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THE EFFECTS OF LESIONS IN THE SEPTAL FOREBRAIN OR THE
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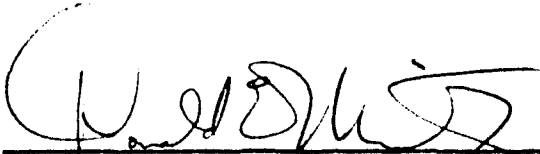
by
MARJORIE^{ANN} CAPLAN

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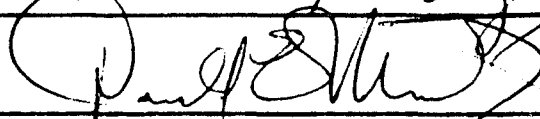
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Abstract

In two experiments, septal lesioned or cingulate lesioned rats were tested on a DRL 8 sec. or DRL 0.6 sec. schedule of reinforcement. Results showed that timing efficiency of septal operates was reduced below control levels when they were required to suppress responding for 1.2 sec. or longer. When reinforcements were periodically and randomly withheld following a correct timing response (nonreinforcing event), response rates for all subjects were higher than they were when every correct timing response was reinforced. The increase in rate was a function of the probability of the nonreinforcing event and was greatest for the septal operates when their baseline reinforcement rate was equal to that of the control animals. The behavior of the septal operates is discussed in terms of the aversive properties of contingent response suppression and of omission of reinforcement for a previously rewarded response. Animals with cingulate lesions were no different than operated or nonoperated controls. These results were taken as evidence against the hypothesis that cingulate lesions enhance inhibitory control, and were discussed in relation to the performance of organized complex sequences of behavior.

Table of Contents

	<u>Page</u>
Introduction	
General introduction and statement of problem.....	1
Anatomy and general background.....	2
Lesion literature.....	6
Rationale for present analysis of septal function.....	14
Evidence supporting the present analysis.....	17
Hypothesis and plan of present experiments.....	21
Experiment 1	
Introduction.....	24
Method.....	24
Results.....	31
Experiment 2	
Introduction.....	65
Method.....	65
Results.....	69
Discussion	
Septal lesions.....	87
Implications for septal functions.....	95
Cingulate lesions.....	99
Summary and conclusions.....	106
Appendix A: Evidence for behavioral assumptions.....	118
Appendix B: Schema for behavioral analysis of aversive events.....	123
Appendix C: Individual data.....	132
Appendix D: Summary tables of analyses of variance.....	144

List of Tables

- Table 1: Summary of procedures followed in Experiment 1.
- Table 2: Values of chi-square and correlation coefficients showing the relation and degree of association between the frequency of responses less than 1 sec. and the frequency of responses between 7 and 8 sec.
- Table 3: Analysis of variance summary table. Differences in per cent efficiency on first and last nonreinforcement days and days immediately preceding for subjects on DRL 8 sec. schedule.
- Table 4: Summary of procedures followed in Experiment 2.
- Table 5: Analysis of variance summary table. Per cent efficiency on first nonreinforcement days at each probability contingency for subjects on DRL 0.6 sec. schedule.
- Table 6: Analysis of variance summary table. Differences in rate on first and last nonreinforcement days and days immediately preceding for subjects on DRL 0.6 sec. schedule.

List of Figures

- Figure 1: Reconstruction of septal lesions in the DRL 8 sec. group.
- Figure 2: Reconstruction of cingulate lesions in the DRL 8 sec. group.
- Figure 3: Cumulative records for one S from each operated group for the first and last sessions during acquisition on DRL 8 sec., and for the first day of each $p(\overline{SR})$ contingency.
- Figure 4: Per cent efficiency, water consumed, and rates during acquisition on DRL 8 sec. for each operated group.
- Figure 5: IRT distributions for each group during acquisition on DRL 8 sec.
- Figure 6: Per cent efficiency for each operated group on DRL 8 sec. during continued DRL 8 sec. training and the successive daily sessions when $p(\overline{SR}) = .20$.
- Figure 7: Correlation diagrams showing the relation between the frequency of responses less than 1 sec. and responses emitted between 7 and 8 sec. for each operated group during the period of continued training on DRL 8 sec.
- Figure 8: Per cent efficiency on reinforcement and alternate nonreinforcement days for each operated group for each probability contingency.
- Figure 9: Rate on reinforcement and alternate nonreinforcement days for each operated group during each probability contingency.
- Figure 10: IRT distributions on the first nonreinforcement day for each probability contingency for each operated group.
- Figure 11: IRT distributions on last nonreinforcement day.
- Figure 12: Reconstruction of septal lesions in the DRL 0.6 sec. group.

- Figure 13: Reconstruction of cingulate lesions in the DRL 0.6 sec. group.
- Figure 14: IRT distributions for first and last sessions on DRL 1.2 sec. and DRL 0.6 sec., respectively, for each operated group.
- Figure 15: Per cent efficiency, water consumed, and rates during continuous reinforcement, DRL 1.2 sec., and DRL 0.6 sec. for each operated group.
- Figure 16: Per cent efficiency on reinforcement and alternate nonreinforcement days for each operated group for each probability contingency.
- Figure 17: Rates on S^R and alternate $\overline{S^R}$ days for each operated group during each probability contingency.
- Figure 18: IRT distributions on first $\overline{S^R}$ day for each probability contingency for each operated group.
- Figure 19: IRT distributions on last $\overline{S^R}$ day for each probability contingency for each operated group.
- Figure 20: Schematic representation of behavioral analysis of aversive events.
- Figure 21: Efficiency ratios for individual S_s from each operated group on DRL 8 sec. on reinforcement days and nonreinforcement days.
- Figure 22: IRT distributions for one rat from each operated group on DRL 8 sec.
- Figure 23: Response rates for individual S_s from each operated group on DRL 0.6 sec.
- Figure 24: IRT distributions for one rat from each operated group on DRL 0.6 sec.

THE EFFECTS OF LESIONS IN THE SEPTAL FOREBRAIN OR THE
CINGULATE CORTEX ON THE TIMING BEHAVIOR OF RATS

Introduction

General introduction and statement of the problem

The effects of damage to the septal forebrain or the cingulate cortex have been interpreted either as affecting (1) the subject's emotional responsivity and motivational level (emotionality hypothesis) or (2) the ability of the animal to withhold or inhibit a response (response inhibition hypothesis). These two hypotheses, which have been presented as alternative explanations of the observed behavior, may not be mutually exclusive. Bard (1950) and Bard and Mountcastle (1948) have suggested that the limbic system, two prime components of which are the septal forebrain and cingulate cortex, may play a restraining role in emotional responsivity. The hypothesis put forth by Bard and Mountcastle includes the operation of elements involved in both emotion and response inhibition. The studies thus far performed to test these theoretical positions, however, have not adequately defined either concept. In order to

achieve adequate specification of the variables involved, it is necessary to develop an analysis of the normal behavior resulting from given stimulus operations, and then a detailed analysis of changes in this behavior resulting from damage to particular anatomical structures.

Anatomy and general background

The septal area is delineated as that area dorsal and anterior to the anterior commissure, immediately ventral to the genu and body of the corpus callosum. It occupies the anteromedial wall of the hemisphere and extends to the lateral ventricle. It is composed of a heterogeneous group of cells and fibers which receives projections from the olfactory bulb, the frontal region, the olfactory tubercle, the amygdala, hippocampus, thalamus, and hypothalamus (Crosby, Humphrey, & Lauer, 1962). It in turn projects to all of these structures (except the olfactory bulb), and also to the midline nucleus of the thalamus, habenula, and certain regions of the midbrain tegmentum (Powell, 1963). It thus constitutes a way-station in which fibers interconnecting most limbic system structures synapse.

The septal forebrain was initially implicated in the mediation of affective behavior by Brady and Nauta (1953), who demonstrated that animals with lesions in this area displayed an extreme "hyperemotional reactive state" until approximately twelve days postoperatively. This hyperreactive state did not appear in control animals with lesions in the

cingulate cortex, or in nonoperated control animals. The "septal syndrome" was thus defined as increased irritability and reactivity to such events as handling, capture, prodding with a pencil or forceps, jangling of keys, and appeared following extensive destruction of septal tissue. Brady and Nauta (1953, 1955) further described the behavior of septal rats as being wild and fierce, exhibiting hyperreactivity to all sensory stimulation, especially tactile. King (1958, 1959) replicated and extended these findings, reporting slight strain differences between hooded and albino rats in postoperative duration of the syndrome. These results supported the transitory nature of the syndrome, in that it declined and eventually disappeared anywhere from one week to two months following surgery.

These early findings were explained by the emotionality hypothesis, which initially posited an increase in emotional responsivity produced by the septal lesion. This hypothesis proposed that increased reactivity to noxious stimulation was responsible for changes in performance observed on behavioral tasks following destruction of the septal area. An increase in the motivational level of the septal animal was posited to explain those results which could not be accounted for by the emotionality hypothesis.

Another structure which appears to be implicated in emotional responsivity is the cingulate cortex. This cortical area was first shown to exert effects on emotional

behavior opposite to those of the septal area when Bard and Mountcastle (1948) found that removal of the cingulate gyrus in cats and dogs resulted in decreased emotional responsivity. The cingulate cortex is the midline structure immediately dorsal to and bordering on the corpus callosum along its anterior-posterior extent. It is divided into an anterior region, rostral and dorsal to the genu of the corpus callosum, a posterior or supracallosal region, bordering the body of the corpus callosum, and a retrosplenial region, dorsal and posterior to the splenium of the corpus callosum. The cingulate gyrus receives its primary connections from the anterior nuclei of the thalamus, but also possesses extensive afferent and efferent associations with all parts of the surrounding cortex.

The importance of the anterior region of the cingulate cortex and its apparent opposition to the role of the septal forebrain in the control of behavior was investigated by Kaada in his electrical stimulation studies (1951, 1960). His findings led to the formulation of the second major hypothesis which has been advanced to account for changes in behavior following destruction of either one of these two limbic system areas. Kaada showed that electrical stimulation of the subcallosal area¹, immediately anterior to and directly

¹The term "subcallosal" is used interchangeably with "septal" to designate that area anterior and dorsal to the anterior commissure. These regions have been shown to be functionally equivalent and to share the fiber systems be-

below the genu of the corpus callosum, yields inhibitory effects upon autonomic and somatomotor activity. These results were in contrast to the facilitatory effects obtained upon stimulation of the area above the corpus callosum, including the anterior cingulate gyrus. The "response inhibition" hypothesis maintains that the anterior cingulate cortex and the septal area exercise facilitatory and inhibitory influences, respectively, over autonomic and somatomotor responsivity. Since stimulation of the anterior cingulate cortex enhances somatomotor activity, it would be expected that damage to this area would impair performance in a situation which requires the animal to actively make a response in order to avoid aversive events. However, it would have no effect in a task requiring inhibition of a response, such as in passive avoidance or punishment. Conversely, lesions in the subcallosal area would be expected to facilitate performance in situations in which inhibition of a response is not required, but impair performance in the passive avoidance situation, where inhibition of a response is required.

McCleary (1961) tested this hypothesis and found that rats with bilateral lesions in the subcallosal area exhibited normal approach to a food dish which had previously been shocked, while subjects with bilateral lesions in the

lieved responsible for mediating the electrophysiological and behavioral effects obtained when either area is stimulated or destroyed.

anterior cingulate cortex were comparable to normals in their avoidance of the dish. The converse effects were demonstrated in a shuttle-box avoidance task: subcallosal animals were either equal or superior to normals in response to the conditioned stimulus, while cingulate animals were either deficient or never did acquire the avoidance response. Thus, McCleary's results tended to support the general hypothesis that the function of the septal area is inhibitory, and that its destruction impairs the animal's ability to suppress responding. Conversely, the function of the anterior cingulate region was indicated as being facilitatory, for when it was destroyed that animal had difficulty in making a required response.

Lesion literature

The major problem present in any attempt to reconcile the two theoretical positions is the lack of analysis of the stimulus situations in which postoperative behavior has been observed. These stimulus conditions have been categorized as either positive or negative, depending upon whether a noxious stimulus such as shock was employed. However, the type of reinforcer used is not an adequate criterion for differentiating between positive and negative reinforcing situations. The condition in which an animal is reinforced by food for the performance of some response cannot, just

by the operation of presenting food, be termed "positive," as opposed to labeling a situation in which a noxious stimulus is employed "negative." The response to any given reinforcing event will depend upon the contingencies upon which that event is dependent, as well as upon the type of reinforcer used. A common factor in the lesion studies will be shown to be increased reactivity to a stimulus event, or to the contingencies with which that event is associated in septal animals, and either no change or decreased reactivity in cingulate animals.

The studies in which shock has been used as a stimulus event have been designed according to the conditioned emotional response technique of Estes and Skinner (1941), the punishment paradigm in which the occurrence of shock is contingent upon the emission of some response of the animal (also termed passive avoidance; Mowrer, 1960), and the active avoidance paradigm according to which the animal must make a response in order to avoid the occurrence of the negative reinforcer.

Brady and Nauta (1953, 1955) and Trafton (1967) showed that animals with lesions in the septal forebrain were deficient in the retention of a "conditioned emotional response" (CER) which was preoperatively learned to a clicker stimulus which was terminated concomitantly with shock to the feet. The CER here consisted of "complete immobility and crouching (freezing)" and was usually accompanied by defecation upon

presentation of the conditioned stimulus. The deficiency in retention of the CER did not appear in control animals with lesions of the cingulate cortex, or in nonoperated control animals.

King (1958) first demonstrated that acquisition of a two-way shuttle-box avoidance response was more rapid in rats sustaining damage to the septal forebrain than it was in normals or in operated control animals. Krieckhaus, Simmons, Thomas, and Kenyon (1964) and Kenyon and Krieckhaus (1965) have replicated this finding and shown in addition that the effect is seen in different strains of rats, hooded as well as albino.

The facilitation of the avoidance response was also shown to be independent of lesion size or amount of spontaneous activity as measured by the number of crossings made in the shuttle-box during the adaptation period prior to the initiation of avoidance training. There was no difference between septal and control animals on the latter measure. McCleary (1961) presented evidence suggesting that the more rapid acquisition of the avoidance response was also present in cats with septal lesions, and Buddington, King, and Roberts (1967) demonstrated this phenomenon in the squirrel monkey.

The findings obtained by McCleary (1961) with regard to septal or cingulate destruction have thus been upheld and extended by subsequent studies. Results obtained by Lubar

(1964) offer further support for the opposing influences exerted by these structures upon behavior. He found that animals with combined lesions of the septal and cingulate areas were less deficient in performance on a passive avoidance task than were animals with lesions in the subcallosal area alone. Peretz (1960) also found that cingulectomized rats were slower than controls in the acquisition of a shuttle-box avoidance response when either shock or oscillation was used as the noxious stimulus.

The results cited thus far can be used to support either major theoretical position. Interpretations may be limited, however, because they are derived primarily from experiments in which a noxious stimulus was employed. Therefore, the results of those studies using a positive reinforcer have provided the criteria for defining the role of the septal forebrain and the cingulate cortex as being involved in emotional or inhibitory functions. The factors operating in these studies are considered to be those primarily involved in response inhibition.

Several designs have been used to investigate the behavioral changes resulting from cingulate or septal damage in animals performing a positively reinforced instrumental response. Performance in various types of mazes has been investigated (Thomas, Moore, Harvey, & Hunt, 1959; Thomas & Slotnick, 1962, 1963; Peretz, 1960; Wolfe, Lubar, & Ison, 1967; Green & Levinthal, 1967); on several types of discrim-

ination tasks (Peretz, 1960; Schwartzbaum, Kellicutt, Spieth, & Thompson, 1964; Zucker, 1965; Schwartzbaum & Donovanick, 1968; Green & Schwartzbaum, 1967); and on several different schedules of reinforcement (Ellen & Powell, 1962a, 1962b; Ellen, Wilson, & Powell, 1964; Harvey & Hunt, 1965; Burkett & Bunnell, 1966; Schwartzbaum & Gay, 1966; Carey, 1967a, 1967b).

Thomas et al. (1959) divided their rats with septal lesions into "irritable" and "nonirritable" groups on the basis of behavior in an open-field test. They demonstrated a relationship between this behavior characteristic and impaired maze performance in a Lashley Type III maze. "Irritable" Ss made twice as many errors as controls; behavior of these subjects included "long periods of intense exploratory sniffing, and periodic bursts of energetic running back and forth in the same alley." These behaviors decreased as training progressed. Septal animals were slower than controls on all time scores except latency of leaving the start box, but showed no difference in number of trials required to reach the acquisition criterion. Thomas and Slotnick (1962, 1963) observed no differences in maze performance between rats with lesions in the cingulate cortex and control animals. Green and Levinthal (1967) used a three-unit multiple U-maze designed to test the "choice" behavior of rats for alternative paths to a goal, each path differing in length and position relative to the goal compartment. Rats with lesions in the

septal forebrain were found to consistently choose the longest, though most continuous, path to the goal. The control animals, however, shifted to another path, which was the shortest but required an "abrupt" motor adjustment at the choice point.

Schwartzbaum et al. (1964) have presented evidence showing that septal lesions markedly increased responding during a discrimination in the presence of the negative stimulus and during extinction, while reinforced responding decreased slightly. However, cingulate lesions, while reducing the rate of reinforced responding on the variable interval schedule, resulted in more rapid extinction and had no effect on responding during the nonreinforced stimulus. A follow-up study investigating the effects of septal lesions on acquisition of a simultaneous brightness discrimination showed an increase in the number of perseverative errors of septals over controls, but no differences in trials to criterion or in number of initial incorrect responses.

More recent data obtained by Zucker (1965), using a Wisconsin General Test Apparatus, showed that cats with septal lesions were deficient on the acquisition and first reversal of a successive object discrimination task, but not on acquisition or reversal of a simultaneous object discrimination task. This worker also reported that the performance deficit was correlated with impairment on a passive avoidance task (avoidance of an electrified food dish) which he used as

a screening device prior to the beginning of the experiment to separate his animals into different subgroups. Schwartzbaum and Donovanick (1968) have presented evidence indicating that rats with the septal area destroyed were impaired only on reversals of a spatial discrimination task. Their acquisition scores on the original task were not affected, nor were original learning or reversals of a brightness discrimination task. Interestingly, septal lesions also blocked acquisition of a spatial alternation task on which subjects were required to alternate responding between two levers on every trial. This task may be considered analogous to reversal of a spatial discrimination task, except that the animal has to reverse his response every trial. The errors on both spatial problems were manifest in perseverative responses, i.e., persistent responses to the previously rewarded lever, and more rapid performance time as judged by time to complete the number of trials constituting a session.

Several studies have investigated the behavioral results of cingulate or septal damage in animals working in a bar-pressing situation for positive reinforcement. Results have indicated that rates and patterns of responding are differentially affected by the lesions, depending upon the schedule used. However, these studies have generally failed to examine the properties of the reinforcement contingencies used to generate the behavior.

Ellen and Powell (1962a) investigated the effects of septal lesions on a multiple fixed-interval and fixed-ratio schedule. Animals with lesions in the gyrus cinguli constituted one of their operated control groups. Their results indicated that the septal animals exhibited a significantly higher rate of responding during the FI contingency but not during the FR. Animals with cingulate lesions were not different from nonoperated controls. The animals with septal lesions showed a transitory loss in temporal discrimination during the FI contingency but a permanent increase in terminal rates prior to the delivery of reinforcement. Ellen and Powell concluded that the hyperexcitability displayed by septal animals depends not only on the lesion but also on the reinforcement contingencies used.

Schwartzbaum and Gay (1966) have replicated this finding in rats responding on a 1-min. FI schedule for reinforcement consisting of an 8 per cent sucrose solution. These investigators found that immediately postoperatively, septal rats more than doubled preoperative baseline rates. The temporal distribution of responses for these rats illustrated an increase in terminal rates prior to the delivery of reinforcement, and a resumption of responding earlier than controls following delivery of reinforcement.

In another study employing a schedule in which an animal is reinforced only for a response separated from the previous response by a predetermined delay interval (DRL),

Ellen et al. (1964) found that animals with septal lesions were impaired in acquisition of the required temporal discrimination. Animals with cortical, hippocampal, or callosal lesions were comparable to normals in their acquisition of the discrimination. Septal animals showed a high and equal likelihood of responding after pauses of up to ten seconds, after which time no impairment in temporal control of responding was evidenced. These findings led the authors to revise their earlier position regarding motivational factors and to emphasize the fact that septal lesions caused a decrement in the animal's ability to withhold a response.

The finding that septal rats are unable to suppress responding during periods when reinforcement is not available on a DRL contingency has also been reported by Burkett and Bunnell (1966) and by Carey (1967a). Carey, using water reinforcement on a DRL 15 sec. schedule, further illustrated that increasing deprivation in a control group of rats did not account for the disruption of DRL performance in septal animals. This latter finding is in contrast with results obtained by Harvey and Hunt (1965), who showed that response rates of septals and controls on a continuous reinforcement schedule or an FI 15 sec. schedule could be equalized by differential prewatering prior to the beginning of the daily session, or by differential deprivation.

Rationale for present analysis of septal function

On the basis of findings discussed thus far, it appears

that a nonreinforcing event affects the ability of a septal animal to withhold a response. Heightened activation or excitability results when the subject is not reinforced for a response which was previously rewarded, or when the animal must learn a response which prevents immediate access to the goal object. This increased reactivity was manifest in both the maze and discrimination studies as persistent responses to the incorrect stimulus (perseverative errors), or as a preference for the most continuous path to a goal (Green and Levinthal, 1967). The increased activation following non-reinforcement was seen in accelerated response rates, or disturbances in the temporal distribution of responses by septal animals who were responding on intermittent schedules of reinforcement. Several studies have indicated that the increase in "vigor" of ongoing behavior may be the unconditioned response to the omission of reinforcement, or to a decrease in the density of reinforcement (Amsel, 1958, 1962; Thompson, 1962; Wagner, 1963; Tacker & Way, 1968; Staddon & Innes, 1966; Ferster, 1958; Pliskoff, 1961, 1963). Notterman and Mintz (1965) have suggested that "the increase in vigor following nonreinforcement...is a biological trait resulting from the process of genetic selection."

Considerable experimental evidence is available that the studies using a positive reinforcer may have contained aversive properties. Several studies have shown that behavior similar to that obtained when shock is used as the

reinforcing agent also results when time-out from, or omission of, positive reinforcement is superimposed upon a positively reinforced instrumental response. Two of these studies demonstrated that subjects would escape from stimuli previously associated with food reinforcement which was no longer available (Adelman & Maatsch, 1956; Wagner, 1963). Several other studies have found that matching-to-sample accuracy can be increased by making time-out contingent upon an incorrect response (Zimmerman & Ferster, 1963). Further evidence of the aversiveness of omission of reward can be derived from Azrin, Hutchinson, and Hake (1966), who reported that when periods of responding for food on a continuous reinforcement schedule were alternated with periods of extinction, pigeons actively attacked another bird, and some even a stuffed model present in the experimental chamber. A study by Nigro (1966) has shown that time-out from positive reinforcement in a concurrent two-lever situation can serve as an effective punisher during the extinction of shock-avoidance responses. McMillan (1967) reported that responding was suppressed in the presence of a stimulus which signalled response-contingent time-out from positive reinforcement.

The present analysis of behavior resulting from destruction of the septal area is thus based upon two assumptions which have received empirical support: (1) that response acceleration is the unconditioned response to omis-

sion of positive reinforcement, and (2) that omission of reward constitutes an aversive event.² The analysis then postulates that destruction of the septal forebrain results in greater sensitivity, or a lowered threshold for reaction to stimulus changes, and to aversive events. The specific behavior which reflects this hypersensitivity will depend upon what the unconditioned response to the stimulus event is in the absence of any contingency, and upon the specific contingencies which control the behavior in a given situation.

Evidence supporting the present analysis

The hypothesis that destruction of the septal forebrain results in greater sensitivity to stimulus changes has received direct support from an experiment conducted by Lints (1965), in which he demonstrated lower "flinch-jump" thresholds to electric shock in septal lesioned rats than in controls. Wetzel, Conner, and Levine (1967) recently demonstrated that septal lesioned rats exhibited a higher probability of fighting (rearing with physical contact by slapping or biting) in response to periodic trains of shock (cf. Ulrich & Azrin, 1962) than operated controls. The fighting response induced by shock persisted beyond the period of heightened emotionality, as rated on the emotionality scale developed

²Both of these findings are further documented in Appendix A.

by King (1958).

Electrophysiological evidence supporting the notion of enhanced reactivity to light stimulation has recently been obtained by Lorens and Brown (1967). These workers showed that stimulation of the septal area attenuated photically evoked cortical potentials, thus suggesting that destruction of this area would potentiate these reactions. Enhanced reactivity to photic stimulation was shown to be a definite factor controlling the behavior of subjects with the septal forebrain destroyed in several experiments reported by Schwartzbaum, Green, Beatty, and Thompson (1967). Their stimulus conditions consisted of light-on CS or light-off CS in the compartment in which S was stationed. In addition to showing that the avoidance performance of septal rats was superior to that of controls regardless of illumination conditions, these workers also demonstrated a high probability of responses which reflected increased light aversion. They offer the presence of this enhanced aversive reaction to light as an explanation of the severe impairment obtained by Rich and Thompson (1965) in retention and relearning of an avoidance response which required the rats to jump up and cling to the walls of the apparatus in response to a bright light-on CS located on the ceiling. This meant approach or full exposure to the aversive light-on CS, which characteristic may have interfered with successful avoidance of the shock. That the impairment was not due to a decrease in the

"conditioned emotional response" to the light was evidenced by the observations of "frequent squeaking, abrupt changes in respiration," and orientations toward the top of the box in response to onset of the light.

A schema for the behavioral analysis of aversive events is presented in Appendix B. In terms of this analysis, the effect of septal lesions may be to enhance the reinforcing value of a stimulus (or class of stimuli). Where several types of stimuli are simultaneously controlling behavior, the final emitted response will depend upon the relative reinforcing value of these stimuli. Thus, studies which showed impaired acquisition of an active avoidance response (Kenyon & Krieckhaus, 1965; Rich & Thompson, 1965; Vanderwolf, 1964; McNew & Thompson, 1966) as opposed to the superior performance of septal animals usually obtained may be due to increased sensitivity to the stimuli present in the situation. Where performance of septal animals has been shown to be superior to that of controls, the increased aversiveness of CS onset and the enhanced positive properties of CS termination are compatible with the response required to escape the noxious CS. Where performance of septal animals is inferior to that of controls, results may be due to the incompatibility of the shock-avoidance response with approach to the noxious CS. For instance, in the Kenyon and Krieckhaus one-way avoidance experiment (1965), two 100-watt bulbs were used to light the apparatus at the junction of the compartments

of their shuttle-box apparatus and the rats would have to approach these in order to cross the barrier, similar to the contingency requirement in the Rich and Thompson study. That the one-way vs. two-way variable is not as important except insofar as aversive characteristics of handling are concerned was shown by Zucker (1965) when he demonstrated superior performance of septal lesioned cats in a one-way task when a buzzer CS was used and handling between trials was eliminated.

The facilitatory effect of increased sensitivity to stimulation is shown also in the studies showing increased resistance to extinction of the avoidance response (LaVaque, 1966) even when it was punished (Zucker & McCleary, 1964; McNew & Thompson, 1966). That is, CS onset in these studies was more aversive than the shock used to punish the response. Other investigators have shown that a punishing shock will suppress responding if it is intense enough (Harvey, Lints, Jacobsen, & Hunt, 1965; Schwartzbaum *et al.*, 1967; Zucker, 1965). The study by Harvey *et al.* (1965) found that performance of the conditioned emotional response was impaired in septals only when low intensity shock was associated with the CS, and suppression would have competed with responding for water reward. They interpreted their results in terms of an increased thirst drive produced by the lesion and proceeded to show that increasing water deprivation of controls also resulted in lack of suppression to the CS. This inter-

pretation encounters difficulties, however, in explaining impaired CER performance where the animal is not also performing a response to obtain positive reinforcement (Brady & Nauta, 1953; Trafton, 1967). The difficulty here is believed due to inability to specify exactly what the "dominant response" in the situation is. Schwartzbaum and Gay (1966) have stated that the high emotionality ratings obtained by their septal subjects "reflect primarily somatic reactivity in the form of startle responses followed by exaggerated movement or freezing responses." Brady and Nauta's (1953) suggestion that the observed impairment in their septal animals may be due to the elicitation of an "unconditioned movement reaction" by the clicker CS, which was "specific to their hypersensitive physiological state," is consonant with the uncertainty in specifying the "most likely" response which will appear in this situation.

Hypothesis and plan of present experiments

The hypothesis for the present experiments regarding behavior of subjects following destruction of the septal forebrain is thus based on three conclusions derived from previous studies: (1) that nonreinforcement is followed by acceleration of ongoing behavior; (2) that nonreinforcement is an aversive event; and (3) that septal animals are hyper-reactive to aversive events. The prediction was then made that septal animals would respond most rapidly when reinforcement for a previously rewarded response was withheld.

