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EFFECTS OF SEPTAL LESIONS ON LATENT INHIBITION AND HABITUATION OF THE ORIENTING RESPONSE IN RATS

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Abstract. In Experiment I, the latent inhibition effect; i.e., retardation of conditioned response acquisition when a previously presented but not reinforced stimulus is subsequently used as the conditioned stimulus, was investigated in normal and septal-lesioned rats. Normal animals subjected to 30 nonreinforced CS presentations prior to CS-shock pairings, were retarded in active avoidance acquisition compared to normal animals given no nonreinforced CS presentations. The same manipulation failed to produce such a difference in septal-lesioned rats. In Experiment II, while drinking, thirsty normal and septal-lesioned rats were exposed to the same stimulus which served as CS in Experiment I. The course of suppression of on-going drinking was used as a measure of orienting response habituation. Since no differences in habituation were found between normal and septal-lesioned subjects, the deficiency of septal-lesioned rats in latent inhibition cannot be due to impairment of orienting response habituation. These results, in addition to other septal deficits, were discussed with respect to a theory of septal deficiency which suggests that septal lesions result in an impairment in situations which involve a discontinuity of response and reinforecement.

INTRODUCTION

In a recent review article, Fried (13) suggested that septal lesions result in four dissociable patterns of behavioral alterations; increased intake of palatable solutions, increased aversion to unpalatable solutions, impairment of the utilization of proprioceptive stimuli, and finally, impairment of dampening of responses developed during motivational situations resulting from overresponding to positively motivating stimuli. The last two patterns may serve as substitutes for the concepts of response perseveration or response inhibition impairment which have previously been used as explanations of a variety of behavioral deficits pro-

duced by structural and functional lesions of the septal area (28, 45). These behavioral deficits have been observed in spatial discrimination reversal (35), passive avoidance responding (19), spontaneous alternation (8), performance on DRL schedules (12), and response extinction (3).

Although most of these findings are comfortably handled either by a "response perseveration" hypothesis or by the set of hypotheses proposed by Fried, some experimental results are less easily explained regardless of which alternative is chosen. For example, in a spontaneous alternation task, septal rats tended to perseverate to exteroceptive stimuli rather than to their previous responses when the two were made incompatible (5, 6). This result could hardly have been predicted by any of the hypotheses suggested above. The response inhibition hypothesis has also been strained by demonstrations that septal rats maintained a lower and more efficient rate of responding in a bar-pressing Sidman avoidance task (31, 39) and by the findings that after the introduction of a cue light signalling the end of the delay interval, the performance of septal rats in a DRL task dramatically improved (11). These results led to the hypothesis that septal rats are deficient in the utilization of response produced proprioceptive stimuli (11) which, in the case of DRL performance, may be necessary for the initiation of collateral behaviors which fill the delay period. In testing this hypothesis, van Hoesen, MacDougal, Wilson and Mitchell (42) used discrete trial DRL task in which subjects were provided with exteroceptive stimuli signalling the onset of the timing interval thereby eliminating the need for proprioceptive cues. This procedure did not, however, eliminate the deficit of septal rats, which suggests that a proprioceptive deficit may be an insufficient explanation.

It is interesting to note that investigators of the septal functions have focused their attention on the response aspect of the stimulus-organism-response chain. When the stimulus aspect was included, its discussion centered on response produced proprioceptive stimuli or on sensory reactivity rather than on the nature of the contingency to be learned. This bias has resulted from the exclusion of learning tasks which do not require motor responding. It seemed important therefore to investigate the involvement of the septal area in learning tasks for which response oriented hypotheses are inadequate. Perceptual learning tasks (22) in which no reinforcers are involved provide such a paradigm.

EXPERIMENT I

Exposure to a stimulus in the absence of reinforcement produces the latent inhibition effect (1, 27); i.e., retardation of the acquisition of a conditioned response when the preexposed stimulus becomes the conditioned

stimulus. Rate of response acquisition in this paradigm is relevant only in that it allows estimation of the effect of preexposure. Although it has been suggested that the latent inhibition effect results from acquisition of a motor response during preexposure, which competes with the subsequent learning of the conditioned response (26), empirical evidence argues against this explanation (33, 34). Weiss and Brown (43) suggested that in the preexposure phase, subjects learn that their behavior is not correlated with the occurrence or termination of the stimulus and that the stimulus is not correlated with other environmental changes. In the acquisition phase, learning is retarded because subjects must first unlearn what was learned in the preexposure phase before learning of the new contingencies may proceed. The latent inhibition effect may therefore be considered a result of perceptual learning that had occurred during the preexposure phase.

