group consisted of rats sustaining bilateral lesions of the septal region of the forebrain. All subjects were housed in individual cages and given constant access to food and water.

Surgery

Surgery was carried out under Equi-Thesin anesthesia administered intraperitoneally. A preoperative dose of .1 cc. bicillin was given intramuscularly to guard against possible infection resulting from surgery. Bilateral septal lesions were made by intracerebral insertion of an electrode which was insulated except for 0.5 mm. at the tip. The stereotaxic coordinates for the lesions, as determined from the stereotaxic atlas by de Groot (1959), were anterior-posterior +8.0 mm., lateral $\pm$0.5 mm., and dorsal-ventral +1.0 mm. A direct current of 2.0 ma. was passed through the electrode for 20 seconds to produce the lesion, the circuit being completed by an anal electrode. A two-day recovery period was allowed following surgery.

Apparatus

The apparatus was a two-way shuttle box identical to that employed by Meyer _et al_. (1970). It consisted of two compartments separated by either a partition with a 3 X 4-in. doorway or a 4-in. high hurdle. In each unit were two overhead 15-w. fluorescent lamps, the light from which was diffused by 1/4 in. translucent plexiglass. A mirror-pane on the front wall of both compartments permitted observation of the subjects. The floor was composed of 3/16 in. stainless steel grid bars spaced 1/2 in. apart. The CS was a buzzer which was 20-db. SPL above the white noise background masker SPL of 60-db. The buzzer was mounted 7 in. above the top center of the apparatus. CS duration was 5 sec. The US was a .6-.8 ma. ac scrambled footshock presented for .2 sec duration at the rate of 1 shock every 2.0 sec. by a mechanical device designed to deliver intermittent shock.

Procedure

Training procedures were identical to those used by Dalby and Shuttlesworth (1971). On day one, the subject was permitted free exploration of the apparatus for the first five minutes and the experimenter recorded the number of crossings between the two compartments. Following this the CS was presented alone for 25 trials spaced by a 30 sec. ITI. The CS presentations were five sec. in duration. The experimenter recorded the number of crossings made by each subject during the occurrence of the CS and during the ITI for each trial.

On day two, training began. The subject was placed in the compartment which he occupied at the conclusion of pretraining. The CS was presented for five sec. or until the subject crossed into the other compartment. If, at the end of five seconds, the subject had not crossed, intermittent shock was administered and continued with the CS until the subject moved to the other compartment. Successive trials were presented 30 sec. after a shuttle response was made. One half of the subjects were trained in the doorway situation and the remaining subjects were trained in the hurdle condition. Training continued with 25 trials per day until the subject met the learning criterion of making nine avoidance responses out of any 10 successive trials. During training the experimenter recorded whether an escape response or an avoidance response was made on each trial and the number of crossings made during the ITIs.

Histology

After reaching the 9/10 learning criterion operated subjects were given a lethal dose of sodium pentobarbital and perfused intracardially with .9% saline followed by 10% formalin. The brain was removed from the skull and placed in formalin for several days. It was then embedded in cellodin and serially sectioned at 30 micra. Every tenth section through the septum was saved, mounted, and stained with cresyl violet. The sections were then examined to determine the locus and extent of the lesion.

Figure 1 presents a diagrammatic representation of the lesions in anterior (a), middle (b), and posterior (c) sections of the septum. The lesions were generally bilateral and symmetrical in placement. Damage typically started just posterior to the genu of the corpus callosum, coursed ventrally to the level of the anterior commissure, dorsally to the corpus callosum, laterally to the caudate nucleus, and posteriorly to the descending columns of the fornix. On the first postoperative day of training 93% of the operated subjects displayed some degree of hyperreactivity when handled.