In order to observe the expected increase in rate clearly, the DRL schedule of reinforcement is used as a baseline schedule. The contingencies of this schedule require that the subject suppress responding for a predetermined delay interval in order to be reinforced. The DRL schedule normally generates a steady low rate of responding which maximizes predictability of the animal's responding at a given point in time. Prior to this time, probability of responding is near zero, so that rapid response bursts which may occur are readily discernible. Several studies have demonstrated that these bursts are most frequent following nonreinforced bar presses, and that the closer in time the "missed" reinforcement is to the DRL criterion, the greater is the effect (Sidman, 1956; Stamm, 1964; Farmer & Schoenfeld, 1964). Therefore, according to the experimental procedure, after response rates stabilize, a reinforcement (food pellet) will be periodically omitted when it is "due," i.e., when the animal responds after the appropriate delay interval. It is predicted that response bursts following this event will be most rapid and frequent for septal animals.

It is further postulated that response rates for cingulate lesioned animals will not change or will decrease following the nonreinforcing event, if it is true that the anterior cingulate gyrus and the septal region exert opposing influences upon behavior. This prediction is based upon findings by Schwartzbaum et al. (1964), who showed that rats

with anterior cingulate lesions extinguished a food-reinforced response more rapidly than controls. Stamm (1964) has also shown decreased excitability in cingulate lesioned animals, as evidenced in fewer interresponse-times-less-than-two-seconds than controls when the DRL schedule on which the subjects (monkeys) were working was lengthened by sixty seconds.

Experiment 1

Introduction

Animals in the first experiment were tested on a DRL 8 sec. schedule of reinforcement. Pilot work had shown that animals with lesions in the septal forebrain could acquire and maintain normal timing behavior if the delay interval was of a low value. It was thus believed that the relative frequency of reinforcements obtained by septal animals would be equal to that of normals, so that any change in baseline rates which occurred as a result of the nonreinforcement procedure would be comparable between the groups. The pilot studies had further indicated that the relative frequency of reinforcement obtained on the baseline schedule was an important variable determining the degree of disruption in timing behavior when the nonreinforcement procedure was introduced.

Method

Subjects

Fifteen male albino rats of the Sprague-Dawley strain, approximately 180 days old at the beginning of the experiment, were housed in individual cages and were allowed ad lib food and water for three weeks, during which time daily weights were recorded. At the end of this time, mean body

weights were calculated and the Ss were placed on a restricted diet consisting of two Purina Lab Chow pellets, totaling approximately 7 gm., given daily until the Ss were reduced to 85 per cent of their free-feeding weights. This weight was maintained throughout the course of the experiment by supplementing daily food intake received in the experimental chamber with Purina pellets following each session. Water was continuously available in the home cage.

Apparatus

The experiment was conducted in a Scientific Prototype single-lever operant conditioning apparatus (Model A-101) with a food cup located $1\frac{1}{2}$ in. to the left and slightly below the lever, and an opening through which a calibrated water tube could be inserted located about 2 in. to the right of the lever. A force of 27 gm. was required to close the microswitch in the lever. A single light bulb behind a diffusing milk glass was located 4 in. directly above the lever. The brightness of the glass, measured with an Ilford photometer, was 2.0 log ft. lamberts. The apparatus was located in a Scientific Prototype sound-proof chamber (Model SPC-300).

Programing of reinforcement contingencies and recording of experimental data were accomplished using BRS solid state modules. Thirty-two counters were used to record time between successive responses, and a running time meter was used to record total session time required for each rat to obtain a predetermined number of reinforcements (.045 gm. Noyes pellets). Other counters recorded total responses made and

total reinforcements obtained during the session.

Procedure

Prior to surgery, all subjects were magazine-trained and shaped to press the lever for food reinforcement. Following acquisition of the bar-press, on two successive days, all Ss were placed into the experimental chamber and allowed to obtain 100 reinforcements on a continuous reinforcement schedule.

Subjects were then randomly assigned to three groups of five rats each for surgery. Operated Ss underwent surgery under pentobarbital sodium anesthesia supplemented with chloral hydrate. Ss in the septal group were given bilateral lesions in the septal forebrain. These were produced electrolytically by 2.0 ma. anodal current applied for 30 sec. through a stereotactically guided stainless steel electrode, insulated except for 0.5 mm. at the tip. The ear bar of the stereotaxic instrument was used as the indifferent electrode. The lesions for this group were placed according to Groot (1959) coordinates 1.9 mm. in front of bregma, 0.5 mm. lateral to the sagittal suture, and 5.0 mm. below the surface of the skull at this point.

Subjects in the cingulate group received a series of closely spaced electrolytic lesions along the midline cortex extending from 3.5 mm. in front of bregma to 1.3 mm. posterior to bregma. A strip of skull was removed on either side

of the sagittal suture and the electrode was inserted at one location; a lesion was then made at two or three successive depths, depending on the vertical extent of the cortex at that A-P location. This procedure was repeated at 1.5 mm. intervals along the anterior-posterior extent of the lesion site until a continuous ablation of the midline cortex on both sides of the sagittal suture was complete. Two ma. was applied through the electrode for 20 sec. at each lesion site (technique after Slotnick, personal communication).

The third group was designated as the control group and consisted of two rats receiving sham operations and three unoperated controls. The sham operations included drilling of the skull and insertion of the electrode into the brain for the septal animal according to the appropriate coordinates without passage of current, and removal of the strips of skull for the cingulate operated control.

Following recovery from surgery and during the course of training, a pneumonia epidemic caused the death of three subjects, two of the cingulate operated animals and one of the normal controls. The final n's for each of the groups was thus as follows: septal, $n = 5$; cingulate, $n = 3$; control, $n = 4$.

Behavioral testing procedure

DRL acquisition.--One week after completion of surgery, all animals were placed on a DRL 8 sec. schedule of reinforcement. This meant that a minimum interval of 8 sec. had

to elapse between successive bar-presses in order for reinforcement to be obtained. If an animal pressed the bar before completion of the interval, the clock was reset and timing of the interval was re-started. During this phase of DRL acquisition, the number of reinforcements obtained during each daily session was kept constant for all animals, and was gradually increased over sessions until a maximum of 160 reinforcements per session was being obtained. This procedure insured that each animal received a constant number of reinforcements throughout the course of the experiment. Session length was thus determined by the time it took for the S to obtain the number of reinforcements available for a given session.

There were six daily sessions per week for forty days. A calibrated water bottle was present in the experimental cage at all times during the session. Animals were run under conditions of no illumination in the experimental chamber, the only possible source being stray light entering through the vent for the blower located in the sound-proofed chamber in which the operant conditioning apparatus was housed. This condition of minimizing illumination was designed to maximize visibility of the light located over the bar when it was illuminated. During the acquisition phase, this light was automatically turned on at random times for 1 sec. during specified sessions according to a 0.2 probability in order to allow adaptation to occur.

Nonreinforcement procedure.--On the forty-first session, a new procedure was introduced whereby 20 per cent of the programmed reinforcements were withheld following a correct timing response. Omission of reinforcement was accomplished by a random probability generator which inactivated the feeder 20 per cent of the time that the animal allowed the DRL interval to elapse. This nonreinforced correct response was accompanied by two additional stimulus events: (1) the click from a second feeder mechanism, and (2) a light over the bar to which the subjects had previously been adapted.

Recording apparatus was arranged so that time between successive responses was recorded independently for those responses following a correct timing response which was reinforced and for those responses following a correct timing response which was not reinforced. Thus, separate and independent interresponse time distributions were obtained following normal reinforcement conditions, and following programmed omission of reinforcement. The size of the interresponse time class interval was 1 sec., except for the first eight sessions of acquisition, when it was 0.8 sec.

The "nonreinforcement procedure" was instituted on alternate days for a period of eight days. On alternate days, 20 per cent of the animal's correct timing responses were not reinforced, and interresponse times following this event were recorded in one bank of sixteen counters until the animal allowed another DRL interval to elapse. At this time,

if this response was reinforced, another set of counters was activated, and remained so until another reinforcement was withheld. The alternate day procedure was used to allow assessment of baseline changes in DRL timing behavior, and assure that any disruption in behavior which might occur following the nonreinforcement procedure was specific to this experimental operation and was not a general disturbance of DRL timing behavior.

Stability of performance: nonreinforcement procedure-- successive days.--The regular DRL 8 sec. schedule was reinstated following the nonreinforcement sessions for a total of twenty-one sessions. Following re-stabilization on this schedule, the nonreinforcement contingency was again introduced, this time on successive days, for a total of fourteen sessions. The purpose of this procedure was to assess possible habituation effects to the nonreinforcement contingency.

Nonreinforcement procedure--alternate days.--The procedure for the final phase of this experiment involved systematic variation of the probability of withheld reinforcement on alternate days for a period of eight days each. The probability of nonreinforcement was 0.5 on alternate days during the first eight-day period, 0.8 during the second, and 1.0 during the third. The parametric variation in the probability of withheld reinforcement was introduced in order to determine if there would be systematic changes in behavior

following this event for the different groups.

In order to determine if the light which had been paired with the "nonreinforced-but-correct response" had acquired any stimulus control over behavior, it was omitted following a response during the two days of extinction, and differences in responding during "light" and "no light" days were examined. A summary of the procedures followed is presented in Table 1.

Following completion of behavioral testing, all animals were sacrificed by perfusion with saline and 10 per cent formalin solution. The brains were removed and placed in formalin for approximately one week, after which time they were cut by the frozen section technique in 48μ . sections in the frontal plane. Every fifth section was stained with cresyl violet. These were examined with a projection microscope and reconstructions were drawn showing exact limits of the lesions.

Results

Anatomical results

Histological analysis of the brains of rats with septal lesions showed two patterns of septal damage, distinguishable on the basis of the posterior extent of the lesions. Reconstruction of the maximum and minimum lesions is shown in Figure 1. All of the septal lesioned brains showed extensive destruction of the subcallosal area, including the medial

Table 1

Summary of Procedures Followed in Experiment 1

<u>Procedure</u>	<u>Contingency</u>	<u>Stimulus Conditions</u>	<u>No. of Sessions</u>
1. DRL Acquisition	All IRTs > 8 sec. reinforced	No illumination	40
2. Nonreinforcement procedure	20% IRTs > 8 sec. not reinforced on alternate days	Magazine click, light over bar with nonreinforced IRT > 8 sec.	8
3. Stable DRL 8 sec. performance;	All IRTs > 8 sec. reinforced	No illumination	21
Nonreinforcement procedure	20% IRTs > 8 sec. not reinforced, successive days	Magazine click, light over bar with nonreinforced IRT > 8 sec.	14
4. Nonreinforcement procedure	50% IRTs > 8 sec. not reinforced, alternate days	Same as above	8
Nonreinforcement procedure	80% IRTs > 8 sec. not reinforced, alternate days	Same as above	8
Nonreinforcement procedure	100% IRTs > 8 sec. not reinforced, alternate days (extinction)	Same as above, Sessions 4 and 8; no light, Sessions 2 and 6	8

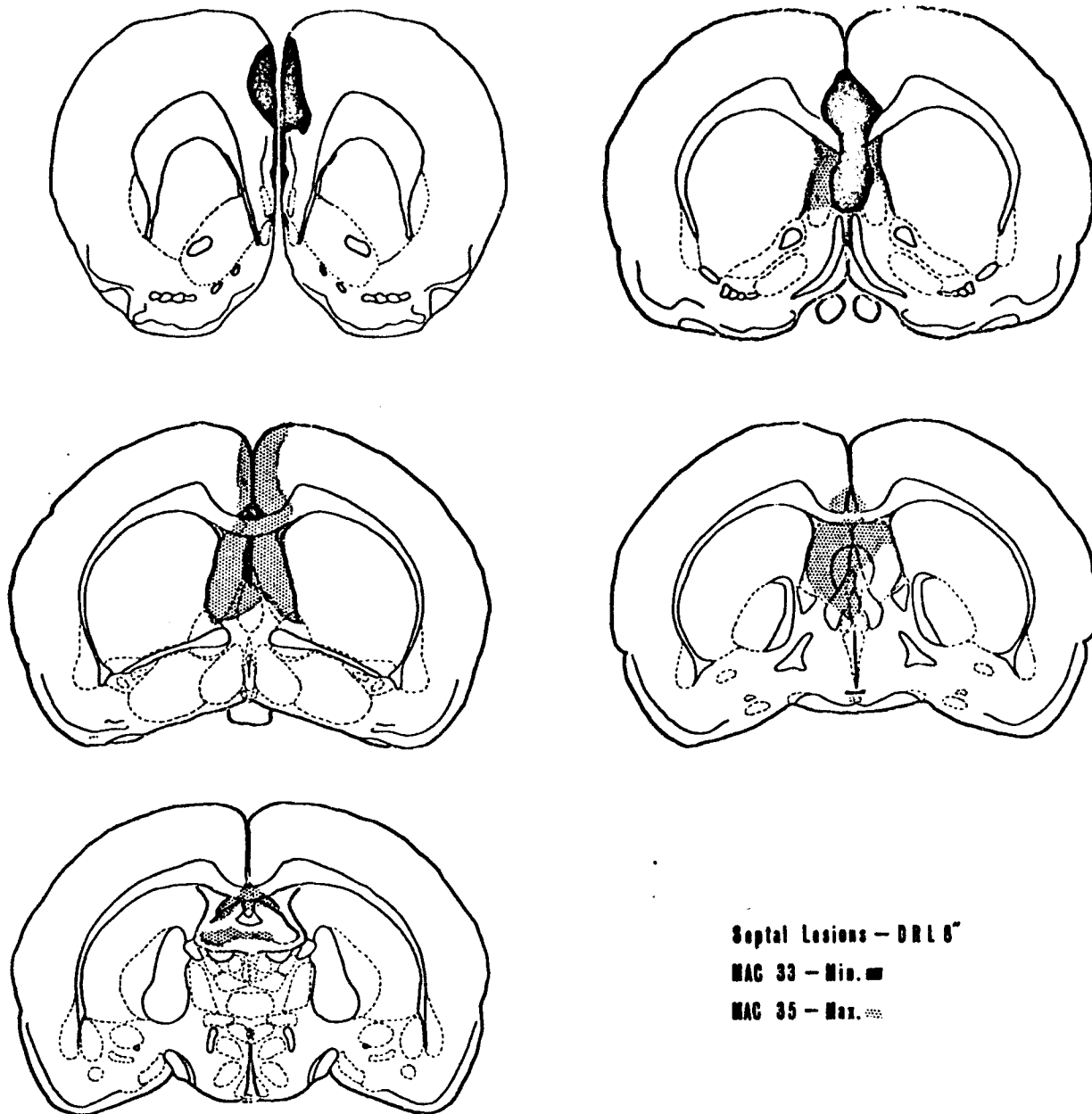
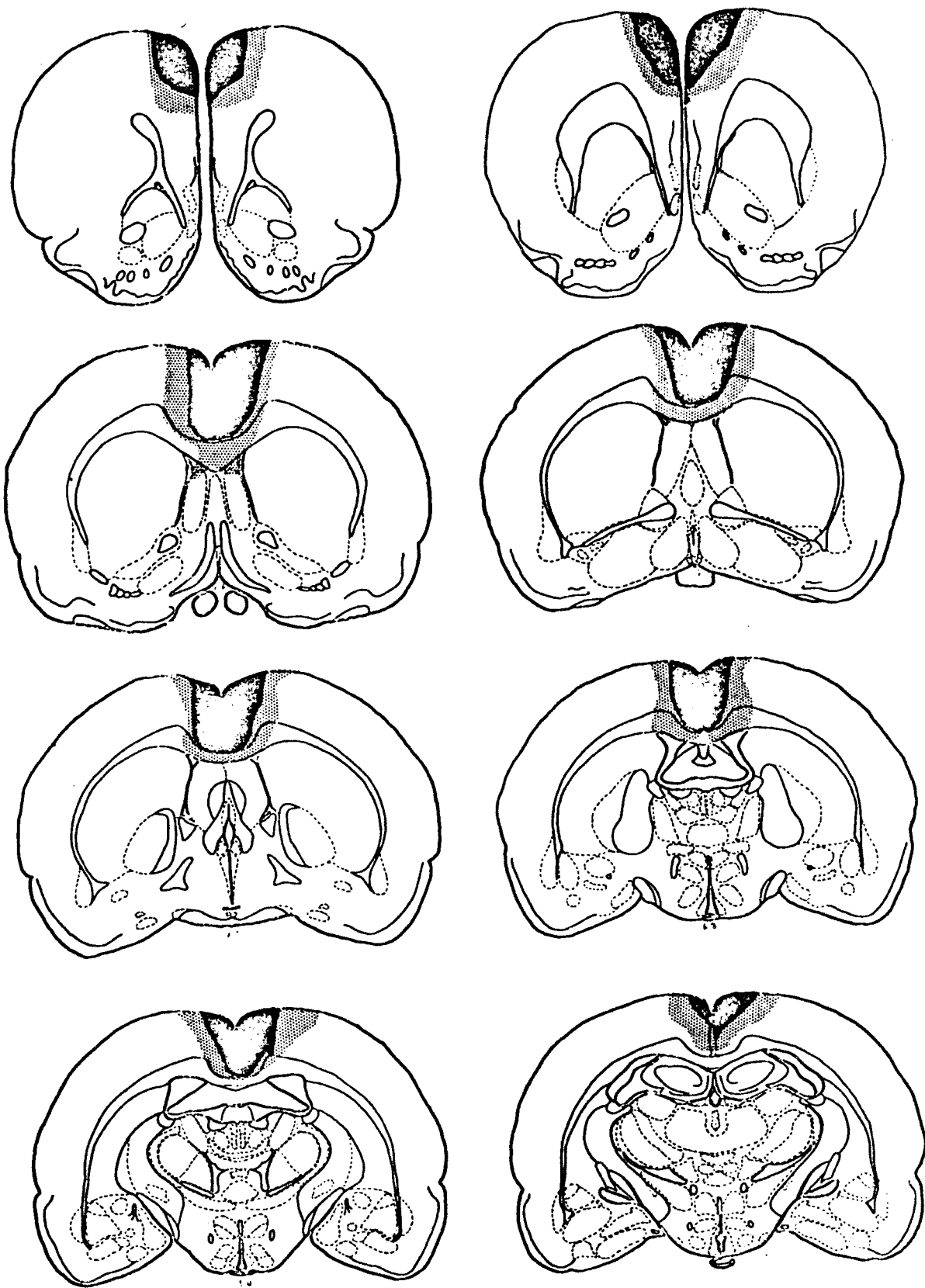


Figure 1.--Reconstruction of septal lesions in the DRL 8 sec. group. Area of maximal damage is stippled and minimum is indicated by solid black.

septal nuclei, most if not all of the lateral septal nuclei, a small portion of the anterior hippocampus, the medial olfactory tract, the olfactory hypothalamic tract, the nucleus and tract of the diagonal band of Broca, and the septohypothalamic tract. All brains also sustained some damage to the anterior part of the superior fornix, the corpus callosum, and the cingulate cortex in the immediate vicinity of the electrode site. The lesion for MAC 33 was the only one which deviated from this general pattern. Damage here was restricted to the midline, destroying most of the medial septal nuclei and medial portions of the lateral septal nuclei. The lesions for MAC 35 and 37 extended far enough posteriorly to include damage bilaterally to the fornix and fornix columns, the septal nucleus triangularis, the precommissural stria terminalis, and the septohabenular and corticohabenular tracts.

The anterior-posterior extent of the cingulate lesions was fairly constant for all animals. The main difference was in the lateral and vertical extent of the lesions. Reconstruction of these lesions is shown in Figure 2. Cingulate damage included bilateral destruction of the posterior portion of cortical area 24, area 23, and the dorsal region of pregenual area 32, as described for the rat by Krieg (1946). Areas 10, 6, and 4 in the immediate vicinity of cingulate areas 23 and 24 sustained at least minimal damage, being most extensive for MAC 45. Slight gliosis was noted in the anteroventral and anteromedial thalamic nuclei. Differences in be-



Cingulate Lesions - DRL 8⁺
 MAC 43 - Min. mm
 MAC 45 - Max. mm

Figure 2.--Reconstruction of cingulate lesions in the DRL 8 sec. group.

havior as a result of lesion variability are noted in Appendix C.

Behavioral data

The cumulative records in Figure 3 show the changes in response rate which occurred during acquisition and the non-reinforcement phases of the experiment. When response rates had stabilized at the end of acquisition, the septal animals were responding slightly more rapidly than either the cingulate or control animals. These differences in rates increased as reinforcements were periodically withheld according to the specified probability following a correct timing response.

Figure 4 shows that at the beginning of acquisition, all of the groups demonstrated poor timing behavior, as gauged by the relative number of responses which were reinforced. This ratio, or per cent efficiency, is a measure of the animal's accuracy in spacing his responses to meet the DRL requirement. It is defined as the

$$\frac{\text{frequency of interresponse times} > 8 \text{ sec.}}{\text{total number of interresponse times}} \times 100.$$

During acquisition, all responses greater than 8 sec. were reinforced.

A Kruskal-Wallis analysis of variance between groups indicated no significant differences in efficiency ratios during the first six sessions ($H = .321$, $p > .10$). Performance improved for all three groups as training proceeded

Figure 3.--Cumulative records for one S from each operated group for the first and last sessions during acquisition on DRL 8 sec., and for the first day of each p(SR) contingency. Reinforcements are indicated by vertical deflection of response pen and reinforcement omissions are indicated by vertical deflection of event pen. Duration of nonreinforcement indicated by time event pen is deflected.

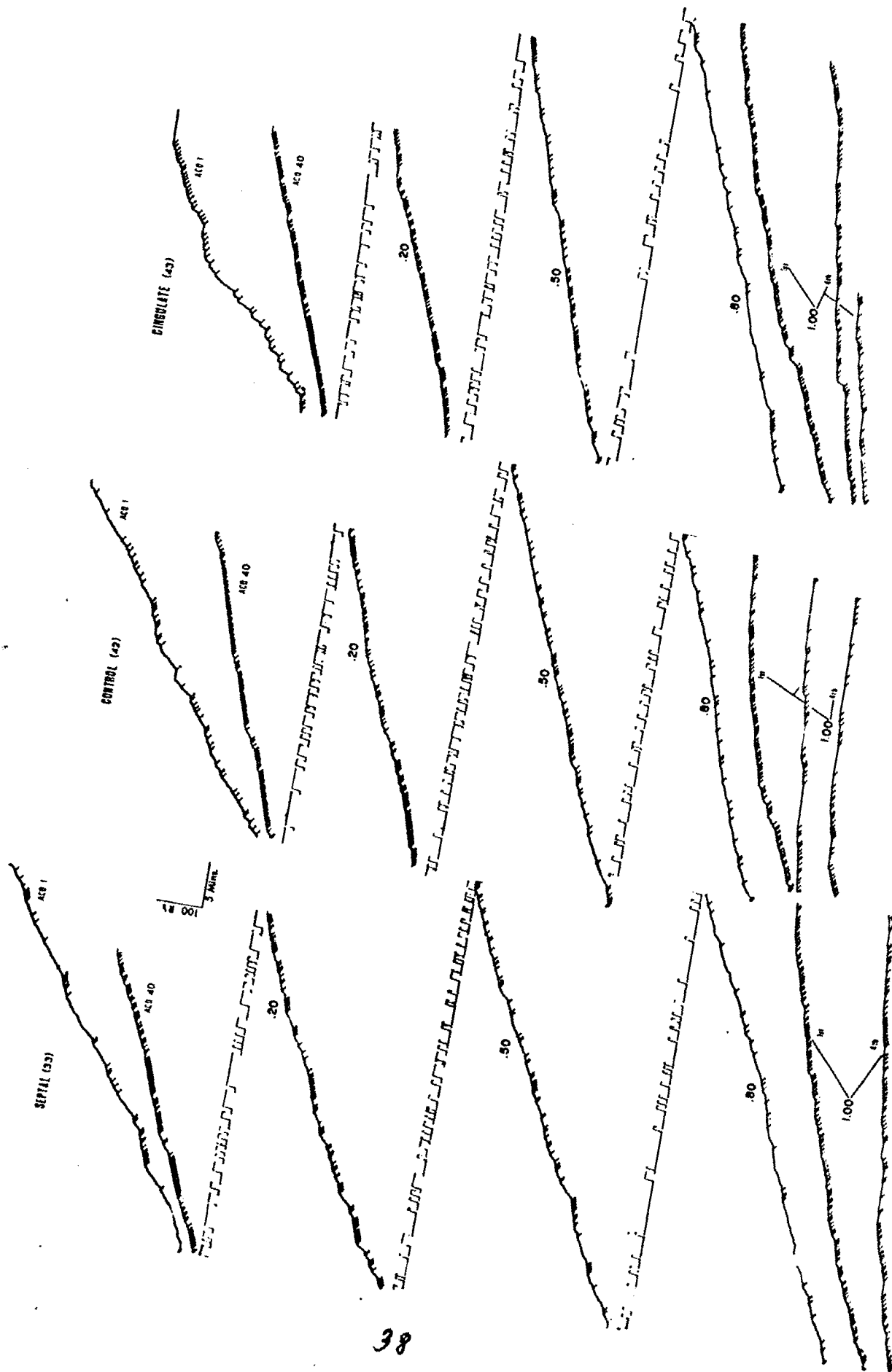
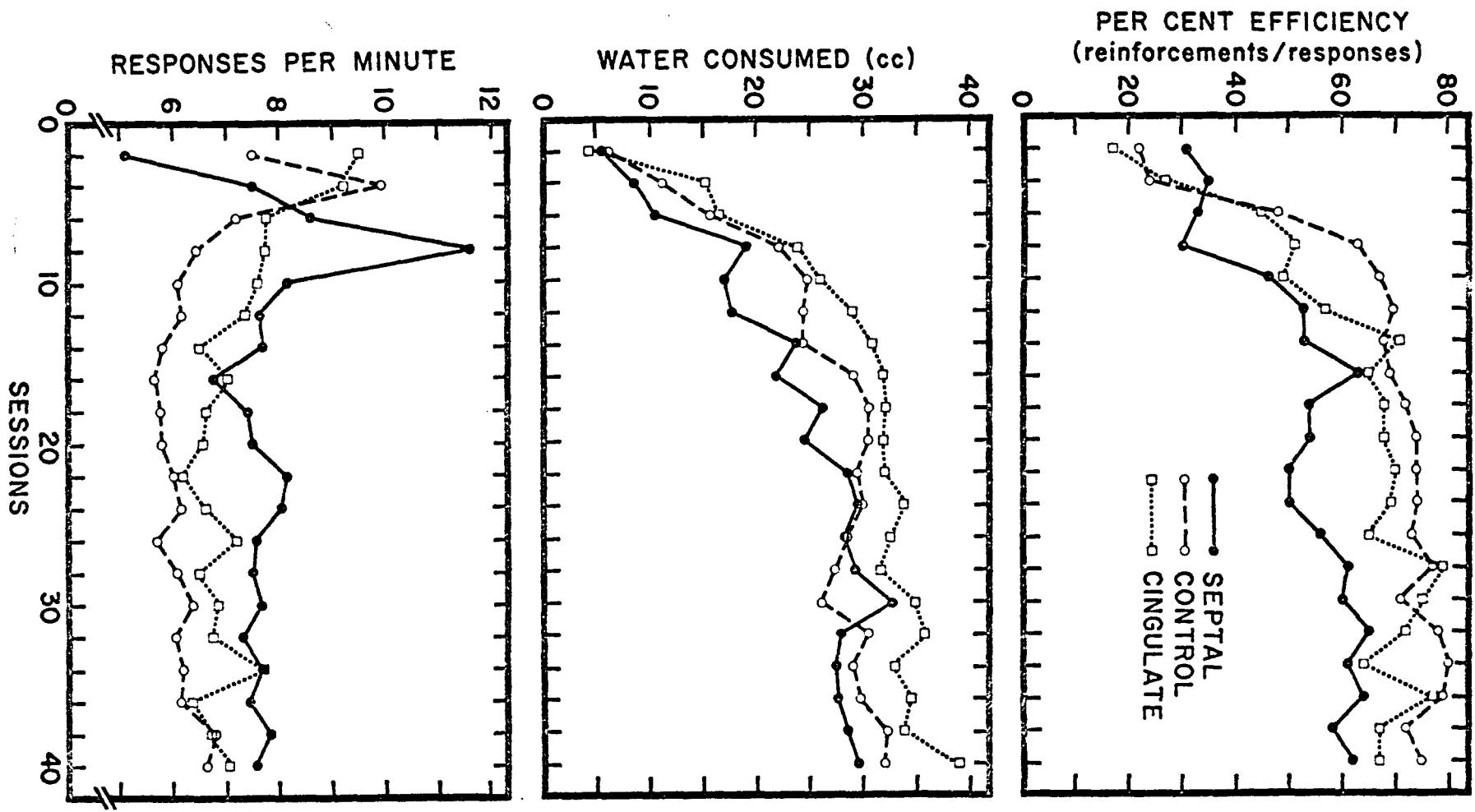


Figure 4.--Per cent efficiency, water consumed, and rates during acquisition on DRL 8 sec. for each operated group. Each data point is the mean of two successive daily sessions.