Methods

The subjects were 32 male Long–Evans rats weighing between 250 and 300 g at the beginning of the experiment. The animals were housed individually and maintained on ad lib. food and water. Sixteen rats received bilateral septal lesions and the remaining 16 were subjected to control surgical procedures. All operations were performed under sodium pentobarbital anesthesia (50 mg/kg) supplemented by atropine sulfate to reduce respiratory complications. The coordinates for the lesions were 1.3 mm anterior to the bregma, 0.5 mm lateral to the midline and 5.0 mm ventral to the surface of the dura, with both bregma and lambda on the same horizontal plane. A 2.5 mm anodal d–c was passed through the uninsulated tip of a stainless-steel electrode for 12 sec. Sham operated animals had skull holes drilled and the dura punctured but the electrode was not further lowered and no current was passed. Testing occurred approximately 10 days after surgery.

After the termination of the experiment, subjects were sacrificed with an overdose of sodium pentobarbital and perfused intracardially with normal saline followed by 10% formaline. The brains were then frozen and 80 μm sections were cut and immediately photographed.

The apparatus was a standard shuttle box divided into two compartments by a central partition with an 8 cm circular gate. The center of the gate was located 4.5 cm above the floor. The floor consisted of stainless-steel rods through which the unconditioned stimulus (a 0.5 ma electric current) was delivered. A white noise generator kept background noise constant at 65 db. A loudspeaker mounted above the center partition was used to deliver the conditioned stimulus (a 1300 hz tone at 72 db). The presence of the animal on either side of the center partition was detected

by a microswitch system. The entire apparatus was fitted into a larger sound attenuating chamber. Experimental contingencies were controlled by solid state programming equipment.

Eight septal (Group STP) and eight control (Group CTP) subjects were randomly assigned to the tone preexposure condition while the remaining eight septal (Group SNP) and eight control (Group CNP) subjects were assigned to the non-preexposure condition.

Each subject was given a single uninterrupted session consisting of three phases. Phase I was a 5 min period of adaptation to the apparatus without tone or shock presentation. During Phase II subjects in Group STP and Group CTP received 30 presentations of the tone. The interstimulus interval was 50 sec and the duration of the tone was always 10 sec. For Group SNP and Group CNP, Phase II was identical to Phase I but lasted 30 min. Phase III was the acquisition of avoidance. Trials were signalled by the onset of the tone. If the subject failed to cross to the opposite compartment within 10 sec, shock was continuously delivered until the rats escaped by entering the opposite compartment. Responses occurring before shock delivery, but after tone onset (i.e., avoidances) terminated the tone and prevented the delivery of shock. The intertrial interval was 50 sec. Phase III was continued until the subject reached the criterion of 9 avoidances in 10 consecutive trials. If criterion had not been reached by trial 150, training was terminated and that subject was assigned a criterion score of 150 for the purpose of data analysis.

Results

Figure 1 shows anterior, medial and posterior microphotographs of a typical septal lesion. In most of the subjects, the lesions extended from slightly rostral to the genu of the corpus callosum to the postcommissural columns of the fornix. The lesions extended ventrally from the ventral surface of the corpus callosum to the dorsal aspect of the anterior commissure. All septal lesions destroyed almost completely the precommissural septum which included the medial and lateral septal nuclei. The most caudo-lateral parts of the septal nuclei escaped injury. Except for the columns of the fornix, there was no consistent pattern of damage to structures adjacent to the septum, but occasional damage to the nucleus and dorsal partion of the diagonal band of Broca, anterior commissure, and corpus callosum was observed. No subject was discarded on the basis of histology.

Most animals with lesions displayed increased reactivity to air puffs and the typical "septal rage" when handled, but there was no apparent relationship between the degree of emotionality and other behavioral measures employed.