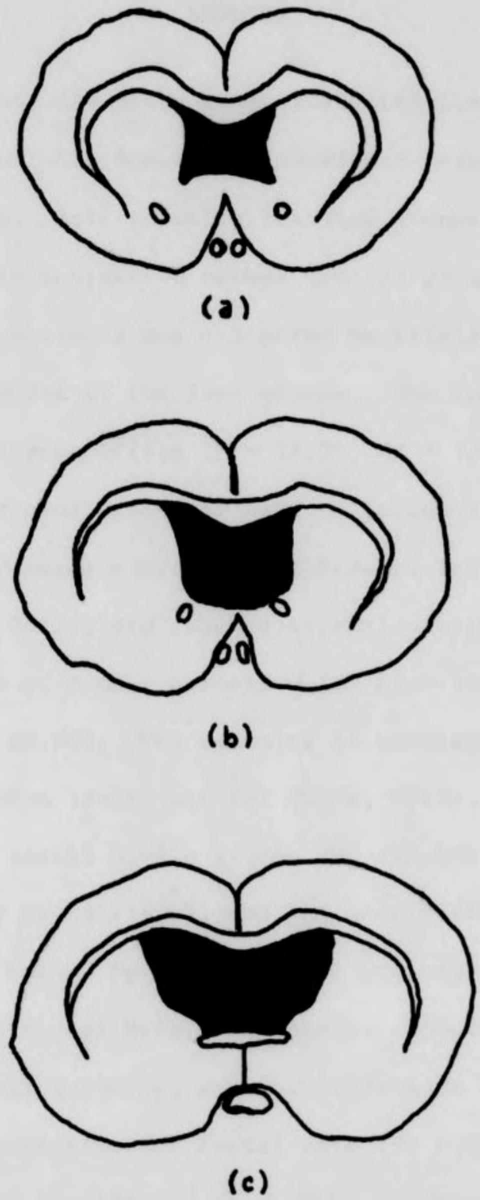

Figure 1. Drawings depicting the locus and extent of the septal lesions.

RESULTS

Figure 2 presents the group mean trials required to reach the learning criterion of nine successful avoidance responses out of any 10 successive trials. Both septally lesioned groups reached criterion faster than did their respective normal control groups.

An analysis of variance was conducted on trials to reach the 9/10 criterion by individuals of the four groups. The analysis indicated only a significant lesion effect ($F = 32.26$, $df = 1/76$, $p < .001$), i.e., there were no significant habit nor Habit X Lesion interaction effects. Thus, both groups of animals with septal lesions learned at similar rates (SD + SH, $\overline{X} = 26.32$) and reached criterion significantly faster than did both groups of normal animals which also learned at similar rates (ND + NH, $\overline{X} = 62.90$). The estimate of variance accounted for (est. ω^2) by the lesion factor was 28% (Hays, 1963).

The normal and septal hurdle groups (NH and SH) were included in an attempt to replicate Dalby (1970), and the mean difference between their learning scores was tested by the Tukey (a) procedure (Winer, 1962). Contrary to the findings of Dalby, the septal animals were facilitated relative to the normal subjects, and the difference between the mean scores at the 9/10 criterion for septal rats (SH = 25.40) and normal rats (NH = 55.90) was significant ($p < .01$).

Shuttle responses that were made during the 5-min. exploration period, habituation trials, and intertrial interval during habituation and avoidance training trials were also tested by separate analyses of variance. During the exploration period, animals in all groups made several