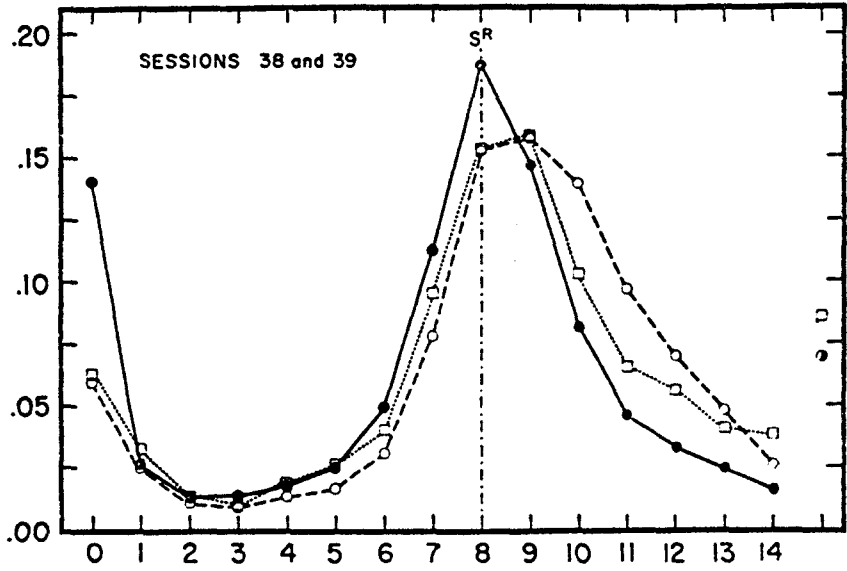
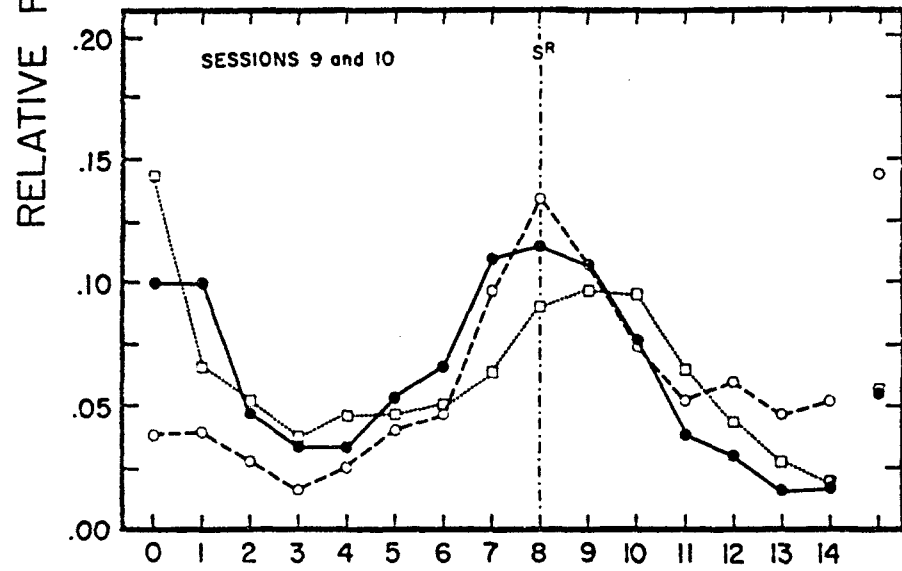
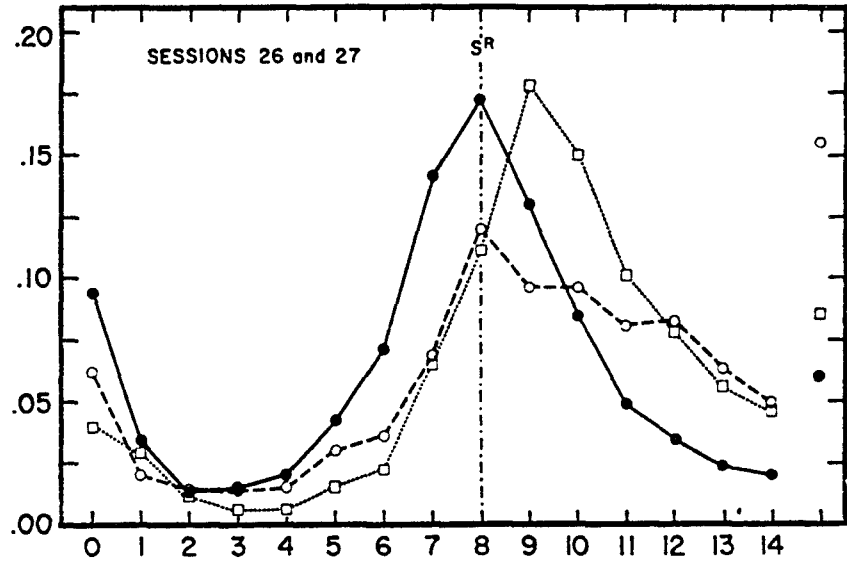
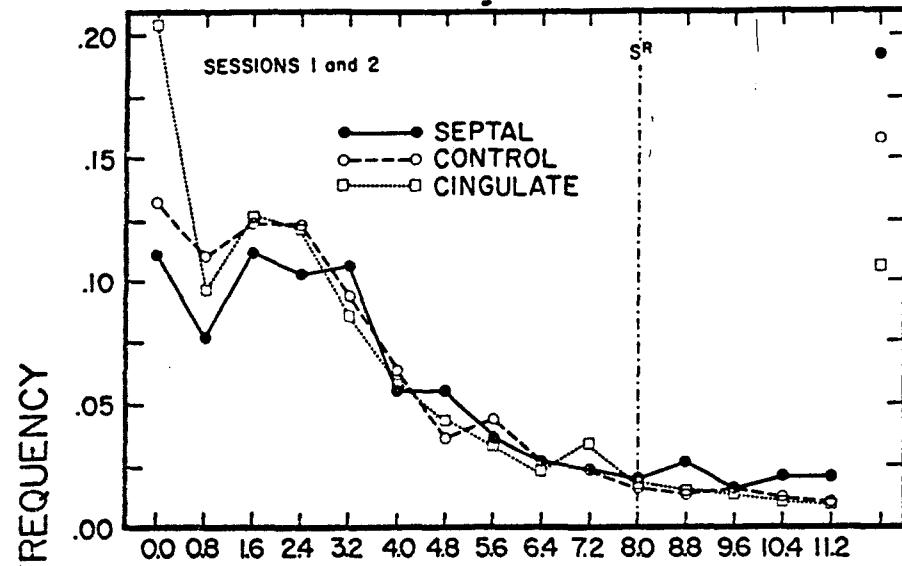
until, by Session 40, the animals demonstrated a fairly stable rate of reinforcement. The efficiency ratios for the three groups were found to be significantly different during the last six sessions of acquisition ($\underline{H} = 13.2, p < .01$).

Figure 4 also shows that the amount of water consumed during a session was approximately equal for all three groups at the beginning of acquisition ($\underline{H} = .729, p > .10$), and increased differentially as efficiency improved. During the last six sessions, this difference was significant ($\underline{H} = 8.96, p < .01$) with the cingulates drinking the most, and septals the least. The finding that timing efficiency seems to be directly related to amount of water consumed is supported by several studies which have demonstrated that if a water bottle is present, animals on a temporal schedule for food will begin to drink between bar presses, therefore supposedly "mediating" the time interval between reinforced responses (Segal & Holloway, 1963; Falk, 1966). Further, if the mediating behavior is prevented after responding has stabilized, timing behavior is completely disrupted (Laties, Weiss, Clark, & Reynolds, 1965).

Differences in response rates during acquisition are more clearly shown in Figure 5, which illustrates how the subjects distributed their responses in time. Each data point represents the relative frequency of responses which were separated by a given interval of time, or, how often the animal waited a certain amount of time before responding

Figure 5.--IRT distributions for each group during acquisition on DRL 8 sec. Class interval size for Sessions 1 and 2 equals 0.8 sec., and for Session 9 and all following equals 1.0 sec. The lower bound of these class intervals is plotted on the abscissa.

6h



INTER-RESPONSE-TIME CLASSES (sec)

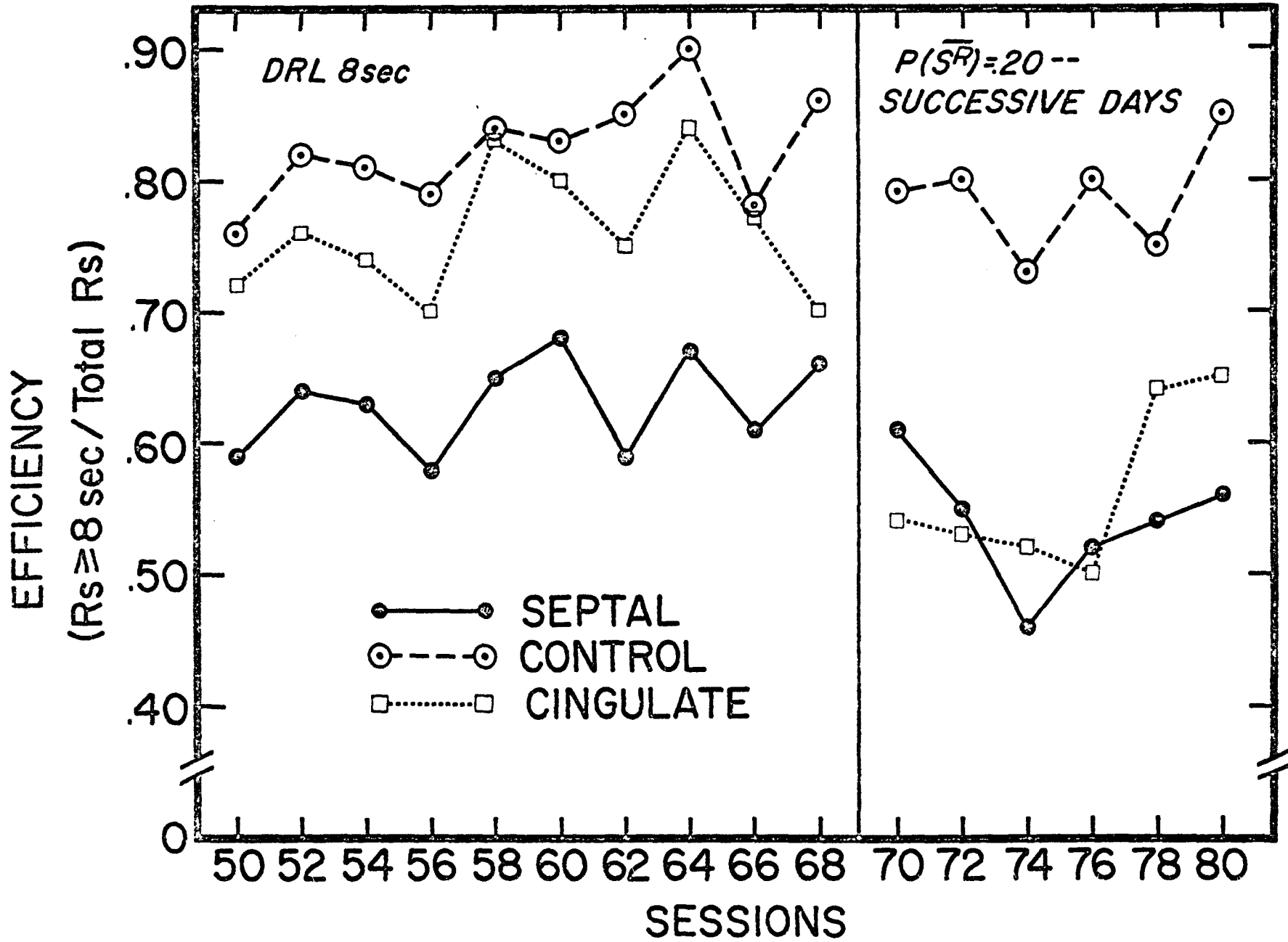
again. These are commonly designated as interresponse time (IRT) distributions.

The improvement in timing behavior which occurred for all groups is shown in Figure 5 as the development of a modal IRT at or around the minimum interval required for reinforcement. There was also a covariation in the frequency of very short IRTs. For the cingulate and control animals, as more responses were made at the appropriate time interval (8 sec.), the frequency of very short IRTs decreased. The frequency of rapid responses increased for the septal animals as timing behavior improved. The major difference in the response patterns between the groups by the end of acquisition was in the frequency of rapid responses, the cingulates and controls being about equal and low, and the septals exhibiting a high frequency of responses separated by no more than 1 sec.

Figure 6 shows that continued training on DRL 8 sec. beyond the first fifty days resulted in only slight improvement in timing behavior for any of the groups. The difference in efficiency among the groups seen at the end of acquisition remained approximately the same. When the nonreinforcement contingency was introduced on successive days (Figure 6), there was an initial decrease in efficiency of timing behavior for all groups. The timing behavior of control subjects gradually improved with exposure to this procedure until their previous efficiency level was recovered. The cingulates also showed a gradual recovery, but not to their

Figure 6.--Per cent efficiency for each operated group on DRL 8 sec. during continued DRL 8 sec. training and the successive daily sessions when the probability of nonreinforcement = 0.2. Each data point is the mean of two successive daily sessions.

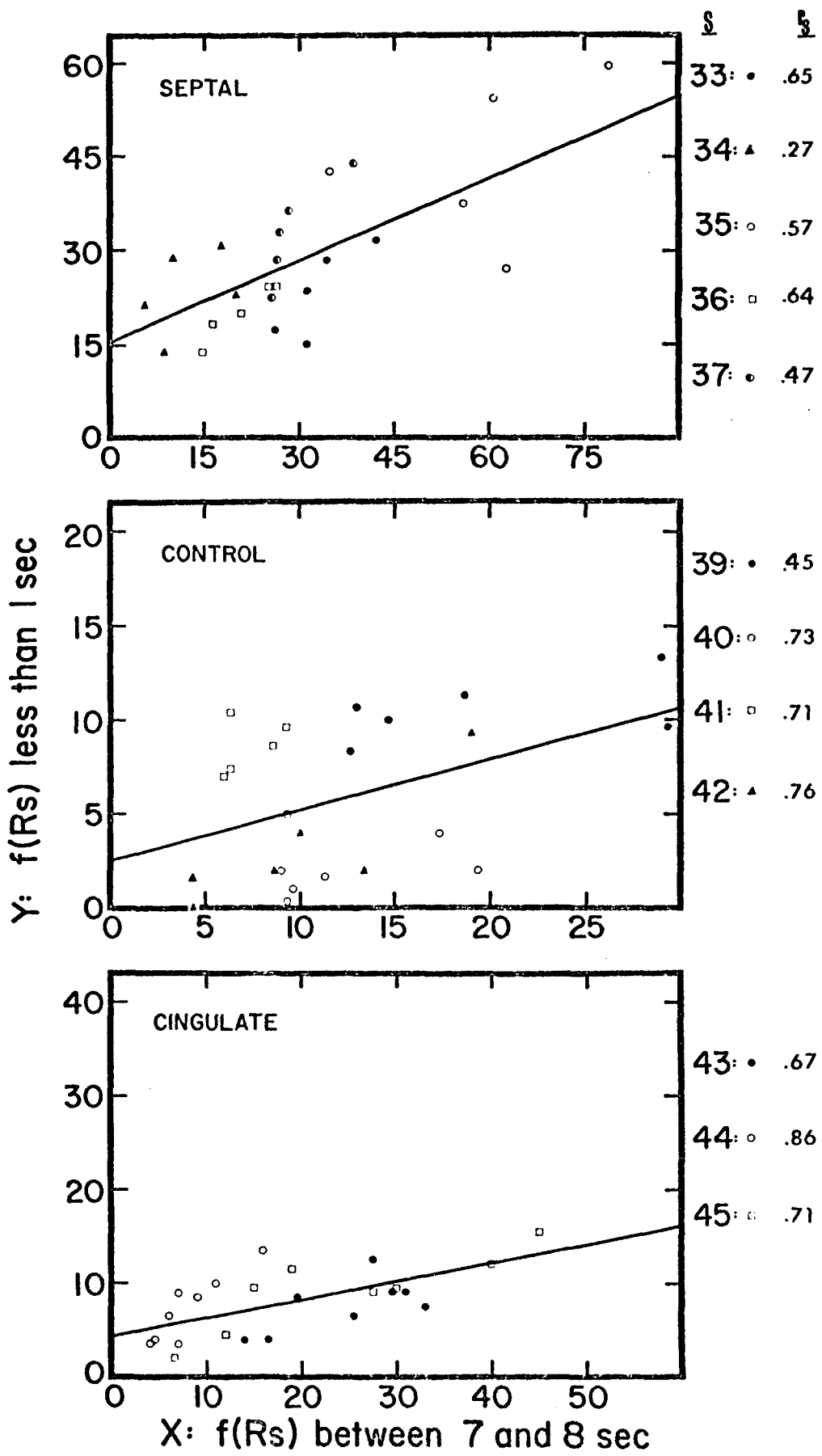
9h



previous level. The septals demonstrated the least adaptation to this procedure although some return toward baseline performance is indicated.

The IRT distributions during the period of continued DRL 8 sec. training were found to be essentially the same as those obtained for the last two sessions of acquisition, i.e., demonstrating a very high frequency of rapid responses (IRTs less than 1 sec.) for the septal animals with a low frequency of short IRTs for both of the other two groups. It has been noted in the literature that these rapid response bursts often follow a long IRT which falls short of the interval required for reinforcement (Sidman, 1956; Stamm, 1964; Ferraro, Schoenfeld, & Snapper, 1965). Correlation diagrams were therefore constructed to determine if the frequency of short IRTs could be related to the frequency of IRTs which were nearly but not quite long enough to be reinforced. Three scatter diagrams are shown in Figure 7 which illustrate the relation between frequency of responses less than 1 sec. (y-axis) and responses emitted between 7 and 8 sec. ("just-missed" responses, x-axis) for each operated group during the period of continued training on DRL 8 sec. Each data point is the frequency of responses in these two time intervals averaged over every two (cingulate) or every three (septal and control) sessions for individual animals. A line of best fit was then calculated and plotted by the method of least squares for each of the scattergrams according to the equation, $X' = r \frac{S_x}{S_y} (Y - M_y) + M_x$ (Guilford, 1956), using the rank

Figure 7.--Correlation diagrams showing the relation between the frequency of responses less than 1 sec. and responses emitted between 7 and 8 sec. for each operated group during the period of continued training on DRL 8 sec. Each data point is the average of every two (cingulate) or every three (septal and control) sessions for individual animals. Individual rank-difference correlations for all sessions during this period are listed in the right-hand margin for each S. The symbol in the center column corresponds to the symbol used for that S in the diagrams.



difference correlation coefficient. (The use of this non-parametric statistic was dictated by the nature of the data.) These coefficients are presented in Table 2, together with the Pearson r 's for comparison purposes.

The correlation coefficients for the three groups were as follows: septals, $r_s = .66$; controls, $r_s = .44$; cingulates, $r_s = .65$. All of these values were significant ($p < .05$). From the regression lines plotted in Figure 7, and from inspection of the scatter of points for individual subjects, it can be seen that the correspondence between these response class frequencies varies depending upon what group the animal is in. For septal animals, sessions with a high frequency of rapid response bursts were accompanied by a high frequency of responses emitted just prior to the criterion delay. Although sequential data were not obtained in the present study, periodic observation of daily response patterns suggested that responses emitted just prior to the criterion delay would be followed by a series of rapid responses, and that the latter event would be followed by an IRT greater than 7 sec. A study by Ferraro et al. (1965) supports these observations.³ One of

³These workers have shown the existence of very definite sequential dependencies between IRTs generated by the DRL schedule. They demonstrated that the further the mode of the IRT distribution was below the criterion delay, the higher the frequency of very short IRTs. Their results showed a high similarity between successive IRTs; that is, that subjects tend to repeat the behavior just emitted, unless the responses are separated by very short time intervals.

Table 2

Values of Chi-Square and Correlation Coefficients
 Showing the Relation and Degree of Association
 between the Frequency of Responses Less Than
 1 Sec. and the Frequency of Responses
 between 7 and 8 Sec.

<u>Group</u>	<u>Chi-Square</u>	<u>r_s</u>	<u>r_p</u>	<u>N</u>
Septals	168.50*	.66**	.74**	25
Controls	44.34**	.44***	.47***	24
Cingulates	31.64	.65**	.64**	24

*p < .001
 **p < .01
 ***p < .05

their results indicated that responses which are separated by very short time intervals are most likely preceded by a nonreinforced IRT which is close to the criterion delay for reinforcement, and is most likely followed by a criterion IRT. In the case of the septal animals in the present study, the high frequency of IRTs which just miss being reinforced and the high frequency of very short IRTs indicates that the most probable event following a short IRT is a near-criterion response rather than one which does meet the DRL requirement. The lower frequency of these response classes for the control and cingulate animals, however, indicates that the long IRT which succeeds a series of rapid responses is more likely to be a criterion IRT.

The rank difference correlations for individual animals between just-missed and very short IRTs for eighteen days during continued DRL training are listed in the right-hand column of Figure 7. All but one of these correlations are high and significantly different from zero (Table L in Guilford, 1956). Therefore, the accuracy of prediction of either one of the response frequencies on the basis of the other is fairly good for any given animal. The degree of variability of individual animals about the regression line reflects differential predictability of these IRT classes on the basis of what group the animal is in. Control animals show greatest variability about the regression line, so that accuracy of prediction for either one of the variables is reduced.

For cingulate animals, there is a high probability that if there are responses which just miss being reinforced, there will be a low frequency of rapid responses. Septal animals will exhibit a high frequency of both response classes.

Figure 8 shows the changes in accuracy of timing behavior which occurred when the nonreinforcement procedure was introduced according to the different probabilities, and Figure 9 shows the concomitant changes in response rates. The solid line functions in each figure show the performance when the probability of nonreinforcement was zero, i.e., on the days when the regular DRL contingency was in effect and all of the animal's responses after IRTs of 8 sec. or more were reinforced. The dashed line functions indicate the changes in efficiency or rate when IRTs greater than 8 sec. were not reinforced 20, 50, 80, or 100 per cent of the time on alternate days.

It can be seen here that reducing the probability of reinforcement for a correct timing response did not have any great effect on normal DRL responding. All of the groups' performance demonstrated fairly constant efficiency and rates on days when regular DRL reinforcement conditions were in effect. It can also be noted that the overall timing efficiency for the septal animals is still about 20 per cent below that of the other groups, with their response rates being correspondingly higher.

PER CENT EFFICIENCY

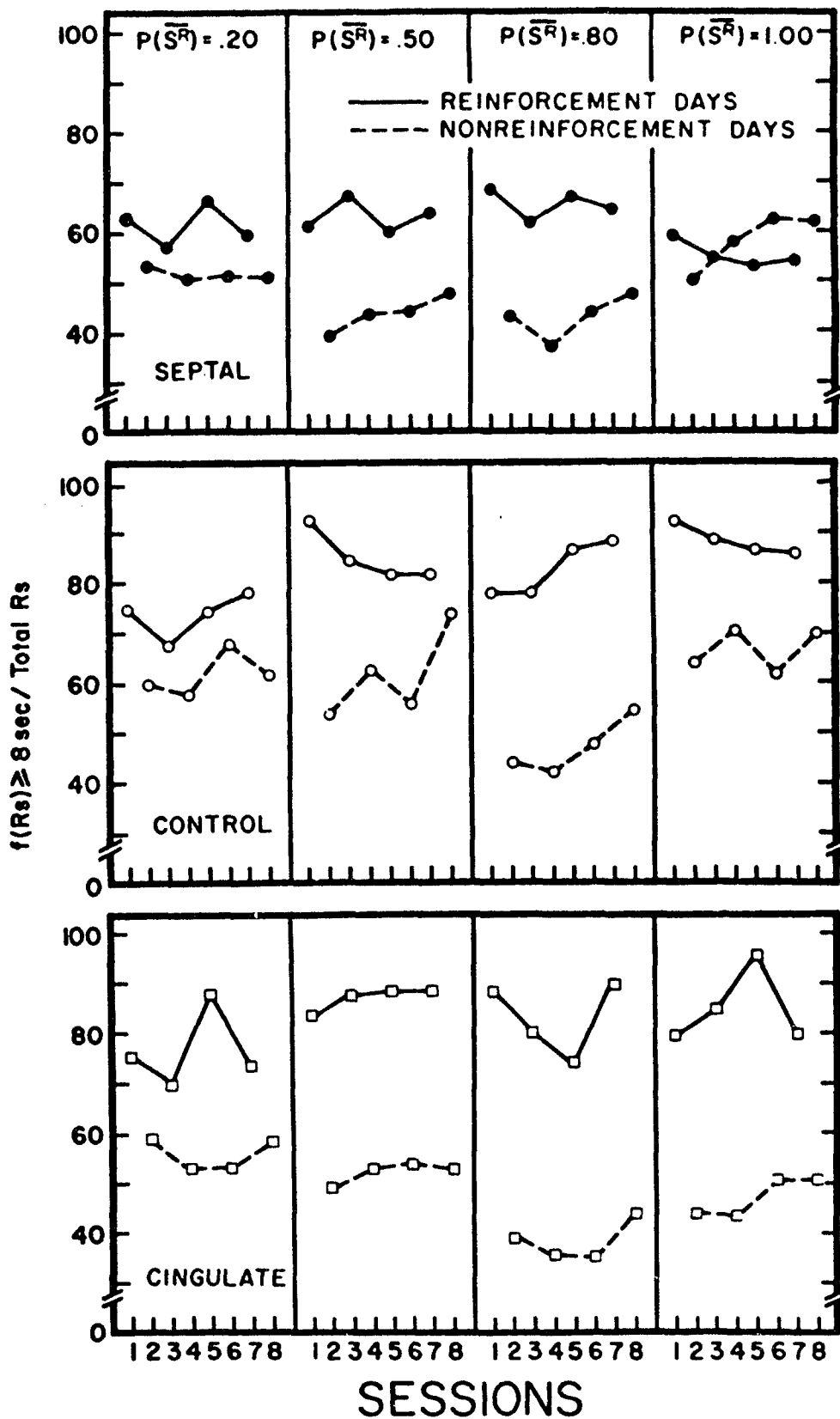
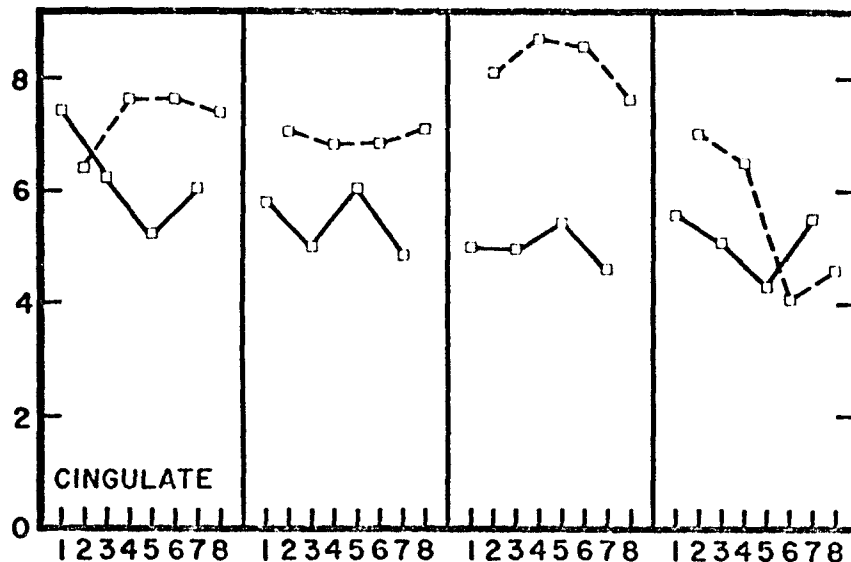
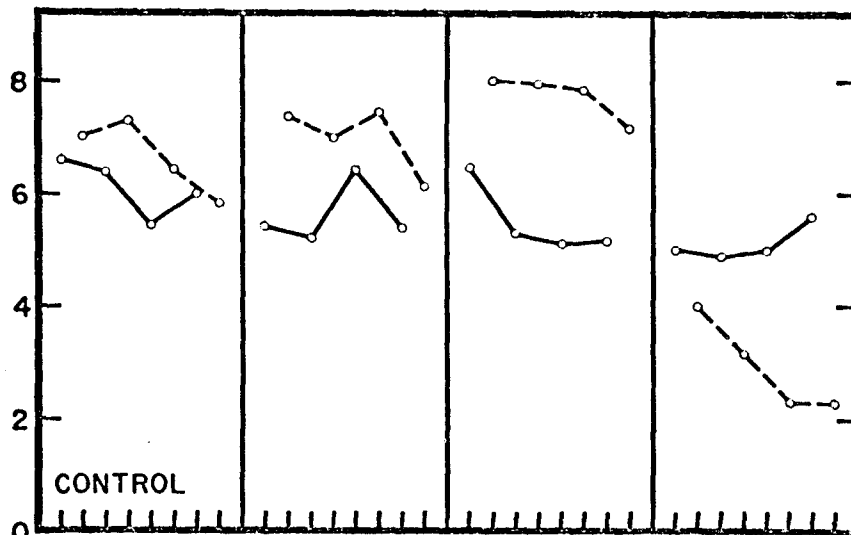
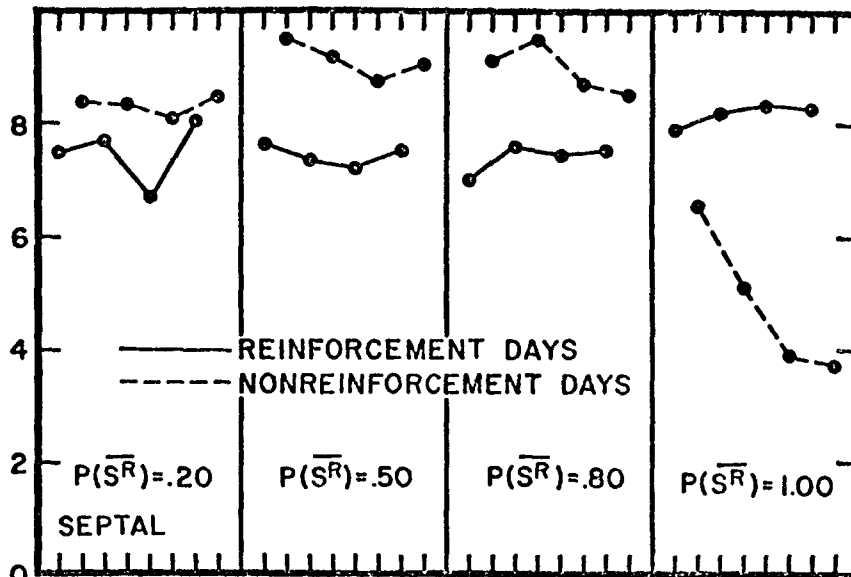


Figure 8.--Per cent efficiency on reinforcement (solid line) and alternate nonreinforcement (dashed line) days for each operated group for each probability contingency. Each data point is the mean performance of \underline{Ss} in each group for the day on which the indicated reinforcement condition was in effect.

Figure 9.--Rate on reinforcement (solid line) and alternate nonreinforcement (dashed line) days for each operated group during each probability contingency. Each data point is the mean performance of subjects in each group.

RESPONSES PER MINUTE



1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8

SESSIONS

Several points can be noted in Figure 8 regarding the differences in efficiency on reinforcement days and nonreinforcement days. The differences in per cent of the IRTs greater than 8 sec. does not appear to differ between groups at any given probability, but these differences become greater for all groups as the probability of nonreinforcement for a correct timing response is increased except during extinction ($p(\overline{SR}) = 1.0$). These observations were confirmed by a 3×4 analysis of variance with repeated measures on one factor (Winer, 1962) which was performed using the differences in efficiency ratios between the first nonreinforcement day at each probability and the day immediately preceding when the regular contingency was in effect as the dependent variable. A difference measure was used because of the baseline differences in efficiency between groups under the regular DRL reinforcement conditions. A summary table of this analysis is presented in Table 3 of Appendix D, together with the results of the same analysis applied to the differences in efficiency ratios between the last reinforcement and nonreinforcement days.

The differences in efficiency between nonreinforcement and regular DRL conditions did not differ among the groups ($F = 1.35$; d.f. = 2, 9; $p > .05$). The effects of increasing the probability of nonreinforcement are quite significant ($F = 62.87$; d.f. = 3, 27; $p < .001$), as is clearly shown by Figure 8. In addition, there is a significant interaction

between operation and probability ($F = 3.77$; d.f. = 6, 27; $p < .01$). This result indicates a differential effect of a particular lesion on DRL responding. The size of the reduction in efficiency with changing probability depends to some extent upon the kind of lesion a subject received or whether he received one at all. Individual comparisons between operated groups revealed no further differences. The analysis of variance for differences between the last reinforcement and nonreinforcement days for each probability showed only a significant probability effect ($F = 31.28$; d.f. = 3, 27; $p < .001$). The effect of increasing the probability of nonreinforcement still produced a significant reduction in efficiency of timing behavior for all subjects.

Performance during the nonreinforcement condition in which probability of nonreinforcement equaled 1.0, or extinction, demonstrated some interesting differences among the groups. Figure 9 shows a marked decrease in rate which occurred for all groups from the first day of extinction to the last. Rate for the septal animals decreased to such an extent that the frequency of IRTs greater than 8 sec. was higher on extinction days than on regular DRL reinforcement days.

The light over the bar, which had been paired with the correct nonreinforced timing response, was introduced during the fourth and eighth sessions of extinction. As shown in Figures 8 and 9, its presence (Sessions 4 and 8) or absence (Sessions 2 and 6) did not seem to affect responding for any

of the groups, therefore indicating that it had not acquired any stimulus control over the behavior in the present situation.

Several properties of the IRT distributions during this phase of the study are shown in Figures 10 and 11. The columns are the operated groups, and the rows are the probabilities of nonreinforcement. The solid line functions are the total distributions of IRTs on days that regular DRL contingencies were in effect. The other two distributions were obtained on the first (Figure 10) or last (Figure 11) days that reinforcement was withheld at each probability contingency. The dashed line function illustrates the distribution of IRTs following every correct timing response which was reinforced, and the dotted line function describes the pattern of IRTs following every correct timing response which was not reinforced. Both distributions include all IRTs until the next 8 sec. IRT, when it was again determined to which class the subsequent behavior belonged. Two general features of these distributions are evident when compared to those obtained on regular DRL days: (1) an increase in the frequency of IRTs less than 8 sec. following a withheld reinforcement, and (2) an increase in long IRTs following a response which was reinforced. The major difference between groups under all reinforcement conditions is in the frequency of these very short and very long interresponse times.

On regular DRL days, the distributions for the septal

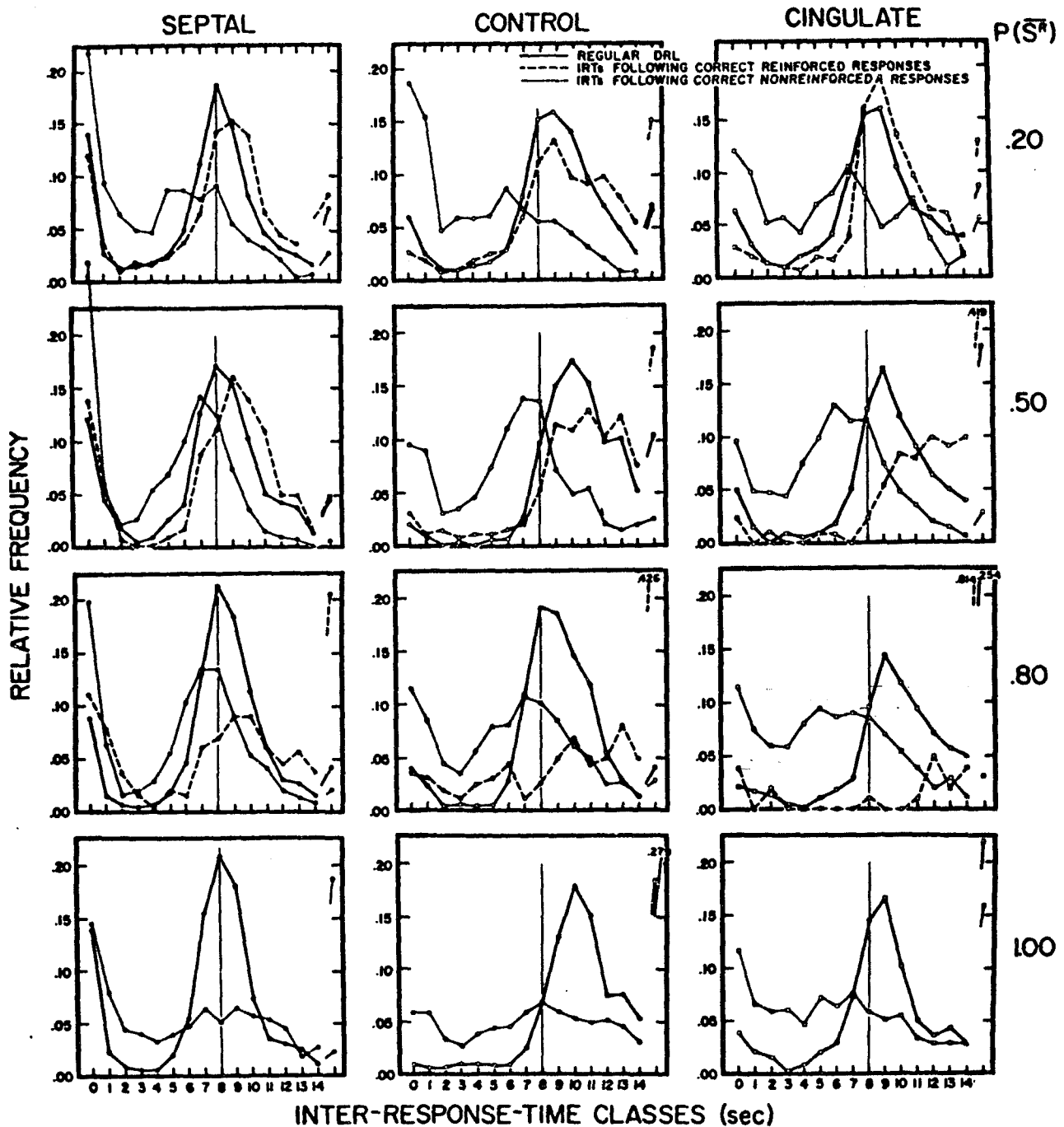


Figure 10.--IRT distributions on the first nonreinforcement day for each probability contingency (rows) for each operated group (columns). Solid line functions represent IRT distributions obtained on a day when regular DRL conditions were in effect. Dashed and dotted line functions represent respectively the IRT distributions obtained following a correct response which was reinforced and one which was not reinforced on the day immediately following.

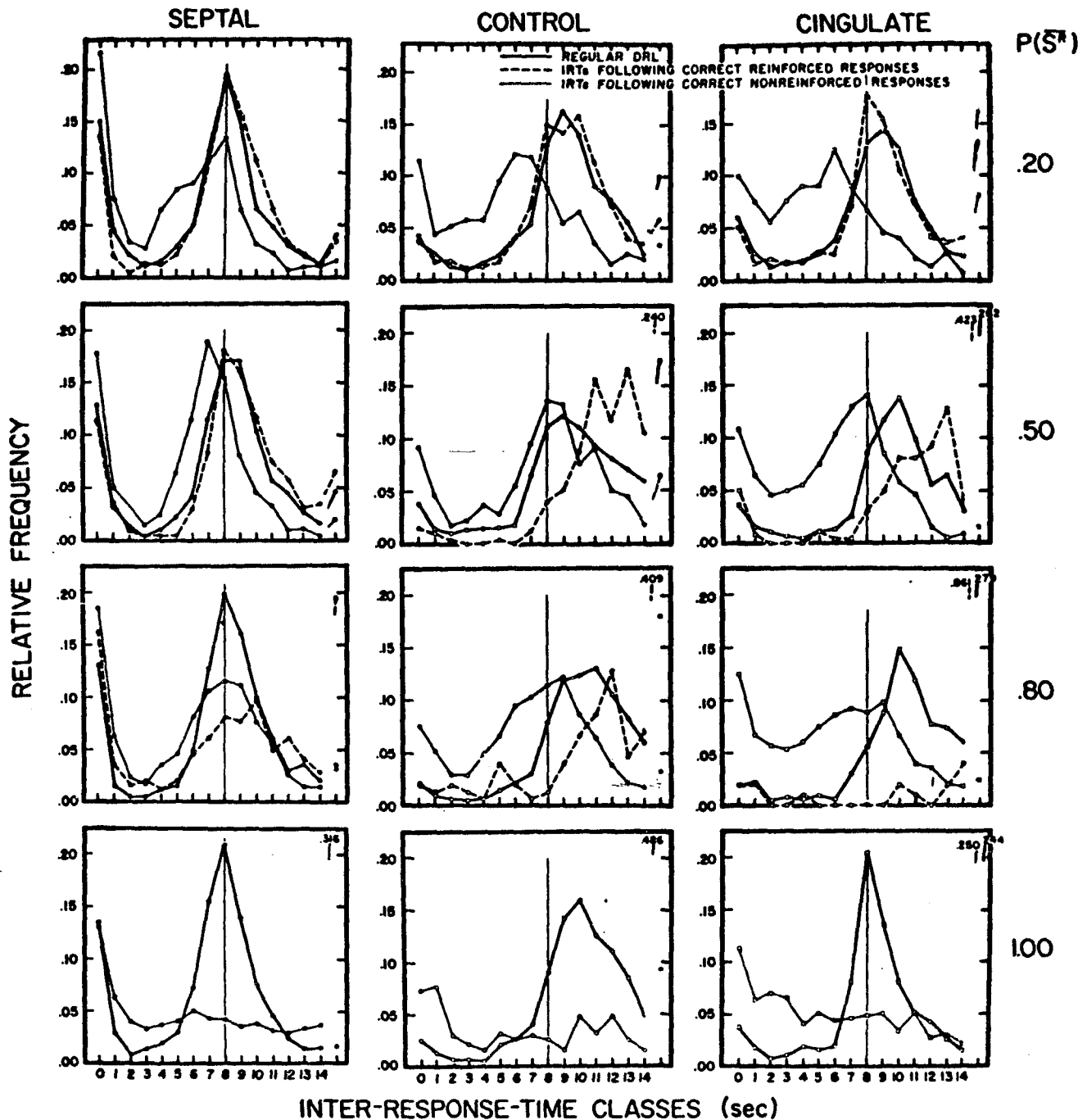


Figure 11.--IRT distributions on the last nonreinforcement day for each probability contingency (rows) for each operated group (columns). Solid line functions represent IRT distributions obtained on a day when regular DRL conditions were in effect. Dashed and dotted line functions represent respectively the IRT distributions obtained following a correct response which was reinforced and one which was not reinforced on the day immediately following.

operates are sharply peaked at the 8 sec. interval, and there are few IRTs exceeding 15 sec. A distinctive feature of this group's behavior was a very high frequency of rapid responses. The distributions for both the cingulate and control groups are flatter with modes occurring at intervals greater than 8 sec. There is also a fairly large number of particularly long IRTs. The tendency for long periods of no-response is most evident for the cingulate animals.

On the first day that the nonreinforcement procedure was introduced at each probability (Figure 10), the response patterns became more variable and there was a marked increase in the number of short IRTs. These effects were most pronounced for the septal operates. Comparison of the nonreinforcement distributions in Figures 10 and 11 shows that there was no great change in response patterns of the cingulate and septal operates from the first to the last days of each probability contingency. The control animals' data show that the increased frequency of rapid responses occurred mainly on the first day when each new probability contingency was introduced. By the last day of the nonreinforcement procedure at each probability, the animals spaced their responses by longer time intervals so that the distributions were shifted back towards the DRL criterion.

The greatest change in the nonreinforcement IRT distributions occurred for all groups during extinction. It was previously noted that accuracy of timing behavior did not

increase markedly during extinction, although all groups showed a decrease in rate. The IRT distributions for this period show that initial exposure to the extinction procedure produced a tendency toward longer and longer periods of non-response, which is most conspicuous for the cingulate and control animals. These long IRTs, combined with a persistent tendency for response bursts, generated flat distributions in the midrange of IRTs. The septal animals did not show a marked increase in the frequency of long IRTs until the last day of extinction (Figure 11).

Figures 10 and 11 show that the effect of random omission of reinforcement was also to increase the time between successive responses following a correct response which was reinforced. The IRT distributions under this condition for the cingulate animals are exceedingly flat with an unusually high frequency of IRTs greater than 15 sec. The septal distributions do not show this maximum until the probability of nonreinforcement is equal to 0.8, and there is still a high frequency of very short IRTs.

The tendency toward long IRTs thus occurs under two conditions: (1) after an 8-sec. or greater IRT which is never reinforced (extinction), and (2) after an 8-sec. or greater IRT which is reinforced intermittently. The cingulate animals show the greatest increase in time between successive responses. The septal animals show the least effect and demonstrate an invariant trend toward rapid responding

under both conditions.

The most important results to be noted in the present experiment are as follows: (1) Under regular DRL conditions, the timing behavior of all groups was similar except for the very high frequency of rapid responses exhibited by septal animals which reduced their efficiency significantly below that of the other two groups. The high frequency of short IRTs emitted by the septal operates was accompanied by a high frequency of near-criterion responses. The frequency of responses in both of these response classes was lowest for the control group. Cingulate animals demonstrated that a high frequency of near-criterion responses was related to a low incidence of very short IRTs. (2) Under the nonreinforcement conditions, timing efficiency decreased for all groups as a function of probability of nonreinforcement. However, the differences in efficiency between nonreinforcement and regular DRL conditions did not differ among the groups. The reduced efficiency on nonreinforcement days was shown to be due to a marked increase in the number of very short IRTs which occurred following a correct timing response which was not reinforced. This effect was most pronounced for the septal operates. A corollary effect of random omission of reinforcement was an increase in the frequency of long IRTs following a correct response which was reinforced. This effect was most pronounced for the cingulate animals.

Experiment 2

Introduction

The results of Experiment 1 indicated that there was no differential disruption in accuracy of timing behavior among groups when the nonreinforcement procedure was introduced. This conclusion is, however, confounded by the fact that baseline timing efficiency was not the same for all the groups. The difference in relative frequency of responses which were reinforced when conventional DRL conditions were in effect makes comparison among groups difficult. Therefore, the delay interval in the second experiment was further reduced so that all subjects were almost always reinforced under regular DRL conditions. Thus, the relative frequency of responses meeting the DRL criterion would be equal for all groups, and differences among groups in disruption of timing behavior could be attributed solely to the type of operation which the subject received.

Method

Twelve male albino rats of the Charles River CD strain, approximately 220 days old at the start of the experiment, were used. The surgical and behavioral testing procedures used were essentially the same as in Experiment 1, with the modifications noted below. The rats were placed on ad lib

food and water for three weeks, during which time daily weights were recorded. They were then divided into groups of four rats each, and operated upon before being reduced to 85 per cent of their ad lib body weights. The surgical procedures remained the same as before for each respective group. Four rats were given bilateral lesions in the septal fore-brain, four in the cingulate cortex, two received sham operations, and two remained as unoperated controls. Following surgery, they were again allowed ad lib food and water for one week, after which time their diet was restricted until they were reduced to 85 per cent of their ad lib body weights.

All subjects were then placed into the experimental chamber for 20 min. and their operant levels of bar-pressing were recorded. On the following day, the rats were shaped and allowed 200 reinforcements on a continuous reinforcement schedule, and another 100 reinforcements on this schedule on the third day. On the fourth day following introduction into the experimental chamber, all rats were placed on a DRL 1.2 sec. schedule of reinforcement. From this time on, session length was determined by the time it took for each rat to obtain 250 reinforcements. Interresponse time class interval size was 0.6 sec.

Following twenty-two sessions on DRL 1.2 sec., the DRL interval was changed to 0.6 sec. The minimum interval required for reinforcement was reduced because of the high frequency of very short IRTs being emitted by some of the

animals, which decreased their efficiency on this schedule. The interval was reduced in an attempt to equate the relative number of responses which were reinforced in each session for all animals. IRT class interval size was maintained at 0.6 sec.

Each animal was run for eight sessions on DRL 0.6 sec. until there was little variation in daily rate output either within or between subjects. During these sessions, the water bottle which had been present in the experimental chamber during the first twenty-two sessions was removed. The cumulative records of these animals showed gross irregularities in responding, with long breaks during which the animals were observed to be drinking. The water bottle was removed in an attempt to stabilize rates.

On the thirty-first session and on alternate days for a period of eight days following, the nonreinforcement procedure was introduced according to a 0.2 probability. Reinforcement contingencies and records of daily responding by each animal were programed as described previously. The probability of nonreinforcement contingency was then introduced on alternate days. There were four successive eight-day periods during which the probability of the withheld reinforcement contingency was 0.2 on alternate days during the first eight-day period, 0.5 during the second, 0.8 during the third, and 1.0 during the fourth. A summary of the procedures followed is presented in Table 4.

Table 4

Summary of Procedures Followed in Experiment 2

<u>Procedure</u>	<u>Contingency</u>	<u>Stimulus Conditions</u>	<u>No. of Sessions</u>
1. Operant level	None	No illumination; water bottle	1
2. Continuous reinforcement	All responses reinforced	Same as above	2
3. DRL acquisition	All IRTs > 1.2 sec. reinforced	Same as above	22
4. DRL acquisition	All IRTs > 0.6 sec. reinforced	Water bottle removed	8
5. Nonreinforcement procedure	20% IRTs > 0.6 sec. not reinforced, alternate days	Magazine click, light over bar with nonreinforced IRT > 0.6 sec.	8
Nonreinforcement procedure	50% IRTs > 0.6 sec. not reinforced, alternate days	Same as above	8
Nonreinforcement procedure	80% IRTs > 0.6 sec. not reinforced, alternate days	Same as above	8
Nonreinforcement procedure	100% IRTs > 0.6 sec. not reinforced, alternate days	Same as above, Sessions 4 and 8; no light, Sessions 2 and 6	8

Following completion of behavioral testing, all animals were perfused with saline and formalin, and their brains sectioned in the frontal plane by the frozen section technique at 48 μ . intervals. Every third section was stained with cresyl violet and examined by use of a projection microscope to determine exact limits of the lesions and any gliosis which might have resulted.

Results

Anatomical results

The general pattern of septal lesions for MAC 3, 5, and 6 was similar to that described previously for septal lesioned animals in Experiment 1. The damaged area included, bilaterally, portions of the fornix and fornix columns and the septal nucleus triangularis. Septal damage to MAC 4 was found to be primarily unilateral, restricted to the left side, including slight injury to the caudate nucleus and putamen dorsomedially in the immediate vicinity of the lateral ventricle. Reconstruction of these lesions is shown in Figure 12.

The pattern of damage for the cingulate lesioned animals was also similar to that described previously for the animals in Experiment 1, except for MAC 14 who only sustained minimal damage to the midline dorsal cortex. Cingulate damage for the other animals in this group included extensive bilateral destruction of the posterior region of cortical

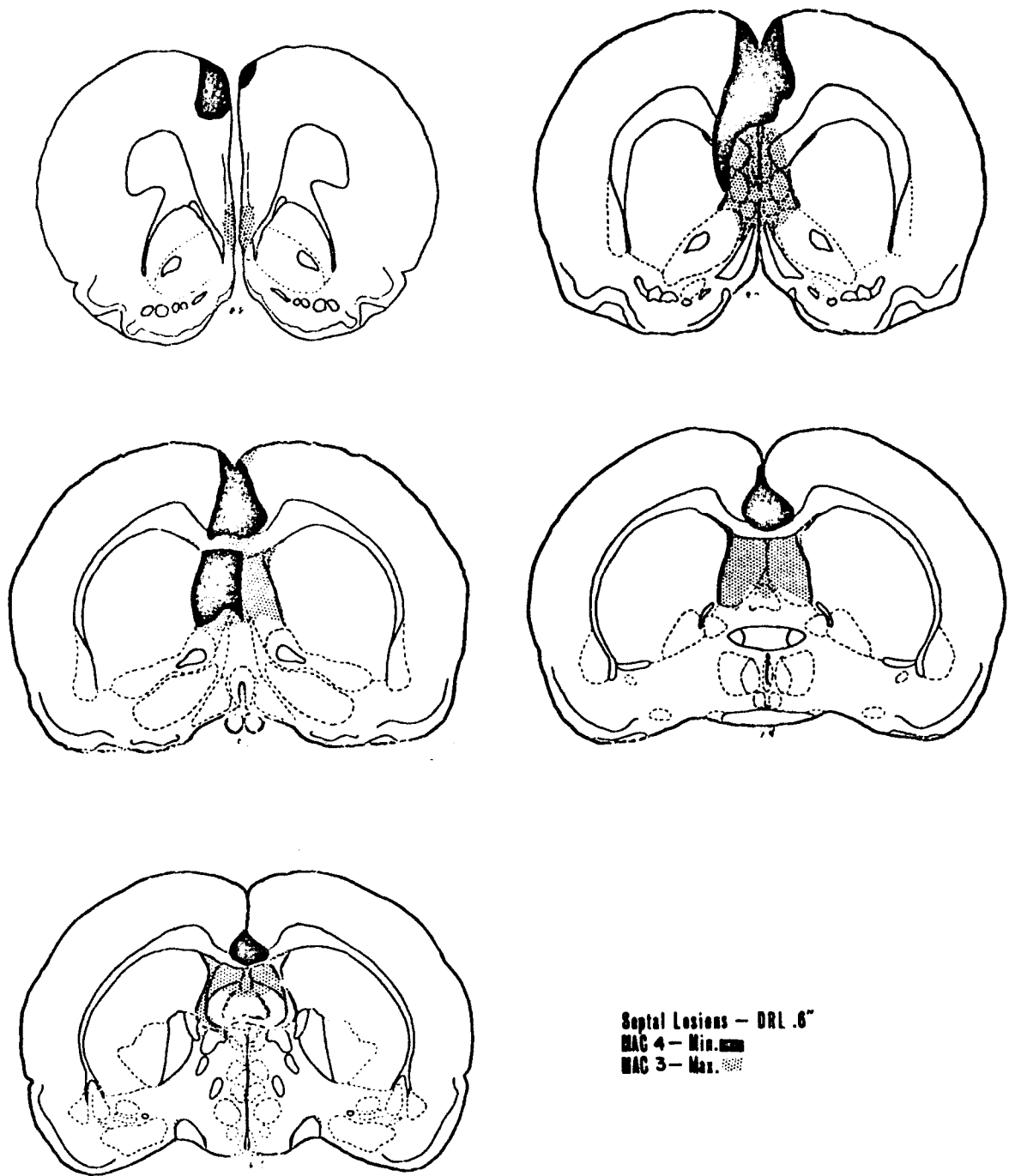


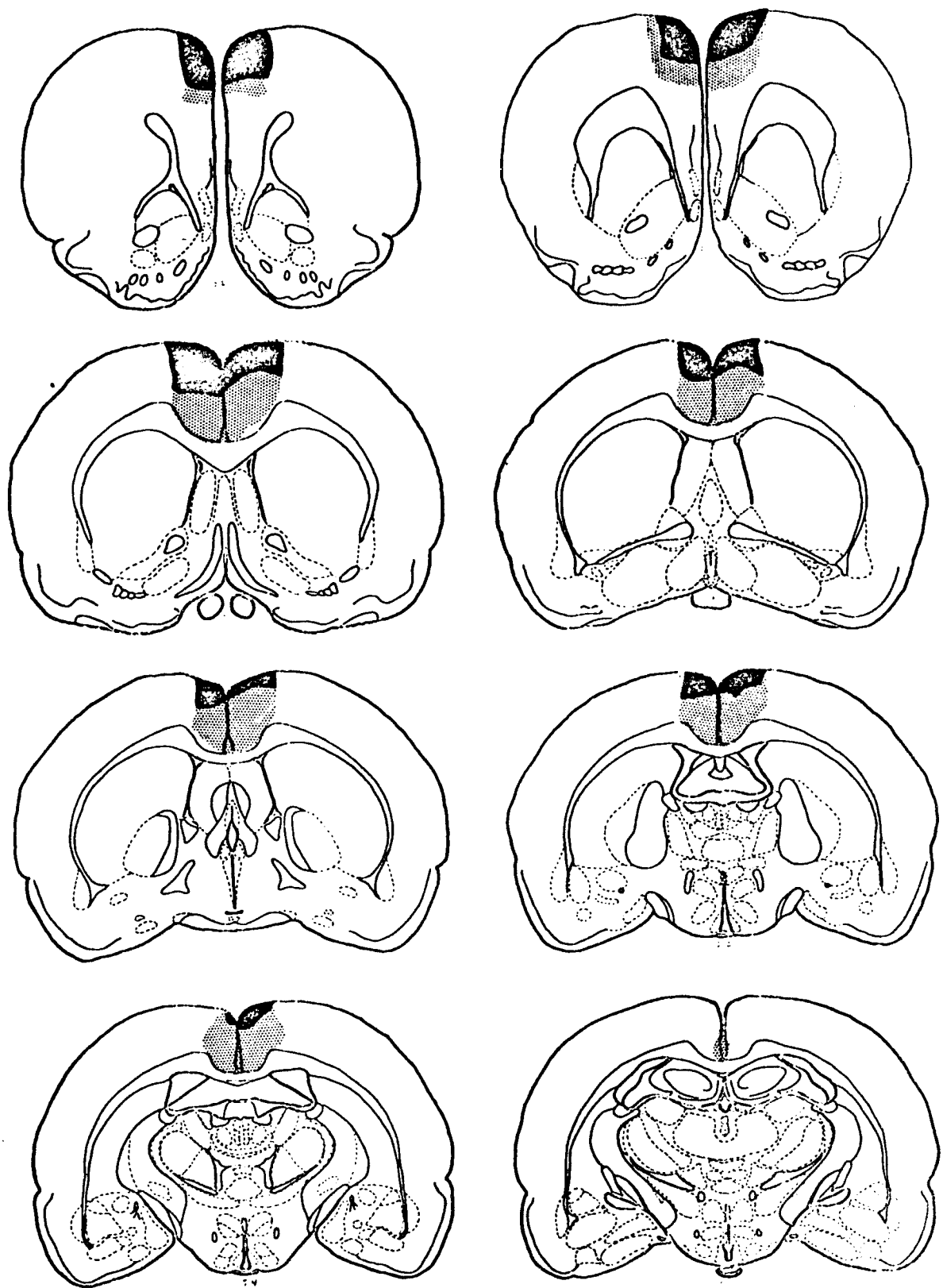
Figure 12.--Reconstruction of septal lesions in the DRL 0.6 sec. group. Area of maximal damage is stippled and minimum is indicated by solid black.

area 24, area 23, and the dorsal region of pregenual area 32, as described for the rat by Krieg (1946). Cortical areas 10, 6, and 4 adjacent to cingulate areas 23 and 24 also sustained minimal damage. Reconstruction of the minimum and maximum extent of these lesions is presented in Figure 13. Differences in behavior as a result of lesion variability are noted in Appendix C.