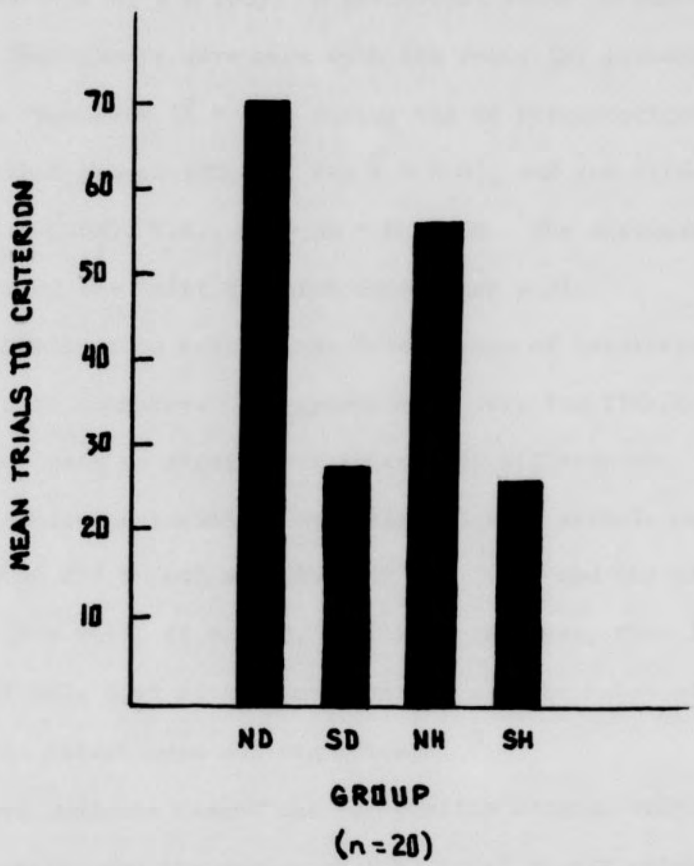

Figure 2. Mean numbers of trials taken by the four groups to reach the 9/10 criterion.

shuttle crossings, but there were no significant intergroup differences ($\overline{X}$ = 8.23).

The analysis of responses made during the habiutation trials in the presence of the CS indicated a significant Habit X Lesion interaction ($F = 5.16$, $df = 1/76$, $p < .05$). A posteriori tests of mean differences between the four groups were made with the Tukey (a) procedure. Group SD made more responses ($\overline{X}$ = 8.1) during the CS presentations than did any of the other groups (ND, NH, SH; $\overline{X}$ = 3.0), and the differences were significant ($p < .05$), i.e., SD $>$ ND = NH = SH. The estimate of variance accounted for by the Habit X Lesion factor was 4.3%.

During habituation trials, the frequencies of intertrial responses (ITRs) were also compared. All groups made very few ITRs/trial ($\overline{X}$ = .37) and there were no significant intergroup differences.

During avoidance training, septally lesioned animals made more mean ITRs/trial than did normal animals (.38 vs. .09), and the difference was significant ($F = 8.15$, $df = 1/76$, $p < .01$). However, this lesion factor accounted for only 8.4% of the total variance. The habit effect and the Habit X Lesion effect were not significant.

The final analysis tested the correlation between trials to reach the 9/10 criterion and the number of ITRs/trial by all animals. The correlation was negative and significant ($r = -.29$, $df = 78$, $p < .01$), and indicated that faster learning was related to a higher incidence of ITRs. Although the correlation was significant, the estimate of variance (r^2) revealed that only 8.4% of the variance was accounted for in the correlation.

DISCUSSION

The functional role played by septal lesions and intermittent shock in the acquisition of a two-way CAR habit by rats can be characterized as one of response facilitation. In studies using continuous shock as the US the facilitative effects of septal lesions on the acquisition of a two-way CAR are well documented (McCleary, 1961, 1966; Kenyon & Krieckhaus, 1965a, 1965b; Krieckhaus et al., 1964; Schwartzbaum et al., 1967; Meyer et al., 1970; Dalby & Shuttlesworth, 1971). Dalby (1970), however, found that the facilitative effects of septal lesions were reversed when intermittent shock was used as the US in a two-way CAR situation. Evidently the combined effects of intermittent shock and septal lesions are contrary to what would have been expected on the basis of the results of prior studies conducted to examine these two factors separately.

The present study, which used intermittent shock and found faster learning by septal animals trained in both the doorway and hurdle tasks, failed to replicate the findings of Dalby (1970) and supports previous experiments which employed continuous shock as the US. Septal lesions in rats clearly result in faster acquisition of the two-way CAR habit regardless of the type of shock used.