Behavioral data

Activity level, as measured by the operant level of bar-pressing, did not differ for septal and control animals, and was greatly depressed for the cingulate operates. The septal operates emitted a total of 116 responses, the controls 120, and the cingulates 36 during the 20-min. operant level period. Response rates increased during one session on a continuous reinforcement schedule to 12.63 responses per minute for the septal rats, 11.77 responses per minute for the cingulates, and 10.57 responses per minute for the controls. The IRT distributions for the continuous reinforcement period showed that the mode occurred at or around 3 sec. for all groups. The only difference among the IRT distributions was in the slightly higher frequency of very short IRTs emitted by the cingulate animals.

Figure 14 shows that introducing the DRL 1.2 sec. contingency produced a decrease in time of occurrence of the modal IRT, so that efficiency decreased (Figure 15) and did



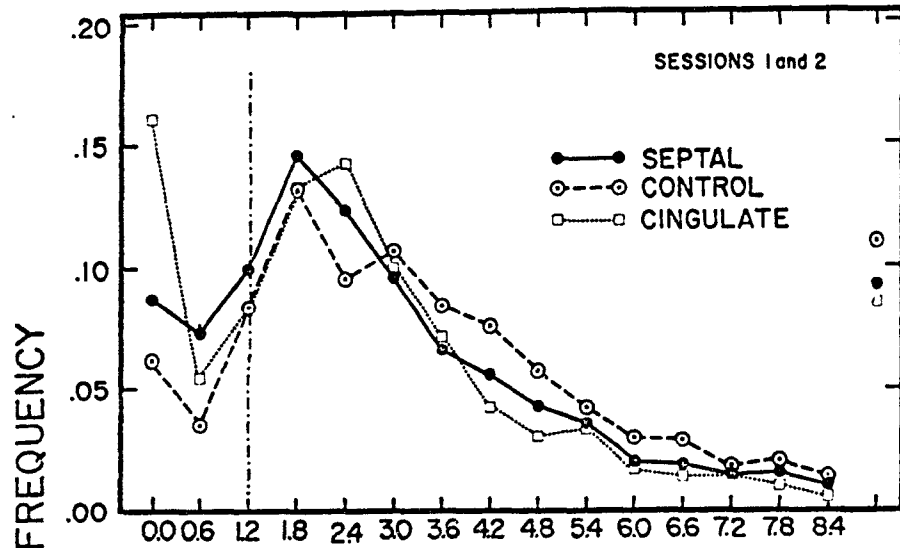
Cingulate Lesions - DRL 6"
 MAC 14 - Min. ■
 MAC 12 - Max. ▨

Figure 13.--Reconstruction of cingulate lesions in the DRL 0.6 sec. group.

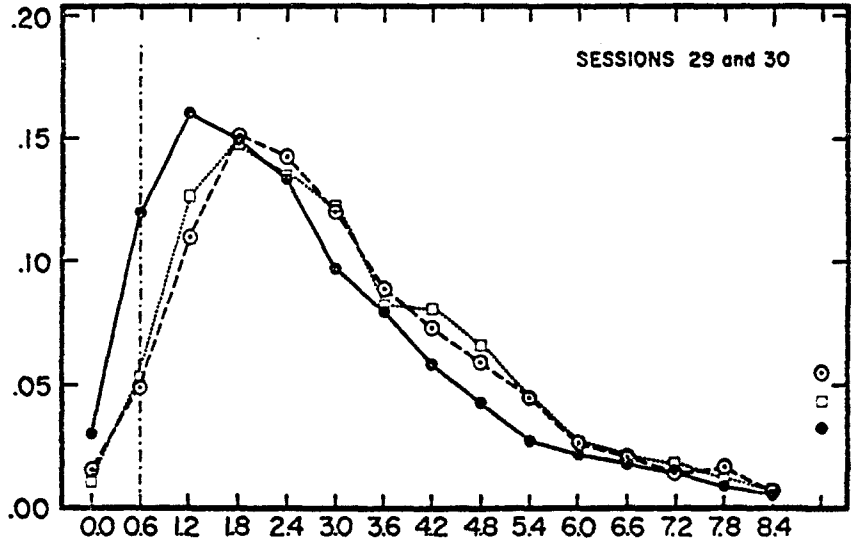
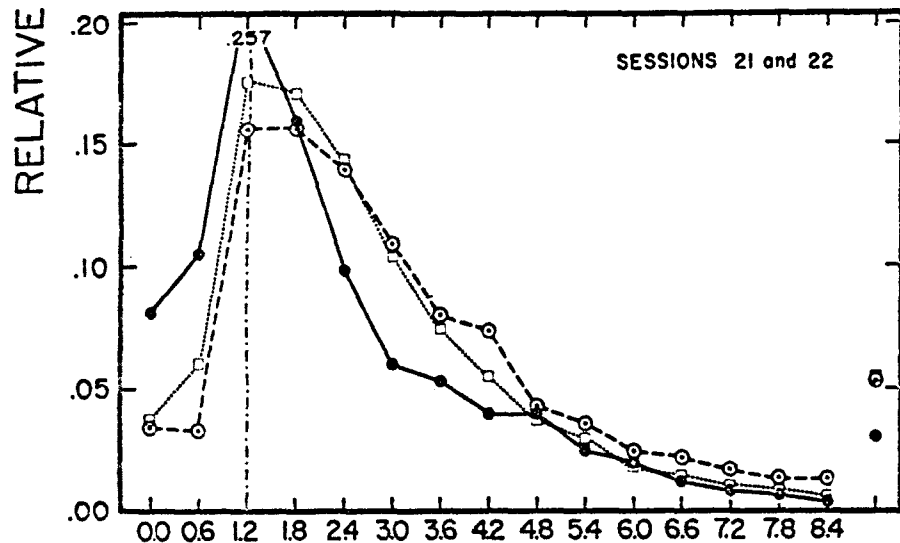
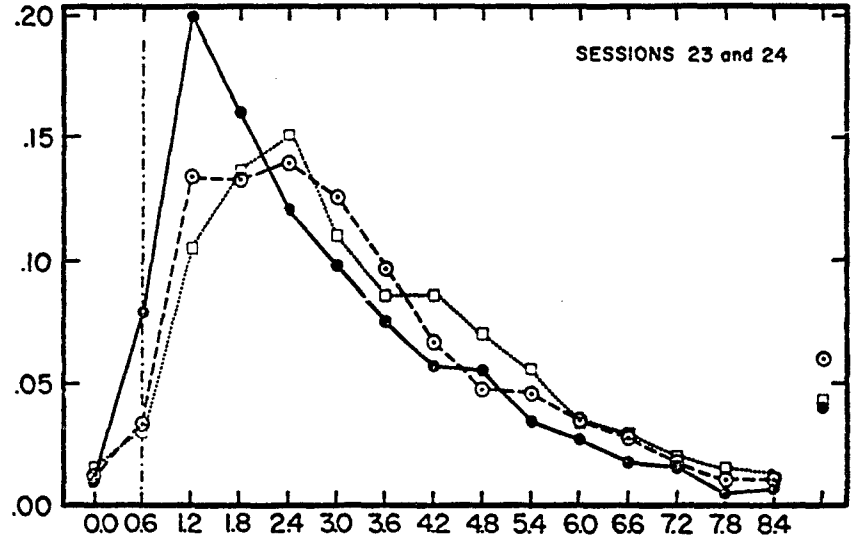
Figure 14.--IRT distributions for first and last sessions on DRL 1.2 sec. and DRL 0.6 sec., respectively, for each operated group. Lower bound of class intervals is plotted on abscissa.

HL

DRL 1.2 sec



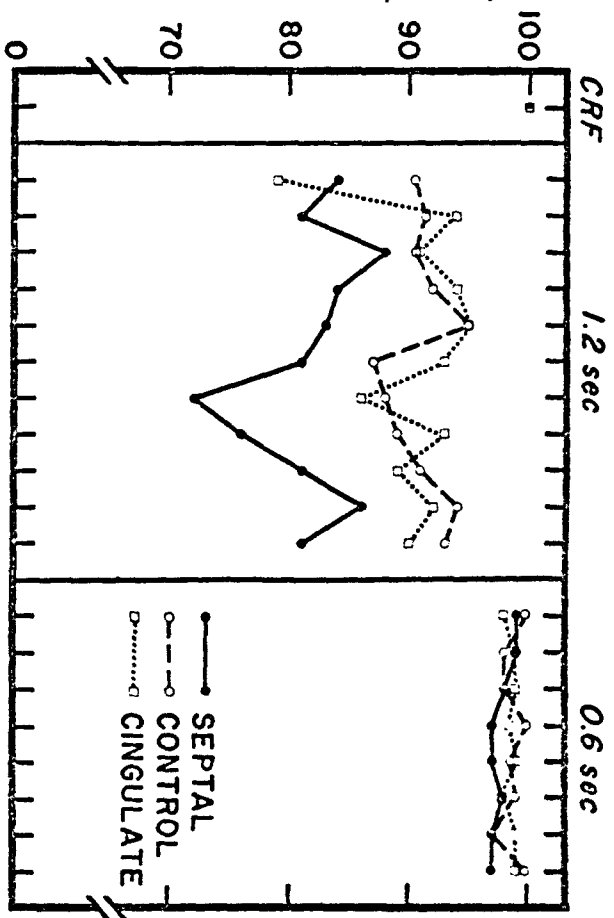
DRL 0.6 sec



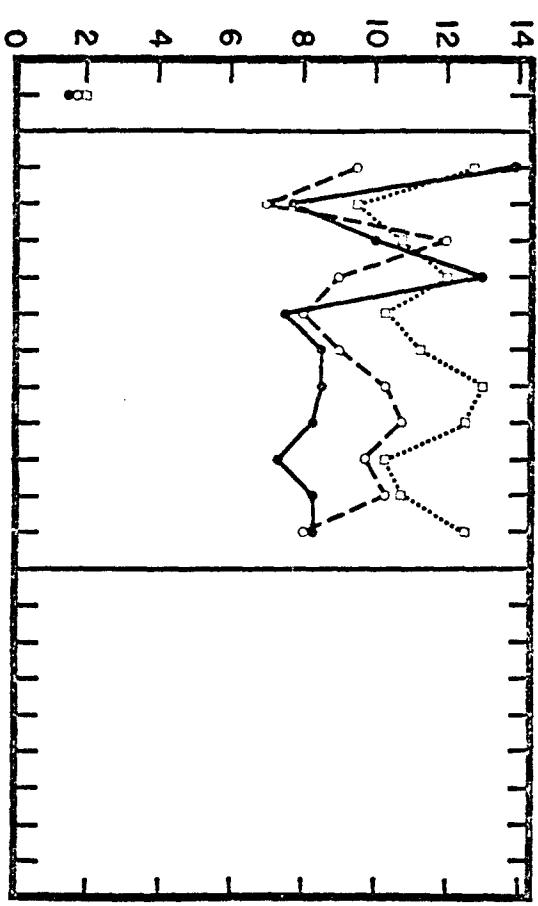
INTER-RESPONSE-TIME CLASSES (sec)

Figure 15.--Per cent efficiency, water consumed, and rates during continuous reinforcement, DRL 1.2 sec., and DRL 0.6 sec. for each operated group.

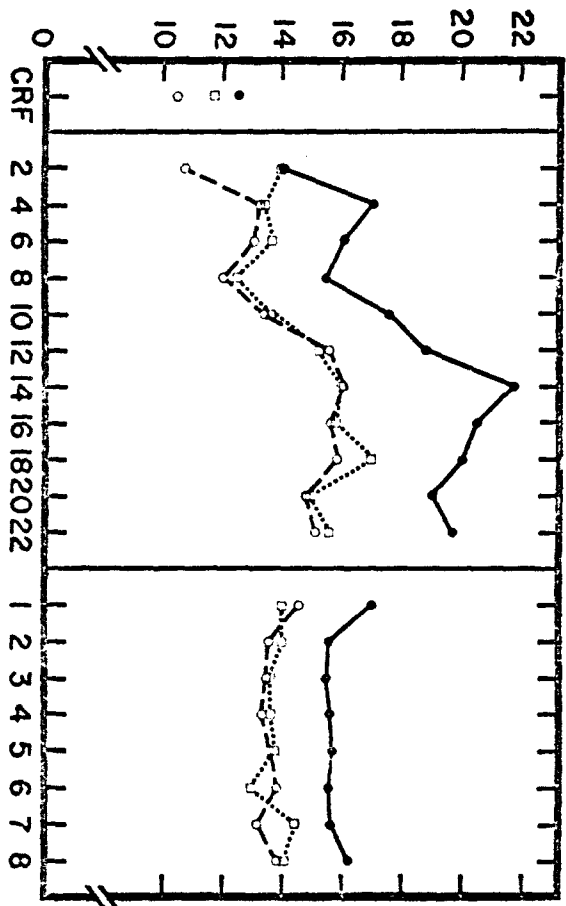
PER CENT EFFICIENCY
(reinforcements/responses)



WATER CONSUMED (cc)



RESPONSES PER MINUTE



SESSIONS

not improve throughout the twenty-two sessions. This decrease was most pronounced for the septal operates, as was the increased response rate which occurred for all groups. A Kruskal-Wallis analysis of variance showed that the differences in rate among the groups were significantly different during the first four sessions of acquisition on DRL 1.2 sec. ($H = 5.70$, $p < .05$) and during the last four sessions ($H = 13.09$, $p < .01$). It can be seen that this difference is due to the high rate of the septal operates, since responding for the cingulates and controls was practically equal.

The IRT distributions in Figure 14 for DRL 1.2 sec. show that the cingulates' high frequency of short IRTs observed during continuous reinforcement was maintained during the first sessions. Otherwise, the distributions are essentially the same. By the last two sessions of training on DRL 1.2 sec., the frequency of IRTs less than 0.6 sec. had decreased for the cingulates and their distribution is similar to that of the controls. The septal operates' higher rate is reflected in the relatively high frequency of IRTs less than 1.2 sec., and in the greater frequency of responses which fall exactly at the DRL contingency.

The second column of graphs in Figures 14 and 15 illustrates the changes in response patterns which occurred when the "just-missed" IRTs were reinforced, i.e., when the DRL requirement was reduced to 0.6 sec. The septal operates markedly decreased the frequency of IRTs less than 0.6 sec.,

although the modal IRT still occurred sooner and was more sharply peaked than for either of the other two groups. Rate for these animals remained constantly higher (Figure 15) but the number of reinforced IRTs (efficiency) for all groups was equal, high, and constant with continued training. A Kruskal-Wallis test showed significant differences between rates for the three groups both during the first and last two sessions on DRL 0.6 sec. ($\underline{H} = 6.97, \underline{p} < .05$; $\underline{H} = 6.51, \underline{p} < .05$, respectively).

The effects of withholding reinforcement are shown in Figure 16. All groups exhibit a sharp decrease in the number of reinforced responses which is related to the probability of nonreinforcement. Results of a 3×4 analysis of variance with repeated measures showed a significant probability effect ($\underline{F} = 44.24, \underline{d.f.} = 3, 27, \underline{p} < .001$), but no among-groups difference in efficiency ratios on the first nonreinforcement days was found. A summary table of this analysis is presented in Table 5 of Appendix D.

Figure 17 illustrates the changes in response rates which occurred on nonreinforcement days. Rate remains constant for all groups on regular DRL days, with septal animals emitting approximately two responses per minute more than either the cingulate or control groups. Response rates for these groups were about equal. When the nonreinforcement procedure was initially introduced, response rates did not differ among groups. With higher probabilities of nonrein-

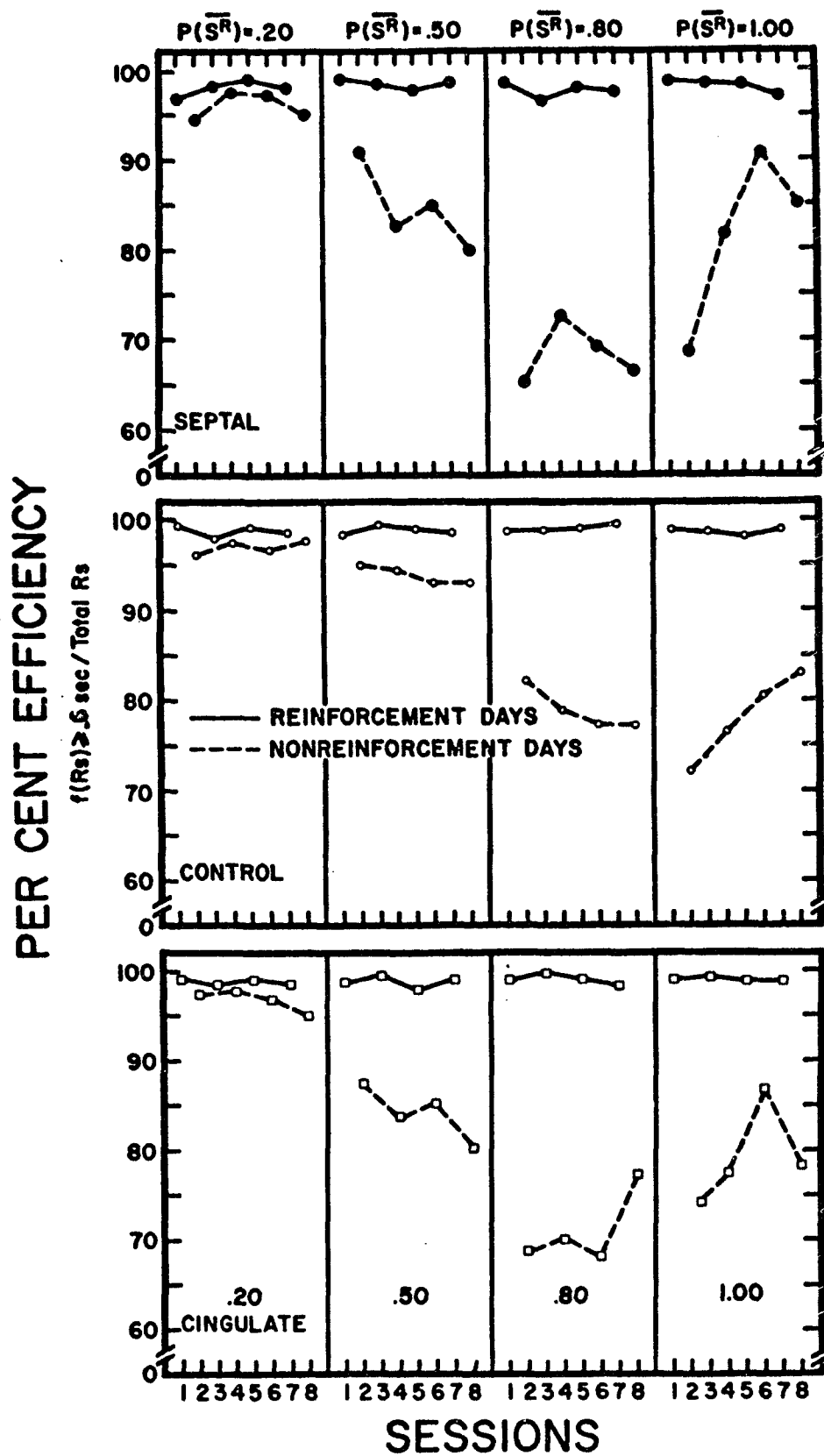
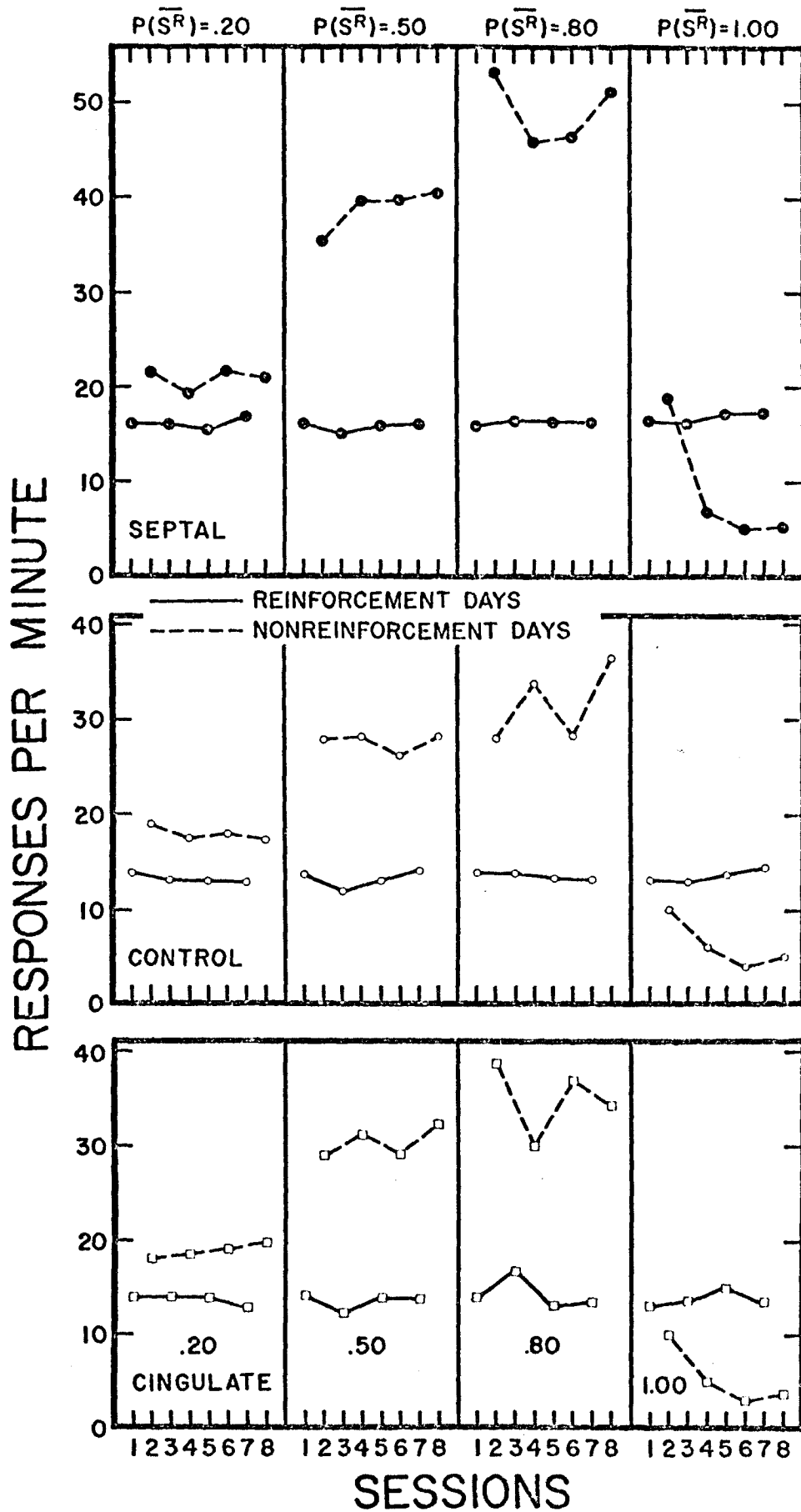


Figure 16.--Per cent efficiency on reinforcement (solid line) and alternate nonreinforcement (dashed line) days for each operated group for each probability contingency. Each data point is the mean performance for \bar{S} s in each group.

Figure 17.--Rates on reinforcement (solid line) and alternate nonreinforcement (dashed line) days for each operated group during each probability contingency. Each data point is the mean performance for Ss in each group.



forcement ($\underline{p} = 0.5$), the rate increase for septal animals was greater than for the other two groups. Extinction occurred rapidly for all groups, rate decreasing on the first day to less than 50 per cent of what it was on the last day of the 0.8 probability contingency. The light, which was regularly paired with the nonreinforced correct timing response, had no effect on rate when it was presented during Sessions 4 and 8.

Response rate seems to be more sensitive an indicator of change when reinforcement is withheld following a correct response, because of the particular timing contingencies of this schedule. This may be explained by the brevity of the IRT interval during which no responses are reinforced (0.6 sec.). Large increases in rates which may occur as a function of increasing probability of nonreinforcement may not produce related changes in the proportion of reinforced responses. A 3×4 analysis of variance, performed on the differences in rates between the first nonreinforcement days and the regular DRL days immediately preceding, verified this analysis. Rates for the three groups differ significantly on the first days of each new probability contingency ($\underline{F} = 4.39$; $\underline{d.f.} = 2, 9$; $\underline{p} < .05$). Individual comparisons between operated groups further revealed a highly significant difference between septal and control animals ($\underline{F} = 49.12$; $\underline{d.f.} = 1, 6$; $\underline{p} < .001$). The presence of a significant interaction indicated that the effects of reducing the probability of rein-

forcement are related to the type of brain damage which the animal sustained ($F = 3.36$; d.f. = 6, 27; $p < .05$). The second analysis between the last reinforcement and last nonreinforcement days indicated that these latter effects had dissipated by the last day of each probability contingency. The effect of changing probability of nonreinforcement was not different among the groups but was still highly significant when compared to regular DRL response rates. Summary tables of these analyses are presented in Table 6 of Appendix D.

Figures 18 and 19 show the effects of withholding reinforcement on the temporal distribution of responses on the first and last nonreinforcement days at each probability contingency, and on the regular DRL days immediately preceding. The major effect to be noted is the greater proportion of short IRTs which occurred on nonreinforcement days. These occurred following a 0.6 sec. or greater IRT which was reinforced and following one which was not. Comparison of Figures 18 and 19 shows that these effects did not vary greatly from the first to the last nonreinforcement days at each probability except for the extinction period. The IRT distributions on regular DRL days are similar among the groups and show little variation day to day. The major difference is the slightly earlier occurrence of the modal IRT for the septal animals.

When the nonreinforcement procedure was introduced, there was an immediate and large increase in the frequency

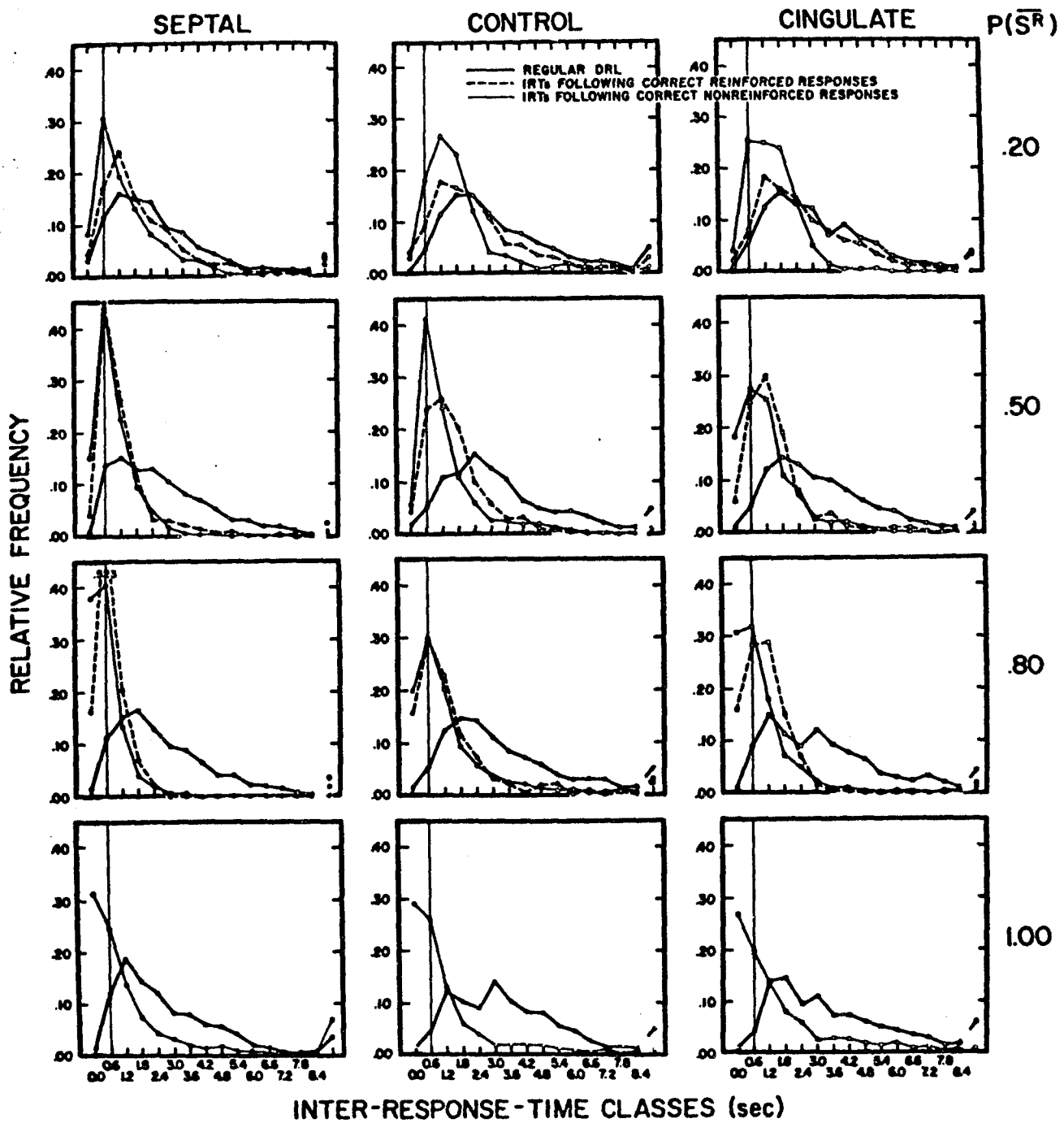


Figure 18.--IRT distributions on first \overline{SR} day for each probability contingency (rows) for each operated group (columns). Solid line functions represent IRT distributions obtained on a day when regular DRL conditions were in effect. Dashed and dotted line functions represent respectively the IRT distributions obtained following a correct response which was reinforced and one which was not reinforced on the day immediately following.

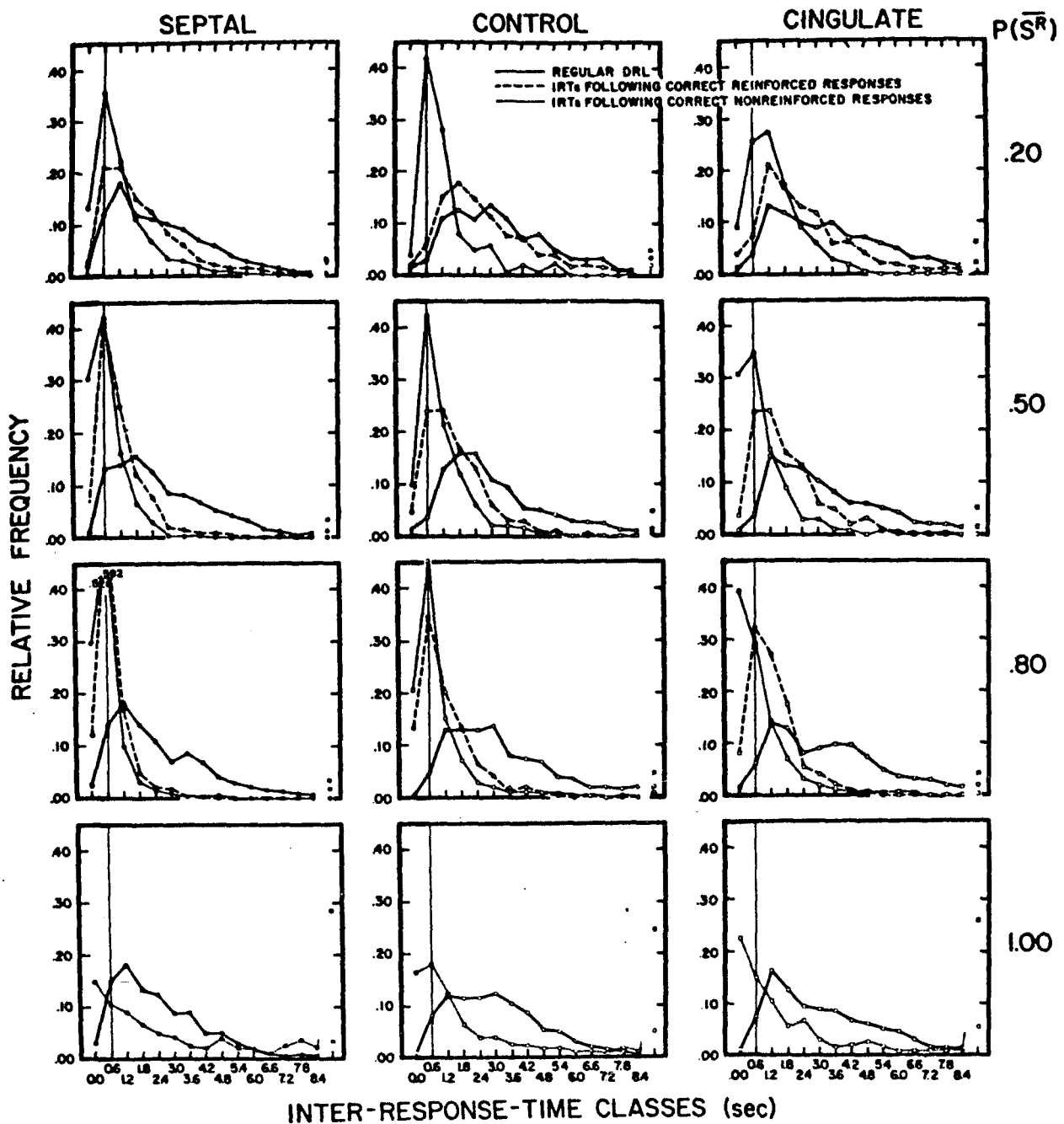


Figure 19.--IRT distributions on last \overline{SR} day for each probability contingency (rows) for each operated group (columns). Solid line functions represent IRT distributions obtained on a day when regular DRL conditions were in effect. Dashed and dotted line functions represent respectively the IRT distributions obtained following a correct response which was reinforced and one which was not reinforced on the day immediately following.

of IRTs less than 1.2 sec. which was greatest for the septal operates. On both the first and last days, the septal and cingulate animals consistently demonstrated a very high frequency of nonreinforced IRTs (less than 0.6 sec.). These decreased on the last day of extinction for all groups except the cingulates, who still produced relatively frequent short IRTs. Differences among groups during extinction are less marked than for any of the other probability contingencies. The major effect to be noted here for all groups is the large increase in the relative frequency of very long IRTs on the last day.

It may be concluded that when the relative number of reinforcements obtained is equal for all operated groups (equal baseline efficiency ratios), the increase in rapid response bursts following a withheld reinforcement for a correct response is greatest for the septals and least for the controls, with the cingulates most generally demonstrating behavior similar to that of the septal operates. The data indicate also that the overall increase in rate following random omission of reinforcement on DRL 0.6 sec. was due to rapid bursting which followed both a correct response which was reinforced and one which was not.

Discussion

Septal lesions

Results obtained in the present experiments demonstrated that septal animals will show an increase in the frequency of rapid responses under either one of two conditions: (1) if reinforcement for a previously rewarded response is withheld, and (2) if they are required to suppress responding in order to obtain a reinforcement. It is postulated that both of the above conditions constitute aversive events (Adelman & Maatsch, 1956; Wagner, 1963; Zimmerman & Ferster, 1963; Azrin *et al.*, 1966; Hearst, Koresko, & Poppen, 1964; Leitenberg, 1966; Nigro, 1966; McMillan, 1967) and that animals with the septal forebrain destroyed are hyper-reactive to aversive events. It is thus proposed that the septal forebrain exerts inhibitory control over behavior which is dependent upon the reinforcing properties of stimuli. In the present study, the aversive properties of non-reinforcement were presumed to increase as the probability of withholding reinforcement increased. The finding that response rates increased as a function of probability supports this assumption. The accelerated response rates exhibited by control animals on nonreinforcement days in the present studies is in agreement with previous reports show-

ing that omission of reinforcement for a previously rewarded response is followed in normal animals by acceleration of ongoing behavior. Staddon and Innes (1966) demonstrated that response rates of monkeys during the second fixed-interval component of a multiple FI schedule of reinforcement were greatly accelerated following nonrewarded completion of the first component. Tacker and Way (1968) reported an increase in the open-field activity of rats immediately following a nonrewarded trial in a runway.

The prediction that septal animals would respond most rapidly when reinforcement for a previously rewarded response was withheld was supported by the results of the second experiment. Septal operates demonstrated the greatest increase in response rate as the probability of withheld reinforcement for a correct response increased. The increase in rate on nonreinforcement days was due to the greater frequency of very brief interresponse times emitted by septal animals following an IRT greater than 0.6 sec. which was intermittently reinforced. Except for the relative frequency of very short IRTs on nonreinforcement days, the IRT distributions for the septal operates, the cingulate operates, and the control animals were very similar. Studies by Thomas et al. (1959), Schwartzbaum et al. (1964), and Zucker (1965), have also demonstrated that septal animals become hyperreactive in response to a nonreinforcing event. The behavior of septal operates in these experiments typically showed persistent

responding to the incorrect stimulus.

The results of the nonreinforcement procedure obtained from septal animals responding on DRL 0.6 sec. are to be contrasted with those obtained from septal operates responding on the DRL 8 sec. contingency. On the latter schedule, septal operates were no different in magnitude of increased rate than either the cingulate or control animals. The difference in magnitude of reduced efficiency demonstrated by septal operates working on the two different DRL schedules may be attributed to the differential baseline reinforcement rates under regular DRL reinforcement conditions. All responses on the 0.6 sec. schedule were almost always reinforced, while septal animals emitted the fewest reinforced responses on the DRL 8 sec. contingency. The results indicate a direct relation between efficiency of timing behavior and the magnitude of change in response rate which occurs when the probability of reinforcement is reduced. Septal operates demonstrated an increase in rate which was greater than control levels only when baseline reinforcement rates were equal.

The inefficient timing behavior demonstrated by septal rats in the present studies under regular DRL conditions when they had to suppress responding for 1.2 sec. or more — supports previous findings (Ellen et al., 1964; Burkett & Bunnell, 1966; Carey, 1967a, 1967b). Results of these studies showed that response rates of septal animals were accelerated above control levels if reinforcement was contingent

upon response suppression. These results may be explained on the basis of the aversive properties of response suppression. Evidence in support of this explanation is obtained from the data showing that the septal operates' operant level of bar-pressing and their rate on one session of a CRF schedule was similar to that of the control animals. The frequency of short IRTs only started increasing after the introduction of a 1.2 sec. delay between reinforcements. The frequency of these short IRTs decreased almost immediately when the "just-missed" IRTs were reinforced (change in second experiment from DRL 1.2 sec. to DRL 0.6 sec.), i.e., when the aversive contingency was removed.

Hearst et al. (1964) have also suggested that response suppression, as is required on the DRL schedule, may contain aversive properties; this conclusion was based on the flat generalization gradients that were obtained from pigeons in a discrimination task when they were differentially reinforced according to a DRL schedule. These gradients were flat relative to those obtained from pigeons reinforced on a variable interval schedule. Hearst et al. do not attempt to define what the properties of the DRL schedule are that may be aversive, but they point to the similarity of the DRL generalization gradients and those produced by the Sidman shock-avoidance schedule which are also characteristically flat. The contingency that requires the organism to suppress responding for a given interval of time in order to obtain

a reinforcement may be the characteristic which makes the DRL schedule aversive. This contingency may be categorized into a general class of operations which can be called "restraint"; e.g., the organism is either physically prevented from responding, or is required to suppress some behavior in order to obtain a reinforcement. Studies demonstrating accelerated behavior following confinement in a goal box are in line with this analysis (DiLollo, Davidson, Hammond, & Donovan, 1968).

The interresponse time distributions for septal and control animals were similar under regular DRL reinforcement conditions when the animals were responding on the DRL 1.2 sec. or the DRL 8 sec. contingencies, except for the high frequency of very short IRIs emitted by septal operates. These results are in agreement with those obtained by Ellen et al. (1964), who demonstrated that rats with septal lesions had a very high response rate on a DRL 20 sec. schedule of reinforcement. These workers showed that most of the responses emitted prior to the criterion delay occurred within five seconds of each other. The occurrence of the short IRIs in the present experiments following contingent response suppression is further indication that these conditions contain aversive properties. The appearance of a modal IRI at or around the DRL criterion for septal rats on the 8-sec. contingency offers further support that responding by septal animals was not random. The inability to suppress responding

was not due merely to a "deficit in inhibition of somato-motor activity" (McCleary, 1961; Kaada, Rasmussen, & Kveim, 1962; Ellen et al., 1964; Carey, 1967a), and more possibly is the result of hyperreactivity to the aversive properties of response suppression. The present results indicated that the frequency of short IRTs was related to the frequency of near-criterion responses; the frequency of both of these IRT classes was higher for septal animals than for the control or cingulate animals. These results may be due to a general increase in activation level induced in septal animals because of increased aversion to response suppression, so that the normal temporal cycle of DRL responding was foreshortened.

The extinction data obtained for the septal operates in the present experiments is somewhat different from that obtained in other studies investigating extinction of a positively reinforced response. In the present experiments, septal animals' response rates declined at least as rapidly as the other groups', and the number of criterion IRTs increased accordingly. Schwartzbaum et al. (1964) found that septal lesions resulted in increased resistance to extinction compared to control rats following discrimination training on a variable interval schedule. Butters and Rosvold (1968) similarly demonstrated increased resistance to extinction in septal monkeys following reinforcement on a 1-min. variable interval schedule. The present results are in agreement with those obtained by Ferraro et al. (1965) using normal

rats. They suggested that the rapid extinction which occurred for their rats responding on a DRL 60 sec. schedule was due to long exposure to the schedule (200 hours) and to the presence of a discriminable stimulus which accompanied criterion responses during conditioning and extinction. Both of these variables operated in the present experiments and may have contributed to speed extinction. This explanation is not clear-cut, however, because of the complex interaction of variables controlling the extinction process. Carey (1967b) has demonstrated that whether resistance to extinction of a bar-press response for water reward on a CRF schedule was increased or decreased in septal animals depended upon the length of time between surgical and testing procedures. Septals emitted more responses than controls in the extinction test if they were operated on before training, but fewer if surgery was performed after training.

The prediction that septal animals would show increased resistance to extinction because of hyperreactivity to withdrawal of reinforcement was therefore not borne out by the present results. The possible aversiveness of this condition for all subjects, however, is suggested by the relatively high frequency of short IRTs evidenced on the first day of extinction. Further indication of the aversive properties of extinction was obtained by Davis and Donenfeld (1967). They showed that actual fighting occurred between pairs of rats working together in a two-lever apparatus when they

were placed in extinction following reinforcement on either a DRL or fixed ratio schedule.

Results of the DRL 8 sec. experiment further support the proposition that septal animals are hypersensitive to the aversive properties of nonreinforcement. These showed that the frequency of the short IRTs did not decrease for the septal animals from the first day of the procedure to the last at each probability contingency. Fewer short IRTs were evidenced by the control animals by the last nonreinforcement day. Terrace (1966b) has demonstrated that certain phenomena associated with discrimination training involving alternate conditioning and extinction also adapt out with extended exposure to the discriminative stimuli. These results supported his conclusion that both of the phenomena (behavioral contrast and the peak shift) were generated by aversive conditions associated with the occurrence of nonreinforced responses in the presence of S⁻.

The finding that septal animals did not manifest a trend toward longer postreinforcement pauses on nonreinforcement days until long after control and cingulate subjects did is further indication of their increased sensitivity to nonreinforcement. The trend toward long IRTs following a reinforced response on nonreinforcement days was seen only when the criterion IRT was equal to 8 sec. In this condition, there was a high probability that a reinforcement would follow a long delayed response and a low probability that a

short IRT would be reinforced, so that response suppression was the most likely response. The result of not reinforcing some of the criterion responses on nonreinforcement days was to increase the likelihood of a long IRT following a reinforced response, therefore supposedly increasing the probability that the long IRT would eventuate in reinforcement. In contrast to this, short latencies were reinforced according to the 0.6 sec. contingency, so that the probability of a reinforcement following a short IRT was high. The effect of omitting occasional reinforcements following a brief latency response was merely to increase the probability of another short latency response, even when the first response had been reinforced.

Implications for septal function

The thesis presented in this paper stated that destruction of the septal forebrain produces increased sensitivity to aversive events. The results of the present experiments and other results cited support this proposition. It was further suggested that the primary function of the septal area is the regulation of inhibitory control over the neural systems which regulate reactivity to the reinforcing properties of stimuli. According to this proposition, septal lesions "disinhibit" reactivity to the reinforcing properties of stimuli. However, the specific behavior which manifests this "release from inhibitory control" will depend on the stimuli, and the contingencies associated with those stimuli,

which control behavior. For instance, the lack of response suppression in septal animals noted in studies using shock, which are designed according to the conditioned emotional response or passive avoidance response paradigms, may possibly be due to the increased reinforcing value of the positive reinforcer (Brady & Nauta, 1955; McCleary, 1961). Studies in which the deficit is obtained and animals are not simultaneously responding for positive reinforcement may be due to an enhanced unconditioned or startle response to the conditioned stimulus (Brady & Nauta, 1953; Trafton, 1967).

The present position is supported by several other investigators who have offered an analysis of septal function which is similar to the one presented here (King, 1958; Harvey et al., 1965; Zucker, 1965; Beatty & Schwartzbaum, 1967). Zucker (1965) postulated that one function of the septal area is to "dampen the increment in response strength which normally is induced by a reinforcement." This explanation proposes that the septal area exerts control over some kind of associative mechanism involved in learning. The present position maintains that the septal forebrain influences reactivity to the reinforcing properties of stimuli. This position is in agreement with the explanation offered by Beatty and Schwartzbaum (1967). They postulated that the primary function of the septal area is the regulation of inhibitory control over a neural incentive-reward system which involves hypothalamic and ventral tegmental components via

the medial forebrain bundle system. This conclusion was based on the finding that adulteration of the drinking water by the addition of quinine HCl or Na saccharine significantly decreased or increased, respectively, the septals' fluid consumption relative to that of controls. However, neither of these concepts as put forth can account for other results obtained showing that the response strength of septal animals for positive reinforcement does not differ from that of controls. Septal animals do not increase rate on a variable interval schedule for food reinforcement (Schwartzbaum et al., 1964; Butters & Rosvold, 1968) or in the fixed ratio component of a multiple schedule for water reward (Ellen & Powell, 1962a). Neither did they demonstrate increased running speed in a straight runway for water reinforcement (Wolfe et al., 1967).

Donovick (in press) has suggested that different neural pathways may be involved in the various behavioral changes which have been reported following septal lesions. This suggestion was based upon results showing that septohippocampal connections are important in response inhibition which is required for successful completion of a task such as reversal of a spatial discrimination. Facilitation of active avoidance problems seemed to be independent of hippocampal activity insofar as the hippocampal theta rhythm did not change during learning. Carey (1967b) has shown the independence of increased water intake and behavior change following septal

lesions, further suggesting the involvement of different neural pathways within the septal region in different behavioral phenomena.

Recent results have indicated that at least some of the behavioral deviations of septal operates may be due to disturbances in pituitary functioning which are mediated through the septal region via hypothalamic connections to the pituitary gland. This gland controls the organism's fluid balance through secretions of antidiuretic hormone (ADH), and the functioning of the adrenal glands through secretions of adrenocorticotrophic hormone (ACTH). Extensive anatomical projections from the septum to the ventral and lateral hypothalamic areas directing pituitary function have been demonstrated (Crosby et al., 1962; Grossman, 1967; Powell, 1963, 1966; Powell & Rorie, 1967). Behavioral studies have reported changes in fluid consumption of septal lesioned rats (Harvey & Hunt, 1965; Pizzi & Lorens, 1967; Carey, 1967a, 1967b; Beatty & Schwartzbaum, 1968; Donovanick & Burrigh, 1968). Some of these results have been accompanied by indications of metabolic disturbances which are symptomatic of malfunction of the pituitary gland (Vilar, Gentil, & Covian, 1967; Lubar, Boyce, & Schaefer, 1968). Results reported by Endroczi and Lissak (1960) demonstrated that destruction of the anterior region of the septum results in markedly elevated corticosteroid levels in venous adrenal blood. This increased activity of the adrenal cortex would result from increased

secretion of ACTH from the anterior hypophysis. The correlation between increased reactivity of septal animals to aversive events and increased pituitary activity is further substantiated by Brady (1966). The results of an extensive series of studies showed increased blood steroid levels in monkeys following exposure to several different types of conditioning techniques using shock. These increased steroid levels were not seen following reinforcement on appetitive schedules.

Although the precise role of the neurologic and parametric variables which interact to control behavior changes associated with septal lesions cannot be accurately defined at the present time, two major trends are indicated: (1) results suggest that there may be several neural "circuits" within the septal region that are critically involved in the mediation of different behavioral phenomena; (2) increased activity of the hypophysis is implicated in reactivity to those stimulus events containing aversive properties.

Cingulate lesions

The prediction was made earlier that cingulate lesioned animals would not show marked changes in response rates during the nonreinforcement procedure. This prediction was based on evidence that monkeys with the anterior cingulate cortex removed did not show the increase in frequency of very short IRTs shown by controls when the DRL schedule on which they were working was lengthened by sixty seconds (Stamm,

1964). Cingulate rats were also shown to extinguish a food-reinforced response more rapidly than controls (Schwartzbaum et al., 1964). Both of these results indicated that cingulate lesioned animals may be less reactive to aversive events than are normal animals. This conclusion was also based on results which reported reduced fear of humans and cagemates in monkeys following removal of the cingulate cortex (Ward, 1948; Glees, Cole, Whitty, & Cairns, 1950). The results of the present studies, however, do not support this conclusion. There were no differences between cingulate and control animals in their responsivity to the nonreinforcing event. Both groups demonstrated an increase in rapid responding on non-reinforcement days which was significantly different from their response rates when regular DRL reinforcement conditions were in effect.

In contrast to the decreased emotionality posited to explain the results described above, results of several experiments testing cingulate lesioned animals in an avoidance task have been interpreted as indicating increased reactivity to noxious stimulation. These studies demonstrated that lesions in the anterior cingulate cortex impair the acquisition and/or retention of active avoidance responses in a two-way shuttle-box task (Peretz, 1960; McCleary, 1961; Thomas & Slotnick, 1962, 1963; Trafton, 1967; Kimble & Gostnell, 1968). The deficits observed in these studies were attributed to an increase in the strength of the freezing response to noxious

stimulation (Thomas & Slotnick, 1963). However, this hypothesis was tested by Trafton (1967), and it was found that animals with the anterior cingulate cortex removed were significantly slower than controls in acquisition of the freeze response as required in the conditioned emotional response paradigm. Kimble and Gostnell (1968) have also reported increased activity of cingulate lesioned rats in an open field.

It therefore seems that another factor besides emotional reactivity is affected by cingulate lesions. Barker and Thomas (1965) have suggested that the deficits seem to be most apparent when performance involves the temporal integration of a sequence of responses. This conclusion was derived from studies which reported disturbances in the performance of responses involved in maternal behavior, such as pup-retrieving and nest-building (Stamm, 1955; Slotnick, 1963) and hoarding activity (Stamm, 1954). The conclusion is corroborated by results showing that behavior in an appetitive learning situation is not affected by anterior cingulate lesions (Peretz, 1960; Thomas & Slotnick, 1962; Ellen & Powell, 1962a). Results obtained by Barker (1967) testing this hypothesis demonstrated that ablation of the anterior cingulate region severely impaired performance for food which was contingent upon the correct completion of a sequence of bar-presses on either two or four levers. It is therefore possible that the deficits observed in shock avoidance behavior may be more concerned with the learning of specific response

sequences than with deviant emotional responsivity to aversive stimulation.

The present experiments did not involve a complex sequence of discrete responses and therefore may not have provided an opportunity for the deficit to appear. The finding that there was no difference between cingulate and control animals in reactivity to the nonreinforcing event supports the contention that reactivity to aversive stimulus events is not the primary characteristic affected by anterior cingulate lesions. Lyon and Harrison (1959) initially made this suggestion based on their results showing that rats with the anterior cingulate cortex destroyed were no different than controls in postoperative recovery time of an escape response from a noxious stimulus (150 dB. noise). They interpreted their results as indicating that the anterior cingulate cortex is less involved in affective behavior than was previously thought.

Notable differences were obtained between cingulate and control animals in the DRL 8 sec. group on nonreinforcement days in the frequency of very long IRTs which occurred following a criterion IRT which was reinforced. The reason for this increase in long IRTs is unclear. To the writer's knowledge, there are no previous reports in the literature of enhanced response suppression following a reinforced response. Wolfe et al. (1967) did report slower running times for cingulate animals in a straight alley for water reward.

Again, however, interpretations of this finding were limited.

Wolfe et al. (1967) also reported no differences in extinction of the running response between cingulate and control rats. They stated that this finding did not support the proposition that cingulate lesions enhance inhibitory control as was postulated by Kaada (1960). The present results did not support the hypothesis formulated on the basis of Kaada's stimulation work either. This hypothesis proposed that the supracallosal region exerts a facilitating influence over somatomotor activity. The results led to the prediction by McCleary (1961) that cingulate lesions should enhance inhibitory control. If this were the case, then it might be expected that cingulate animals would acquire DRL timing behavior sooner than controls, and that they would not demonstrate increased rates following nonreinforcement. Neither of these predictions was supported by the present results.

It is therefore concluded that neither the emotionality hypothesis nor the response inhibition hypothesis is adequate to account for the diverse behavioral phenomena which have been reported to be affected by anterior cingulate lesions. A promising analysis of deficiencies following cingulate lesions is that which proposes that the primary disturbance is in the organized performance of complex sequences of behavior. However, a more precise analysis of the behaviors affected by cingulate lesions and more exact anatomical localization is needed before an accurate definition of dysfunctions result-

ing from cingulate destruction can be achieved.

Summary and Conclusions

Two experiments were conducted which were designed to test the effects of lesions in the cingulate cortex or the septal forebrain on timing behavior generated by the DRL schedule of reinforcement and on reactivity to a nonreinforcing event. In the first experiment, the performance of septal, cingulate, and control rats was stabilized on a DRL 8 sec. schedule of reinforcement. Reinforcements were then periodically and randomly withheld on alternate days following a correct timing response according to a specified probability. The probability of nonreinforcement was varied systematically from 0.0 to 1.0 (extinction). Independent interresponse time distributions were obtained following a correct response which was reinforced and one which was not. These were then compared to the IRF distributions obtained on days when the regular DRL reinforcement contingency was in effect. In the second experiment, septal, cingulate, and control rats were first tested on a DRL 1.2 sec. schedule of reinforcement which was then reduced to 0.6 sec. On the DRL 0.6 sec. schedule, subjects' responses were almost always reinforced. Baseline reinforcement rates were therefore equated for all groups.

Results obtained showed that the behavior of septal operates was inefficient and accelerated above control levels

under either one of two conditions: (1) when they were required to suppress responding for 1.2 sec. or longer, and (2) when reinforcement for a previously rewarded response was withheld. The latter result was obtained only when the baseline reinforcement rate of septals was equal to that of the controls. Under a regular DRL contingency which was 1.2 sec. or greater, the IRT distributions of septal operates demonstrated a very high frequency of rapid responses which were found to be related to a high frequency of IRTs which were nearly but not quite long enough to meet the DRL criterion. Under nonreinforcement conditions, timing efficiency decreased for all groups as a function of the probability of nonreinforcement. The reduced efficiency on nonreinforcement days was shown to be due to a marked increase in the frequency of rapid responses. On the basis of evidence obtained from other studies, contingent response suppression and omission of reinforcement were presumed to constitute aversive events. The results were therefore taken to support the proposition that septal lesioned animals are hyperreactive to aversive events.