In a similar study, Dalby and Shuttlesworth (1971) used the same doorway and hurdle tasks, normal and septal rats, but continuous shock as the US. A comparison of the learning scores between equivalent groups in that study and the present study showed that there were no significant differences between the groups on the basis of continuous vs. intermittent shock. Thus, the combined results of these two studies indicate that intermittent shock does not facilitate the acquisition of a shuttle CAR and therefore opposes the findings of Moyer and Chapman (1966). Furthermore, the facilitated learning of discriminated operant avoidance responses by intermittent shock found by previous investigators (D'Amato, 1966; Biederman _et_ _al_., 1964; Biederman _et_ _al_., 1967; D'Amato _et_ _al_., 1965; D'Amato _et_ _al_., 1966; Hess & Shafer, 1968a, 1968b; Shafer & Hess, 1969) fails to generalize to the shuttle box situation.

Factors other than intermittent shock may be operating to facilitate the acquisition of the two-way CAR. Dalby (1970) has suggested that the presence of a hurdle between the two compartments of a shuttle box facilitates the learning of the CAR response by normal animals relative to normal animals trained in a typical doorway CAR habit. The results of Dalby and Shuttlesworth (1971) support the notion that a hurdle is an important variable in the shuttle box situation because it was found to facilitate the acquisition of a two-way CAR by normal and septal subjects. The use of a hurdle also results in faster learning by normal animals relative to the results of other studies in which a doorway condition was used (Bolles, 1970). However, in the present study, the lack of any significant habit or Habit X Lesion effects does not point to the hurdle as an important variable influencing CAR learning by normal or septal rats.

Dalby (1970) has proposed a fear hypothesis which points out that septal animals are more fearful of being shocked than they are of being shocked in a compartment in which they had received shock on the previous trial. There are two basic implications of this hypothesis: first, the animals are responding on the basis of the fear of being shocked and are not responding due to the nature of the shock type; and second, a heightened degree of responding would also occur during off-shock periods (i.e., the CS-US interval, or ITIs) where there is no direct requirement for an escape response.

The result that septal animals made significantly more ITRs during learning than did normal animals agrees with the previous findings of Dalby (1970) and Meyer et al. (1970). This consistent result that septal animals make more ITI responses suggests that their fear of being shocked constitutes a more salient variable than does their fear of returning to a location where shock was previously delivered. The fact that septal animals made more ITRs when continuous shock (Meyer et al., 1970) or intermittent shock (Dalby, 1970) was used contradicts the fear hypothesis proposed by Biederman et al. (1964). That is, continuous shock is not functionally more aversive than intermittent shock and does not produce more response suppression as reflected in the frequency of ITRs.

The three findings that septal animals learned faster, that septal subjects made more ITRs/trial, and that there was a significant correlation between the frequency of ITRs/trial and learning can be viewed as supporting the enhanced generalization hypothesis of D'Amato et al. (1964). That is, it may be that the higher responding by septal animals during the ITIs may generalize to the CS-US interval and thus account for faster acquisition of the CAR. However, such generalization by itself cannot account for faster learning by septal animals because only 8.4% of the variance was accounted for in the correlation.

Hyperreactivity on the part of septal animals was not restricted to the conditioning trials. During habituation trials septal doorway animals made significantly more crossings than did the other three groups during the CS presentations. This initial hyperreactivity may indicate that the buzzer CS itself was more aversive to septal than to normal animals. Supporting this notion was the absence of any intergroup differences on crossings during the ITIs during habituation trials. However, this initial increased responding by doorway septal subjects cannot account for the subsequent faster acquisition of the CAR. This is so because septal subjects in the hurdle condition learned equally as fast yet made fewer responses to the CS presentations during habituation trials of all the four groups.

In conclusion, the facilitated acquisition of a two-way CAR produced by septal lesions in rats cannot be fully explained from any single standpoint. The most plausible explanations are the fear hypothesis of Dalby (1970) and the enhanced generalization hypothesis of D'Amato *et al*. (1964).

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