Animals with the anterior cingulate cortex removed were no different than controls under most of the experimental conditions. Notable differences were obtained in cingulate subjects working on the DRL 8 sec. contingency in the frequency of very long IRTs which occurred following a criter-

ion IRT which was reinforced. The results were taken as evidence against the hypothesis that cingulate lesions enhance inhibitory control. They were discussed in relation to findings indicating that the primary deficit following cingulate lesions is in the organized performance of complex sequences of behavior.

References

- Adelman, H. M. & Maatsch, J. L. Learning and extinction based upon frustration, food reward, and exploratory tendency. J. exp. Psychol., 1956, 52, 311-315.
- Amsel, A. The role of frustrative non-reward in non-continuous reward situations. Psychol. Bull., 1958, 55, 102-119.
- Amsel, A. Frustrative nonreward in partial reinforcement and discrimination learning: some recent history and theoretical extension. Psychol. Rev., 1962, 69, 306-328.
- Azrin, N. H., Hutchinson, R. R., & Hake, D. F. Extinction-induced aggression. J. exp. Anal. Behav., 1966, 9, 191-204.
- Bard, P. Central nervous mechanisms for the expression of anger in animals. In M. L. Reymert (Ed.), Feelings and emotions: The Moosehart Symposium. New York: McGraw-Hill, 1950. Pp. 211-257.
- Bard, P. & Mountcastle, V. B. Some forebrain mechanisms involved in the expression of rage with special reference to suppression of angry behavior. Res. Publ. nerv. ment. Dis., 1948, 27, 362-404.
- Barker, D. J. Alterations in sequential behavior of rats following ablation of midline limbic cortex. J. comp. physiol. Psychol., 1967, 64, 453-460.
- Barker, D. J. & Thomas, G. J. Ablation of cingulate cortex in rats impairs alternation learning and retention. J. comp. physiol. Psychol., 1965, 60, 353-359.
- Beatty, W. W. & Schwartzbaum, J. S. Enhanced reactivity to quinine and saccharine solutions following septal lesions in the rat. Psychon. Sci., 1967, 8, 483-484.
- Beatty, W. W. & Schwartzbaum, J. S. Consummatory behavior for sucrose following septal lesions in the rat. J. comp. physiol. Psychol., 1968, 65, 93-102.
- Brady, J. V. Operant methodology and the experimental production of altered physiological states. In W. Honig

(Ed.), Operant behavior: Areas of research and application. New York: Appleton-Century-Crofts, 1966. Pp. 609-633.

- Brady, J. V. & Nauta, W. J. H. Subcortical mechanisms in emotional behavior: affective changes following septal forebrain lesions in the albino rat. J. comp. physiol. Psychol., 1953, 46, 339-346.
- Brady, J. V. & Nauta, W. J. H. Subcortical mechanisms in emotional behavior: the duration of affective changes following septal and habenular lesions in the albino rat. J. comp. physiol. Psychol., 1955, 48, 412-420.
- Brethower, D. & Reynolds, G. S. A facilitative effect of punishment on unpunished behavior. J. exp. Anal. Behav., 1962, 5, 191-199.
- Buddington, R. W., King, F. A., & Roberts, L. Emotionality and conditioned avoidance responding in the squirrel monkey following septal injury. Psychon. Sci., 1967, 8, 195-196.
- Burkett, E. E. & Bunnell, B. D. Septal lesions and the retention of DRL performance in the rat. J. comp. physiol. Psychol., 1966, 62, 468-471.
- Butters, N. & Rosvold, H. E. Effect of caudate and septal nuclei lesions on resistance to extinction and delayed alternation. J. comp. physiol. Psychol., 1968, 65, 397-403.
- Carey, R. J. Contrasting effects of increased thirst and septal ablations on DRL responding in rats. Physiol. Behav., 1967, 2, 287-290. (a)
- Carey, R. J. Independence of effects of septal ablations on water intake and response inhibition. Psychon. Sci., 1967, 8, 3-4. (b)
- Crosby, E., Humphrey, T., & Lauer, E. Correlative anatomy of the nervous system. New York: Macmillan, 1962.
- Davis, H. & Donenfeld, I. Extinction induced social interaction in rats. Psychon. Sci., 1967, 7, 85-86.
- DiLollo, V., Davidson, R. C., Hammond, G. R., & Donovan, R. The relative effects of nonreward and response thwarting on the frustration effect. Psychon. Sci., 1968, 8, 31-32.
- Donovick, P. J. Effects of localized septal lesions on hippocampal EEG activity and behavior in rats. J. comp. physiol. Psychol., in press.

- Donovick, P. J. & Burrigh, R. G. Water consumption of rats with septal lesions following two days of water deprivation. Physiol. Behav., 1968, 3, 285-288.
- Ellen, P. & Powell, E. W. Effects of septal lesions on behavior generated by positive reinforcement. Exp. Neurol., 1962, 6, 1-11. (a)
- Ellen, P. & Powell, E. W. Temporal discrimination in rats with rhinencephalic lesions. Exp. Neurol., 1962, 6, 538-547. (b)
- Ellen, P., Wilson, A. S., & Powell, E. W. Septal inhibition and timing behavior in the rat. Exp. Neurol., 1964, 10, 120-132.
- Endroczi, E. & Lissak, K. The role of mesencephalon, diencephalon, and archicortex in the activation and inhibition of the pituitary-adrenocortical system. Acta Physiol. Hung., 1960, 17, 39-55.
- Estes, W. K. & Skinner, B. F. Some quantitative properties of anxiety. J. exp. Psychol., 1941, 29, 390-400.
- Falk, J. L. Schedule-induced polydipsia as a function of FI length. J. exp. Anal. Behav., 1966, 9, 37-39.
- Farmer, J. & Schoenfeld, W. N. Inter-reinforcement times for the bar-pressing response of white rats on two DRL schedules. J. exp. Anal. Behav., 1964, 7, 119-122.
- Ferraro, D. P., Schoenfeld, W. N., & Snapper, A. G. Sequential response effects in the white rat during conditioning and extinction on a DRL schedule. J. exp. Anal. Behav., 1965, 8, 255-260.
- Ferster, C. B. Control of behavior in chimpanzees and pigeons by time out from positive reinforcement. Psychol. Monogr., 1958, 72, 1-38 (Whole No. 461).
- Glees, P., Cole, J., Whitty, C. W. M., & Cairns, H. The effects of lesions in the cingular gyrus and adjacent areas in monkeys. J. Neurol. Neurosurg. Psychiat., 1950, 13, 178-190.
- Green, P. C. & Levinthal, C. F. Effects of subcallosal lesions on "hypothesis" behavior in rats. Psychon. Sci., 1967, 7, 113-114.
- Green, R. H. & Schwartzbaum, J. S. Effects of unilateral septal lesions on avoidance behavior, discrimination reversal and hippocampal EEG. J. comp. physiol. Psychol., 1968, 65, 388-396.

- Gibbon, J. Discriminated punishment: avoidable and unavoidable shock. J. exp. Anal. Behav., 1967, 5, 451-460.
- Groot, J. de. The rat forebrain in stereotaxic coordinates. N. V. Noord-Hollandsche Uitgevers Maatschappij, 1959.
- Grossman, S. P. A textbook of physiological psychology. New York: Wiley, 1967.
- Guilford, J. P. Fundamental statistics in psychology and education. New York: McGraw-Hill, 1956.
- Harvey, J. A. & Hunt, H. F. Effect of septal lesions on thirst in the rat as indicated by water consumption and operant responding for water reward. J. comp. physiol. Psychol., 1965, 59, 49-56.
- Harvey, J. A., Lints, C. E., Jacobsen, C. E., & Hunt, H. F. Effects of lesions in the septal area on conditioned fear and discriminated instrumental punishment in the albino rat. J. comp. physiol. Psychol., 1965, 59, 37-48.
- Hearst, E., Koresko, M. B., & Poppen, R. Stimulus generalization and the response-reinforcement contingency. J. exp. Anal. Behav., 1964, 7, 369-382.
- Kaada, B. R. Somatomotor, autonomic, and electrocorticographic responses to electrical stimulation of "rhinencephalic" and other structures in primate, cat, and dog. Acta Physiol. Scand., 1951, 226, 24, Suppl. 83.
- Kaada, B. R. Cingulate, posterior orbital, anterior insular, and temporal polar cortex. In J. Field (Ed.), Handbook of physiology. Sec. 1: Neurophysiology, Vol. 2. Washington, D. C.: American Physiological Society, 1960.
- Kaada, B. R., Rasmussen, E. W., & Kveim, O. Impaired acquisition of passive avoidance behavior by subcallosal, septal, hypothalamic, and insular lesions in rats. J. comp. physiol. Psychol., 1962, 55, 661-670.
- Keller, F. S. & Schoenfeld, W. N. Principles of psychology. New York: Appleton-Century-Crofts, 1950.
- Kenyon, J. & Krieckhaus, E. E. Enhanced avoidance behavior following septal lesions in the rat as a function of lesion size and spontaneous activity. J. comp. physiol. Psychol., 1965, 59, 460-468.

- Kimble, D. P. & Gostnell, D. Role of cingulate cortex in shock avoidance behavior of rats. J. comp. physiol. Psychol., 1958, 65, 290-294.
- King, F. A. Effects of septal and amygdaloid lesions on emotional behavior and CER in the rat. J. nerv. ment. Dis., 1958, 126, 57-63.
- King, F. A. Relationship of the "septal syndrome" to genetic differences in emotionality in the rat. Psychol. Rep., 1959, 5, 11-17.
- Krieckhaus, E. E., Simmons, H. J., Thomas, G. J., & Kenyon, J. Septal lesions enhance shock avoidance behavior in the rat. Exp. Neurol., 1964, 9, 107-113.
- Krieg, W. J. S. Connections of the cerebral cortex. I. The albino rat. A. Topography of the cortical areas. J. comp. Neurol., 1946, 84, 221-275.
- Latties, V. G., Weiss, B., Clark, R. L., & Reynolds, M. J. Overt "mediating" behavior during temporally spaced responding. J. exp. Anal. Behav., 1965, 8, 107-116.
- LaVaque, F. J. Conditioned avoidance response perseveration in septal rats during massed extinction trials. Psychon. Sci., 1966, 5, 409-410.
- Leitenberg, H. Is time-out from positive reinforcement an aversive event? A review of experimental evidence. Psychol. Bull., 1965, 64, 428-441.
- Leitenberg, H. Conditioned acceleration and conditioned suppression in pigeons. J. exp. Anal. Behav., 1966, 9, 205-212.
- Levine, G. & Loesch, R. Generality of response intensity following nonreinforcement. J. exp. Psychol., 1967, 75, 97-102.
- Lints, C. E. Changes in sensitivity to electric shock following CNS lesions in the rat. Doctoral dissertation, University of Chicago, 1965.
- Lorens, S. A. & Brown, F. S. Influence of the septal area on visual evoked potentials. Exp. Neurol., 1967, 17, 86-90.

- Lubar, J. F. Effect of medial cortical lesions on the avoidance behavior of the cat. J. comp. physiol. Psychol., 1964, 58, 38-64.
- Lubar, J. F., Boyce, B. A., & Schaefer, C. F. Etiology of polydipsia and polyuria in rats with septal lesions. Physiol. Behav., 1968, 3, 289-292.
- McCleary, R. A. Response specificity in the behavioral effects of limbic system lesions in the cat. J. comp. physiol. Psychol., 1961, 54, 605-613.
- McMillan, D. E. A comparison of the punishing effects of response-produced shock and response-produced time out. J. exp. Anal. Behav., 1967, 10, 439-449.
- McNew, J. J. & Thompson, R. Role of the limbic system in active and passive avoidance conditioning in the rat. J. comp. physiol. Psychol., 1966, 61, 173-180.
- Mowrer, O. H. Learning theory and behavior. New York: Wiley, 1960.
- Nevin, J. A. & Shettleworth, S. J. An analysis of contrast effects in multiple schedules. J. exp. Anal. Behav., 1966, 9, 305-315.
- Nigro, M. R. Punishment of an extinguishing shock-avoidance response by time-out from positive reinforcement. J. exp. Anal. Behav., 1966, 9, 53-62.
- Notterman, J. M. & Mintz, D. E. Dynamics of response. New York: Wiley, 1965.
- Peretz, E. The effects of lesions of the anterior cingulate cortex on the behavior of the rat. J. comp. physiol. Psychol., 1960, 53, 540-548.
- Pizzi, W. J. & Lorens, S. A. Effects of lesions in the amygdalo-hippocampo-septal system on food and water intake in the rat. Psychon. Sci., 1967, 7, 187-188.
- Pliskoff, S. S. Rate-change effects during a pre-schedule-change stimulus. J. exp. Anal. Behav., 1961, 4, 383-386.
- Pliskoff, S. S. Rate-change effects with equal potential reinforcements during the "warning" stimulus. J. exp. Anal. Behav., 1963, 6, 557-562.
- Powell, E. W. Septal efferents revealed by axonal degeneration in the rat. Exp. Neurol., 1963, 8, 406-422.

- Powell, E. W. Septal efferents in the cat. Exp. Neurol., 1966, 14, 328-337.
- Powell, E. W. & Rorie, D. K. Septal projections to nuclei functioning in oxytocin release. Amer. J. Anat., 1967, 120, 605-610.
- Rich, I. & Thompson, R. Role of the hippocampal-septal system, thalamus, and hypothalamus in avoidance conditioning. J. comp. physiol. Psychol., 1965, 59, 66-72.
- Schwartzbaum, J. S. & Donovan, P. J. Discrimination reversal and spatial alternation associated with septal and caudate dysfunction in rats. J. comp. physiol. Psychol., 1968, 65, 83-92.
- Schwartzbaum, J. S. & Gay, P. E. Interacting behavioral effects of septal and amygdaloid lesions in the rat. J. comp. physiol. Psychol., 1966, 61, 59-65.
- Schwartzbaum, J. S., Green, R. N., Beatty, W. W., & Thompson, J. B. Acquisition of avoidance behavior following septal lesions in the rat. J. comp. physiol. Psychol., 1967, 63, 95-104.
- Schwartzbaum, J. S., Kellicutt, M. H., Spieth, T. M., & Thompson, J. B. Effects of septal lesions in rats on response inhibition associated with food reinforced behavior. J. comp. physiol. Psychol., 1964, 58, 217-224.
- Segal, E. F. & Holloway, S. M. Timing behavior in rats with H₂O drinking as a mediator. Science, 1963, 140, 888-889.
- Sidman, M. Time discrimination and behavioral interaction in a free operant situation. J. comp. physiol. Psychol., 1956, 49, 469-473.
- Staddon, J. E. R. & Innes, N. K. An effect analogous to "frustration" on interval S^R schedules. Psychon. Sci., 1966, 4, 287-288.
- Stamm, J. S. Control of hoarding activity in rats by the median cerebral cortex. J. comp. physiol. Psychol., 1954, 47, 21-27.
- Stamm, J. S. The function of the median cerebral cortex in maternal behavior of rats. J. comp. physiol. Psychol., 1955, 48, 347-356.
- Stamm, J. S. Function of cingulate and prefrontal cortex in frustrative behavior. Acta Biol. Exp., 1964, 24, 27-36.

- Tacker, R. S. & Way, J. Motivational properties of nonreward. Psychon. Sci., 1968, 10, 103-104.
- Terrace, H. S. Stimulus control. In W. Honig (Ed.), Operant behavior: Areas of research and application. New York: Appleton-Century-Crofts, 1966. Pp. 271-344. (a)
- Terrace, H. S. Behavioral contrast and the peak shift: effects of extended discrimination training. J. exp. Anal. Behav., 1966, 2, 613-617. (b)
- Thomas, G. J., Moore, R. Y., Harvey, J. A., & Hunt, H. F. Relations between the behavioral syndrome produced by lesions in the septal region of the forebrain and maze learning in the rat. J. comp. physiol. Psychol., 1959, 52, 527-532.
- Thomas, G. J. & Slotnick, B. M. Effects of lesions in the cingulum on maze learning and avoidance conditioning in the rat. J. comp. physiol. Psychol., 1962, 55, 1085-1091.
- Thomas, G. J. & Slotnick, B. M. Impairment of avoidance responding by lesions in the cingulate cortex in rats depends on food drive. J. comp. physiol. Psychol., 1963, 56, 959-964.
- Thompson, D. M. The effect of two phenothiazines and a barbiturate on extinction-induced rate increase of a free operant. J. comp. physiol. Psychol., 1962, 55, 714-718.
- Thompson, D. M. Escape from SD associated with fixed-ratio reinforcement. J. exp. Anal. Behav., 1964, 7, 1-8.
- Trafton, C. L. Effects of lesions in the septal area and cingulate cortical areas on conditioned suppression of activity and avoidance behavior in rats. J. comp. physiol. Psychol., 1967, 63, 191-197.
- Ulrich, R. & Azrin, N. H. Reflexive fighting in response to aversive stimulation. J. exp. Anal. Behav., 1962, 5, 511-520.
- Vanderwolf, C. H. Effect of combined medial thalamic and septal lesions on active-avoidance behavior. J. comp. physiol. Psychol., 1964, 58, 31-37.
- Vilar, A. N., Gentil, C. G., & Covian, M. R. Alterations in sodium chloride and water intake after septal lesions in the rat. Physiol. Behav., 1967, 2, 167-170.
- Wagner, A. R. Conditioned frustration as a learned drive. J. exp. Psychol., 1963, 66, 142-148.

- Ward, A. A., Jr. The cingular gyrus. Area 24. J. Neurophysiol., 1948, 2, 13-23.
- Wetzel, A. B., Conner, R. L., & Levine, S. Shock-induced fighting in septal-lesioned rats. Psychon. Sci., 1967, 9, 133-134.
- Winer, B. J. Statistical principles in experimental design. New York: McGraw-Hill, 1962.
- Wolfe, J. W., Lubar, J. F., & Ison, J. R. Effects of medial cortical lesions on appetitive instrumental conditioning. Physiol. Behav., 1967, 2, 239-244.
- Zimmerman, J. & Ferster, C. B. Intermittent punishment of S responding in matching to sample. J. exp. Anal. Behav., 1963, 6, 349-356.
- Zucker, I. Comment on Kenyon and Krieckhaus. Psychon. Sci., 1965, 3, 298. (a)
- Zucker, I. Effect of lesions of the septal limbic area on the behavior of cats. J. comp. physiol. Psychol., 1965, 60, 344-352. (b)
- Zucker, I. & McCleary, R. A. Perseveration in septal cats. Psychon. Sci., 1964, 1, 387-388.

Appendix A

Evidence for Behavioral Assumptions

The present analysis of behavior resulting from septal lesions is predicated upon two major assumptions: (1) that response acceleration is the unconditioned response to omission of positive reinforcement, and (2) that omission of reward constitutes an aversive event. Studies attempting to define omission of reward as aversive are usually confounded by the presence of a contingency whereby the organism is simultaneously performing some response to obtain positive reinforcement. The difficulty encountered involves the fact that in escaping from, or preventing, the occurrence of omission of reward, the subject also maximizes his "time-in" the positive reinforcement condition (Ferster, 1958). Therefore, the escape or avoidance behavior shown may not be evidence of aversion, but may "only indicate that subjects will maintain behavior which leads to positive reinforcement" (Leitenberg, 1965). However, McMillan (1967) has pointed out that the aversive properties of nonreinforcement may be a function of the reduction in reinforcement rate so that it may be impossible to test for these properties independently of a reduction in reinforcement density.

The importance of this statement is emphasized by results of studies showing that time-out will only result in behavior typical of paradigms using shock when the consequence of responding is a decrease in reinforcement density or complete removal of positive reinforcement. Otherwise, the response to omission of reward is not as would be expected on the basis of the criteria generally used for defining an aversive event. These criteria were formulated on the basis of experiments which used shock as the reinforcer. Thus, it was assumed (Keller & Schoenfeld, 1950) that an aversive event would suppress the behavior which produced it (punishment contingency; passive avoidance--Mowrer, 1960), or maintain behavior above operant level which terminated (escape) or prevented (active avoidance) its occurrence. Studies have shown that response suppression will result when the organism can successfully avoid the nonreinforcing event (Ferster, 1958; Nigro, 1966; McMillan, 1967). In these studies, not responding resulted in avoiding a significant decrease in reinforcement density. Other studies have shown that acceleration of ongoing behavior results when the organism cannot avoid the time-out contingency. In the same study in which he reported that chimps suppressed responding in the presence of a pre-time-out stimulus when doing so avoided the time-out, Ferster (1958) also reported an increase in rate in the presence of a stimulus signaling unavoidable time-out. Studies by Pliskoff (1961, 1963) have demonstrated a similar

phenomenon; the relative reduction in reinforcement density on a multiple schedule produced an accelerated rate of responding in the presence of a stimulus preceding a shift to the lower reinforcement frequency component.

Whether a pre-time-out stimulus results in accelerated or decelerated rate therefore seems to critically depend upon the avoidability of the event. Leitenberg (1966) demonstrated that responding in the presence of a stimulus signaling unavoidable shock (conditioned emotional response paradigm) invariably resulted in suppression of responding on a variable interval baseline schedule for food reinforcement, while responding in the presence of a stimulus which signaled unavoidable time-out was consistently accelerated above baseline levels. In contrast to these results, McMillan (1967) demonstrated that responding in the presence of a preshock or pre-time-out stimulus was suppressed to an equal degree when shock or time-out was made response-contingent (punishment or passive avoidance contingency). The fact that suppression does not necessarily result when omission of reward is used in a typical aversive paradigm does not mean that the event may not be aversive. Gibbon (1967) demonstrated that rats would make a response which simultaneously resulted in a shock and made positive reinforcement available. The notion that shock was not aversive because the probability of a response which it followed was increased instead of de-

creased was never raised because of the known noxious properties of shock. It may thus be concluded that in the absence of any contingency for avoidance of omission of reward, the unconditioned response to that event will be response acceleration and this response will be conditioned to a correlated stimulus. This response does not negate the aversive properties of nonreward.

Appendix B

Schema for Behavioral Analysis of Aversive Events

In reviewing the literature attempting to describe the behavior changes which occur following damage to the septal forebrain or cingulate cortex, it was found convenient to conceptualize the effects of various reinforcing events in terms of several continua which might be used to describe the relativity of contingent control of behavior (also Mintz, personal communication). The proposed principle of operation is schematized in Figure 20. Two single stimulus events, whose reinforcing properties are fairly well established, have been included in the schematic for illustrative purposes, but any complex stimulus-response relation may be subject to the same analysis.

The continuum represents an increase or decrease along some dimension of change in the response-reinforcement contingency; the relation could be scaled on the basis of quantifiable parameters of the reinforcer (such as magnitude and frequency), or on the basis of quantifiable parameters of the contingency relation between the response and the reinforcer (such as number of responses required for reinforcement, reinforcements per unit time, etc.). The absolute positive

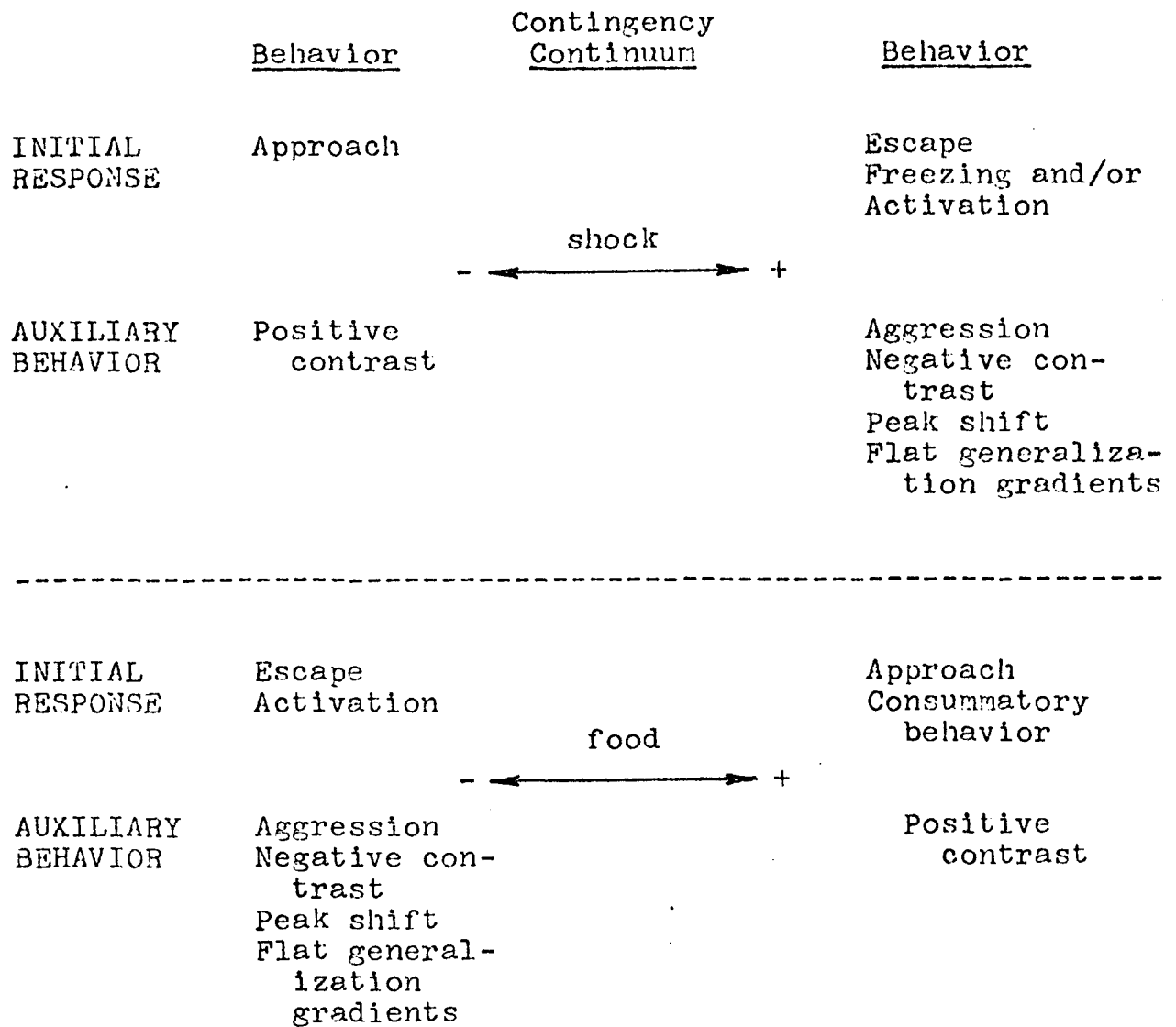


Figure 20.--Schematic representation of behavioral analysis of aversive events. See text for explanation.

or negative reinforcing properties of a single stimulus are defined on the basis of the initial, or unconditioned, response to presentation or withdrawal of the event, in the absence of any contingency.

Inherent in the above rationale is the existence of two classes of positive and negative events which might be called Positive I and II and Negative I and II. These roman numerals designate respectively the classification of stimulus events on the basis of the initial or unconditioned response to the event, in the absence of any contingency (I), and on the basis of changes in behavior resulting from an increase or decrease in the contingency relation between response and reinforcement (II). For example, whether or not an organism will prevent the occurrence of a time-out from a positive reinforcer or will impose one upon himself will depend upon the associated response-reinforcement contingencies (Thompson, 1964; Zimmerman & Ferster, 1963). Where both positive and negative reinforcing events are present simultaneously (CER or passive avoidance paradigms), there is essentially some variant of a "conflict" situation, and behavior will be under the mutual control of the relative contingencies upon which each reinforcer is dependent and the relative strengths of the respective reinforcing events.

The criteria for defining a Positive or Negative I stimulus event specify the absolute differences between reinforcers; these differences may be manifest in the uncondi-

tioned response to the particular stimulus event. However, these criteria may be shown to be both inadequate and impractical when complex reinforcement-response paradigms are considered. In other words, it may not be possible to define an event (or aggregate of events) as positive or negative by subjecting it to test by the simple criteria posed above; for example, those situations involving a total stimulus complex which cannot be merely presented or withdrawn, such as a particular schedule of reinforcement. It may, however, be possible to extend the list of behaviors which can be used to define an "unknown" event as positive or negative on the basis of similarities of the behaviors observed in the "unknown" situation to those observed in one which has previously been defined as positive or negative. These are enumerated as auxiliary behaviors in Figure 20. McMillan (1967) has stated, with regard to the aversive properties of nonreinforcement, that "if it is assumed that shock suppresses behavior when applied as a punisher because it is aversive, then the degree to which time-out mimics the effect of shock under a variety of conditions may reflect the aversive aspects of time-out."

Several types of diverse behavioral phenomena have been described which appear to reflect prior experience with an aversive event since these behaviors are similar in situations using either shock or nonreinforcement (or decrease in density of reinforcement). The most compelling example is

probably that provided by Azrin et al. (1966), who demonstrated that pigeons conditioned to peck a key for food on a continuous reinforcement schedule would "viciously" attack another bird when extinction was introduced. These workers also demonstrated that occurrence of the conditioned key-pecking response was not necessary for the occurrence of the attack; interrupted free food deliveries which were presented according to a regular schedule also produced the attack. These results were similar to those obtained by Ulrich and Azrin (1962), who demonstrated that shock delivered to the feet of an animal results in severe attack. Davis and Donenfeld (1967) have recently reported varying degrees of aggressive responses appearing in pairs of rats working together in a two-lever apparatus when either one or both were placed in extinction following reinforcement on either a DRL 10 sec. or a fixed-ratio-24 schedule of reinforcement. Actual fighting occurred when both members of the pair were placed in extinction.

Terrace (1966a, p. 316; 1966b) has used the appearance of aggressive responses following extinction to support his contention that "behavioral contrast" and the "peak shift" phenomena are both manifestations of emotional responses which appear following exposure to a stimulus which is correlated with nonreinforcement. Both of these phenomena appear in conjunction with discrimination training which involves alternate conditioning (in the presence of S⁺) and

extinction (in the presence of S^-). These phenomena do not occur if discrimination training is conducted without errors. That is, if responses are never allowed to occur to S^- (by controlling its intensity, duration, etc.) and therefore never have to undergo suppression. Behavioral contrast was described by Reynolds (1961) as the change in behavior which occurs in the presence of one stimulus as a result of the change in schedule of reinforcement in the presence of another stimulus. Terrace demonstrated that following conditioning in the presence of S^+ , introduction and nonreinforcement of responses in the presence of S^- "induced" a rate increase in the presence of S^+ when it was re-presented. This behavior change could be demonstrated even after the discrimination had been formed, i.e., when little or no responding occurred in the presence of S^- . Brethower and Reynolds (1962) have previously demonstrated that a decrease in the rate of responding on a variable interval 3 min. schedule for food in the presence of a green stimulus which signaled response-contingent shock was accompanied by an increase in the rate of responding in the succeeding VI 3 min. component of the multiple schedule.

Nevin and Shettleworth (1966) have analyzed these effects in successive components of a multiple schedule for positive reinforcement. They observed that responding in one component of a multiple schedule was dependent upon the schedule of reinforcement correlated with the immediately

preceding stimulus. Positive contrast, an increase in rate, was found to result from responding in a preceding component which was correlated with a low frequency of reinforcement, or extinction. The opposite, or negative contrast (a decrease in rate), resulted when the preceding component was correlated with more frequent reinforcement; in this case, the response rate in the succeeding stimulus was lower than baseline levels. The interesting finding from the present point of view is the differentiation of "positive" and "negative" contrast. On the basis of the continua defined previously, positive contrast would be predicted to result from a shift from a stimulus event having low positive reinforcing value to one possessing greater positive reinforcing properties. Negative contrast, on the other hand, would result from the converse operations. This phenomenon may be useful in defining stimulus events as positive or negative when these properties are not immediately obvious, e.g., in situations where reinforcing properties cannot be defined merely by magnitude or frequency of reinforcement. It is interesting to note in this context that the decrease in rate which resulted from complete omission of reinforcement for the septal animals responding on the DRL 8 sec. schedule of reinforcement was accompanied by an overall increase in rate on the alternate days when the regular DRL conditions were in effect (perhaps an example of positive contrast).

That contrast is not limited to the specific response

which has been extinguished was demonstrated in an experiment by Levine and Loesch (1967) in which they observed increases in the force of bar-pressing for water reinforcement when another, dissimilar response--chain-pulling for food reinforcement--was extinguished. The response intensity on the lever consistently increased when chain-pull extinction was alternated with reinforcement for this response.

Another phenomenon consistently reported in conjunction with discrimination training which involves alternate conditioning and extinction is the shift in the point of response maxima away from the S^- in generalization tests conducted following the discrimination training (peak shift). The assumption that both behavioral contrast and the peak shift were phenomena generated by aversive conditions in the presence of S^- led Terrace (1966a) to infer that these "emotional responses" would adapt out with extended exposure to the discriminative stimuli. This prediction was supported by experiments demonstrating the gradual disappearance of the increased rate "induced" by training not to respond to S^- , and the gradual return of the response maxima to the original S^+ on generalization tests conducted periodically during discrimination training.

Since the behaviors which have been described result when shock is utilized as a stimulus event, it may be possible to use the appearance of these behaviors to classify other nonshock events as aversive. Similarly, positive

events may be defined with respect to the appearance of behaviors which are characteristic of a schedule of positive reinforcement such as food or water. Referring back to Figure 20, moving in either direction along the continua will change the reinforcing properties of the particular contingency according to which the animal is working. The behavior which results will depend upon the specific stimulus conditions. If the stimulus event can be presented or withdrawn, such as food or shock, the behaviors designated as "initial response" can be elicited. In more complex situations, such as schedules of reinforcement, the behaviors designated as "auxiliary behaviors" will result, depending upon the reinforcing properties of the stimulus conditions. The list of phenomena which can be used to classify "unknown" events as positive or negative is therefore extended to include complex behaviors which result from complex stimulus situations.

Appendix C

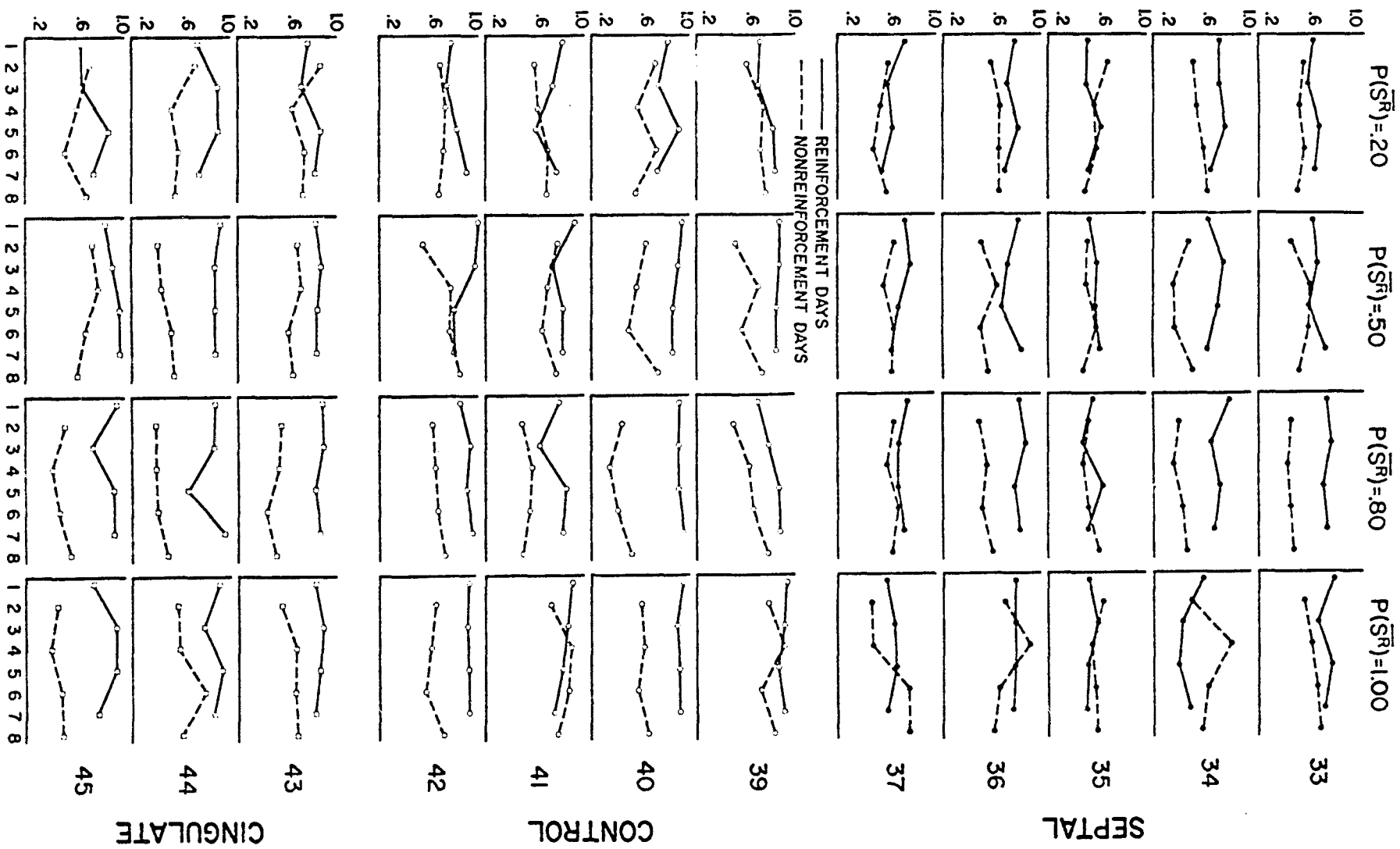
Individual Data

Figure 21 shows changes in efficiency for each S in the DRL 8 sec. group which occurred over days as a function of increasing the probability of nonreinforcement. The solid line functions present the efficiency ratios on the days when the regular DRL 8 sec. contingency was in effect, i.e., when every response equal to or greater than 8 sec. was reinforced. The dashed line functions show how timing behavior changed when every correct timing response was not reinforced according to the indicated probability.

One of the major differences to be noted here is the generally lower accuracy of timing behavior for all of the septal animals on days when all correct timing responses were reinforced. Poorest timing behavior was exhibited by the septal rat MAC 35, who sustained most extensive damage to the fornix complex. This is also the S who exhibited the minimum decrease in efficiency of timing behavior when the probability of reinforcement was reduced to less than 1.0. The other animals increased the frequency of incorrect timing responses when a reinforcement for a correct response was omitted, and the frequency of these increased as a function of the prob-

Figure 21.--Efficiency ratios for individual subjects from each operated group on DRL 8 sec. on reinforcement days (solid lines) and nonreinforcement days (dashed lines). Columns show the probability of nonreinforcement and rows are individual subjects within each operated group.

EFFICIENCY ($R_s \geq 8$ sec / Total R_s)



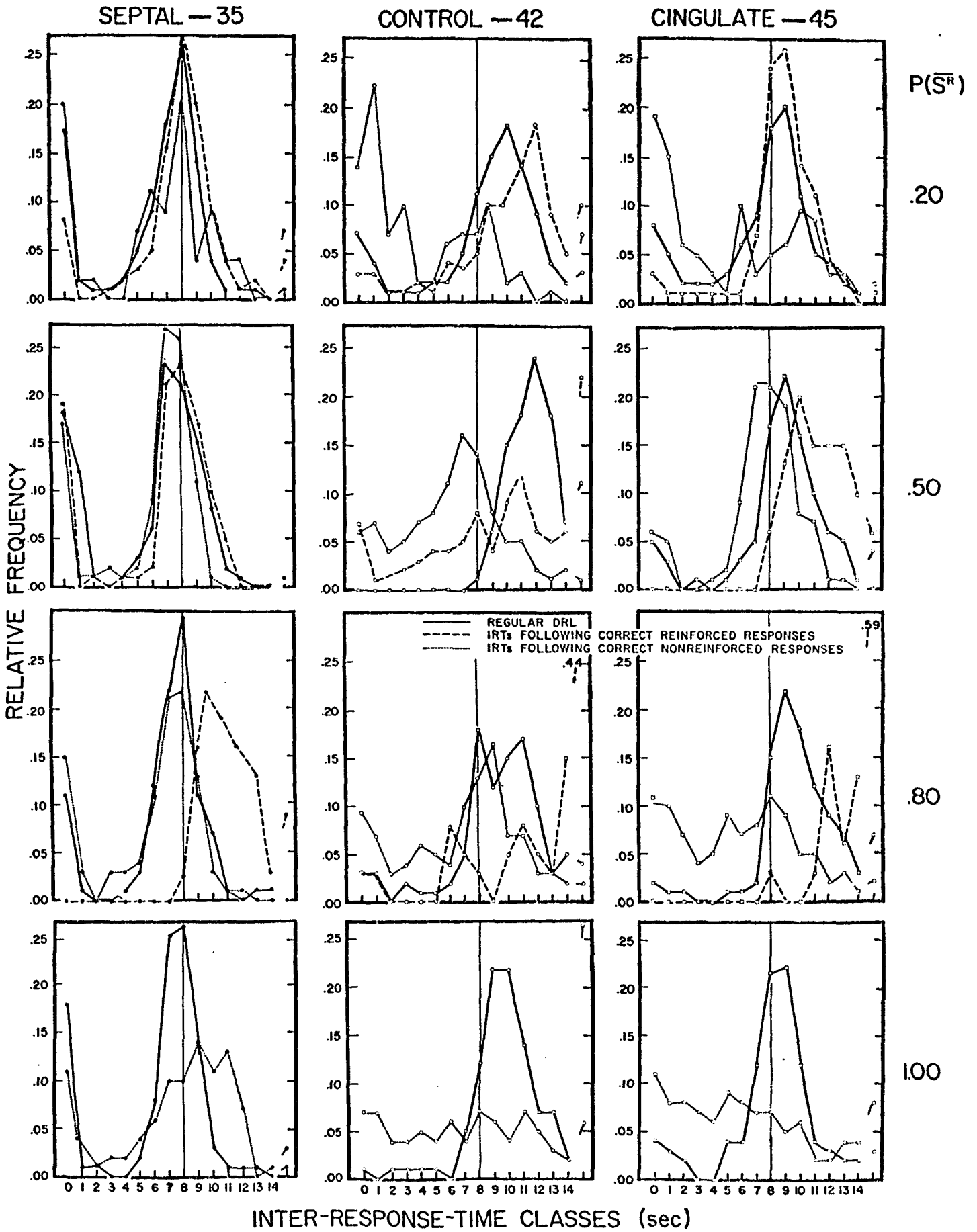
SESSIONS

ability with which the event occurred for most of the SS. The magnitude of the differences in timing behavior of the other septal animals on nonreinforcement days as compared to reinforcement days is similar to that of the control animals and only differs from them with regard to absolute value. On regular DRL days, their reduced efficiency was previously shown to be due to a higher frequency of responses emitted just prior to the interval required for reinforcement and a concomitant high frequency of very short IRTs; on nonreinforcement days, the frequency of incorrect timing responses increases so that absolute efficiency is reduced even below that of the controls. The difference in reduced efficiency from baseline levels is, however, similar to that of the controls.

It can also be seen that all but one of the control animals (MAC 41, normal control) show the "habituation" effect noted before for the group; namely, the fact that the decrease in accuracy of timing behavior is most pronounced on the first day that a new probability contingency is introduced. Efficiency improves over days so that by the last day of each probability contingency fewer incorrect timing responses are being emitted.

Individual IRT distributions are shown in Figure 22 for one rat from each operated group on the DRL 8 sec. contingency. The distributions presented for the septal and cingulate operates are those from animals sustaining most

Figure 22.--IRT distributions for one rat from each operated group on DRL 8 sec. Solid line functions represent IRT distributions obtained on a day when regular DRL conditions were in effect. Dashed and dotted line functions represent respectively the IRT distributions obtained following a correct response which was reinforced and one which was not reinforced on the day immediately following.



damage to the respective target areas. The time between successive responses for MAC 35 shows little variation regardless of reinforcement condition or probability of reinforcement. What seems to be the most important factor here is the very inefficient timing behavior under all conditions, even when probability of reinforcement for a correct timing response is 1.0. The high frequency of very short IRTs and the high frequency of those emitted just prior to the reinforcement interval are to be noted here. The relative frequency of other responses less than 7 sec. is about the same as the other two subjects, and therefore the poor timing behavior of this rat must be attributed to more frequent responding in the latter two time intervals. The distributions of IRTs for the other SS demonstrate no obvious differences from the response patterns noted previously for their respective groups.

The rates for individual animals on the DRL 0.6 sec. contingency are shown in Figure 23, and the IRT distributions for one S from each operated group are shown in Figure 24. The rate for MAC 3 (septal) is just slightly above the control level on regular DRL days; the rest of the septals' and cingulates' rates are similar to the controls. On nonreinforcement days, however, rates for all of the septal animals except MAC 4 increase to a much greater extent than that of either the cingulates or the controls. MAC 4 was previously noted to have sustained minimal damage to

Figure 23.--Response rates for individual subjects from each operated group on DRL 0.6 sec. on reinforcement days (solid lines) and nonreinforcement days (dashed lines). Columns show the probability of nonreinforcement and rows are individual subjects within each operated group.

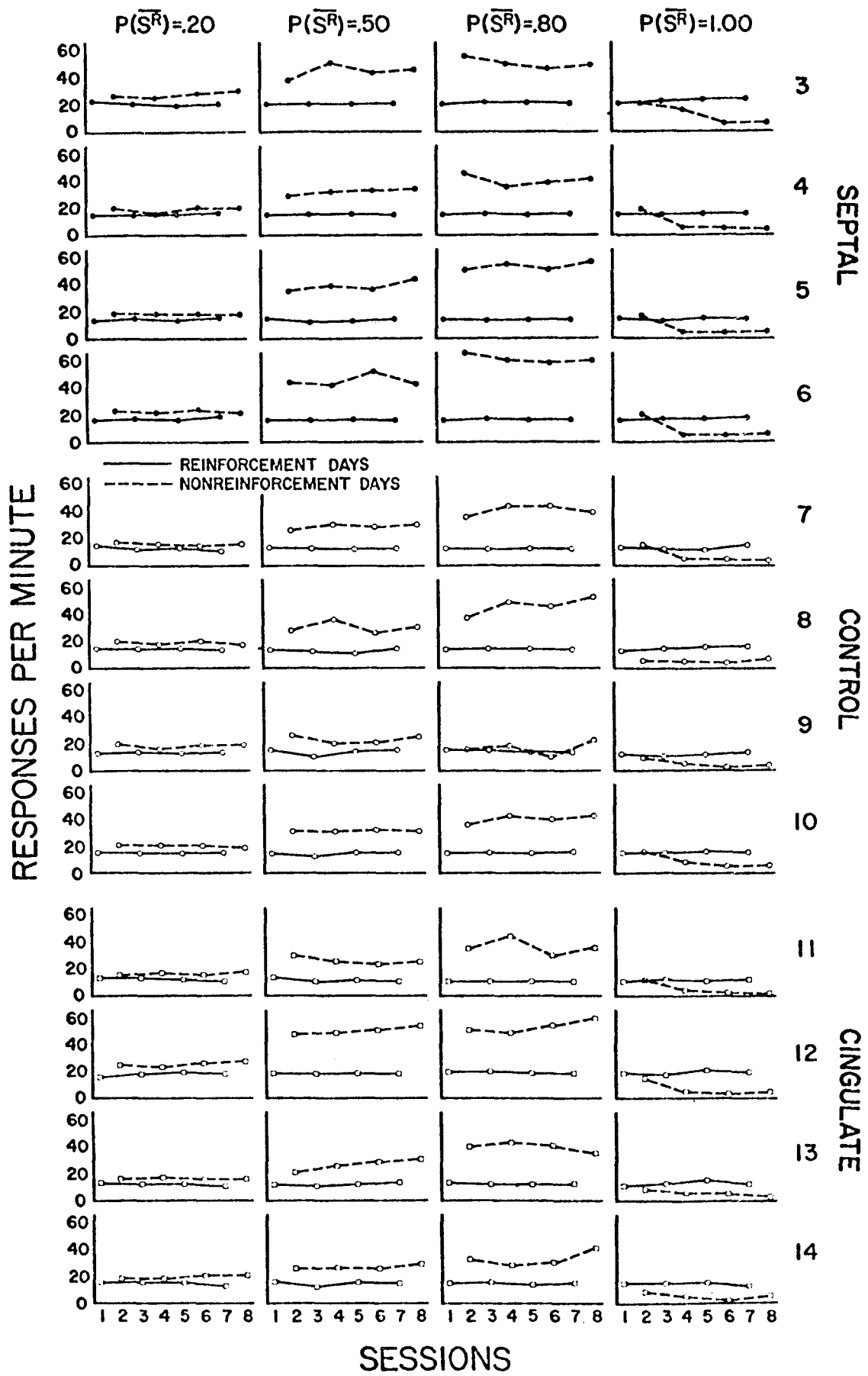


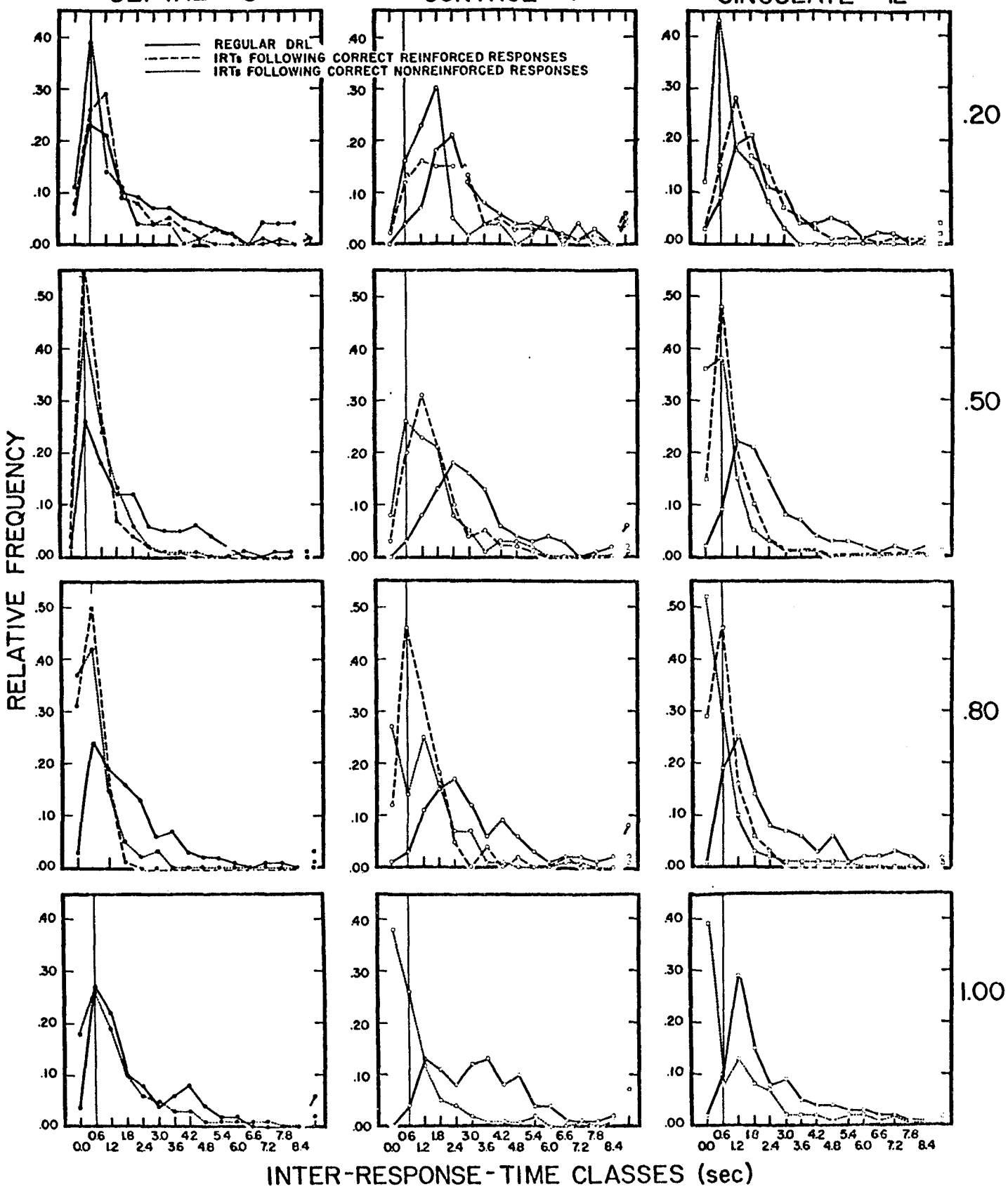
Figure 24.--IRT distributions for one rat from each operated group on DRL 0.6 sec. Solid line functions represent IRT distributions obtained on a day when regular DRL conditions were in effect. Dashed and dotted line functions represent respectively the IRT distributions obtained following a correct response which was reinforced and one which was not reinforced on the day immediately following.

$P(\bar{S}^R)$

SEPTAL—3

CONTROL—7

CINGULATE—12



the septal area, damage here being primarily unilateral and restricted to the cortex immediately above the target area.

The IRT distributions shown in Figure 24 demonstrate that the primary difference in response patterns between animals in the different operated groups is in the frequency of successive responses emitted within a short time period following a correct timing response which was not reinforced and one which was. These were the same differences noted previously for the group. However, here it can be seen that if damage is not restricted only to the cingulate cortex, but includes parts of the surrounding cortical areas as well (MAC 12), the distributions of responses on nonreinforcement days are similar to those of the septal animals. The anterior-posterior extent of the lesion is also a relevant factor. It can also be seen in this figure that at no time does the frequency of responses of the operated control (MAC 7) in the first two class intervals reach the magnitude of the rapid responses emitted by the septal or the cingulate operates.

Appendix D

Summary Tables of Analyses of Variance

Table 3

Analysis of Variance Summary Table. Differences in Per Cent Efficiency on First and Last Nonreinforcement Days and Days Immediately Preceding for Subjects on DRL 8 Sec. Schedule

First Days:

Source of Variation	Sums of Squares	d.f.	Mean Squares	F
<u>Between Subjects</u>				
Operation	1290.44	2	645.22	1.35
<u>Ss</u> within groups	4297.54	9	477.50	
<u>Within Subjects</u>				
Probability	5409.11	3	1803.04	62.87*
Operation x probability	649.01	6	108.17	3.77**
Probability x <u>Ss</u> within groups	774.41	27	28.68	

Last Days:

Source of Variation	Sums of Squares	d.f.	Mean Squares	F
<u>Between Subjects</u>				
Operation	2112.78	2	1056.39	3.22
<u>Ss</u> within groups	2950.91	9	327.88	
<u>Within Subjects</u>				
Probability	2546.41	3	848.80	31.28*
Operation x probability	281.25	6	46.88	1.73
Probability x <u>Ss</u> within groups	732.67	27	27.14	

*p < .001; **p < .01.

Table 5

Analysis of Variance Summary Table. Per Cent Efficiency on First Nonreinforcement Days at Each Probability Contingency for Subjects on DRL 0.6 Sec. Schedule

<u>Source of Variation</u>	<u>Sums of Squares</u>	<u>d.f.</u>	<u>Mean Squares</u>	<u>F</u>
<u>Between Subjects</u>				
Operation	350.00	2	175.00	1.14
<u>Ss</u> within groups	1382.00	9	153.55	
<u>Within Subjects</u>				
Probability	5398.00	3	1799.33	44.24*
Operation x probability	416.00	6	69.33	1.17
Probability x <u>Ss</u> within groups	1098.00	27	40.67	

* $p < .001$

Table 6

Analysis of Variance Summary Table. Differences
in Rate on First and Last Nonreinforcement
Days and Days Immediately Preceding
for Subjects on DRL.6 Sec. Schedule

First Days:

Source of Variation	Sums of Squares	d.f.	Mean Squares	F
<u>Between Subjects</u>				
Operation	481.43	2	240.72	4.39*
<u>Ss</u> within groups	493.51	9	54.83	
<u>Within Subjects</u>				
Probability	5208.58	3	1736.19	73.32**
Operation x prob- ability	477.59	6	79.60	3.36*
Probability x <u>Ss</u> within groups	639.31	27	23.68	

Last Days:

Source of Variation	Sums of Squares	d.f.	Mean Squares	F
<u>Between Subjects</u>				
Operation	148.56	2	74.28	1.25
<u>Ss</u> within groups	536.74	9	59.64	
<u>Within Subjects</u>				
Probability	11,107.02	3	3702.34	101.24**
Operation x prob- ability	317.34	6	52.89	1.45
Probability x <u>Ss</u> within groups	987.31	27	36.57	

* $p < .05$; ** $p < .001$

Autobiographical Statement
of
Marjorie Caplan

I was born December 14, 1940 in Baltimore Maryland where I lived until I started college in 1958. My freshmen year was spent at Lake Forest College in Lake Forest, Illinois. In September, 1959, I transferred to the University of Maryland where I graduated in 1961. During this period, I decided to major in Psychology and enrolled in several summer courses which allowed me to finish college in 3 years. I remained at Maryland for 1 year of graduate study and maintained several jobs working in psychological laboratories around the University. In September, 1962, I transferred to Columbia University where I obtained my Master's degree in June, 1964. Since I had decided to specialize in physiological psychology, I then transferred to Queens College of the City University of New York to work with Dr. John S. Stamm, under whose direction I obtained my Ph.D. in February, 1969. I am presently employed by the Psychology department at Adelphi University in Garden City, Long Island, where I hold the position of Assistant professor. I am also engaged in establishing and maintaining a physiological psychology laboratory there.