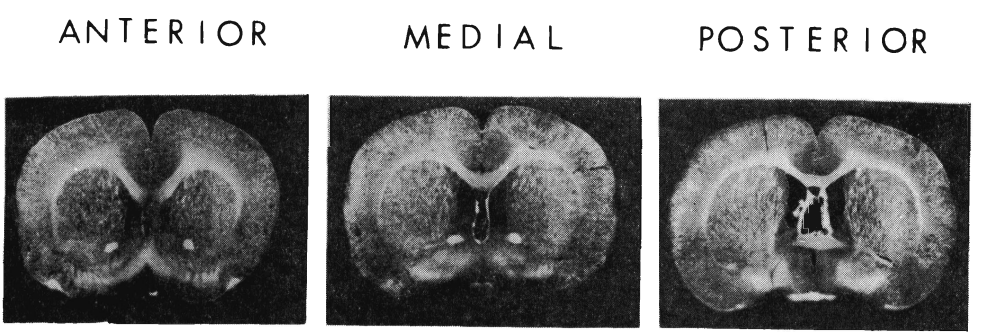

Fig. 1. Photomicrographs of frontally cut sections throughout the extent of a typical septal lesion.

The number of crossings between compartments was used as a measure of exploratory activity during the adaptation and preexposure phase. Figure 2 shows the mean number of crossings as a function of the 5-min blocks into which total adaptation and preexposure time was divided.

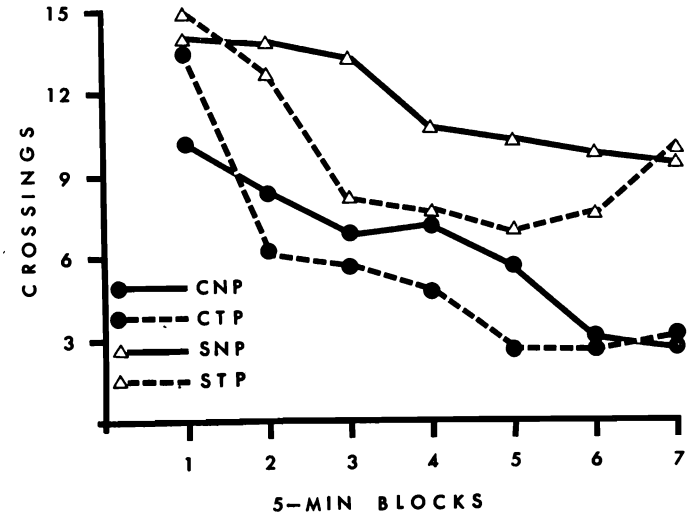

Fig. 2. Mean number of crossings as a function of 5-min blocks of adaptation block 1 and preexposure time (blocks 2–7) for control non-preexposed (CNP), control preexposed (CTP), septal non-preexposed (SNP) and septal preexposed (STP) subjects.

A mixed design analysis of variance, with lesions, tone preexposure and 5-min blocks as main factors, was performed and revealed that the main effect of blocks was significant ($F = 6.59$, $df = 6,168$, $p < 0.01$) as was the main effect of lesions ($F = 4.22$, $df = 1,28$, $p < 0.05$). Neither the main effect of tone preexposure nor any of the first order interactions nor the second order interaction was significant. The main effect of lesion reflected a higher level of exploratory activity of septal rats and the main effect of blocks reflected habituation of this activity. Lack of a significant lesions by block interactions suggests that although septal rats showed an enhanced level of exploratory activity, the habituation of this activity was not slower in septal than in control rats.

Two measures of avoidance learning were used: (i) the number of trials to reach a criterion of four avoidances in five consecutive trials; (ii) the number of trials to reach a criterion of nine avoidances in 10 consecutive trials. Figure 3 shows the mean number of trials required by each group to reach these criteria. A two-way analysis of variance, with lesion and tone preexposure as main factors, was performed for each measure. The analysis of learning trials to the final criterion revealed that there was a significant effect of lesion ($F = 57.75$, $df = 1,28$, $p <$

0.001), a significant effect of tone preexposure ($F = 4.84$, $df = 1,28$, $p < 0.05$) and a significant lesion by tone preexposure interaction ($F = 5.67$, $df = 1.28$, $p < 0.025$). The main effect of lesion reflected the generally faster avoidance learning of septal rats. The main effect of tone preexposure reflected faster avoidance acquisition of non-preexposed subjects.

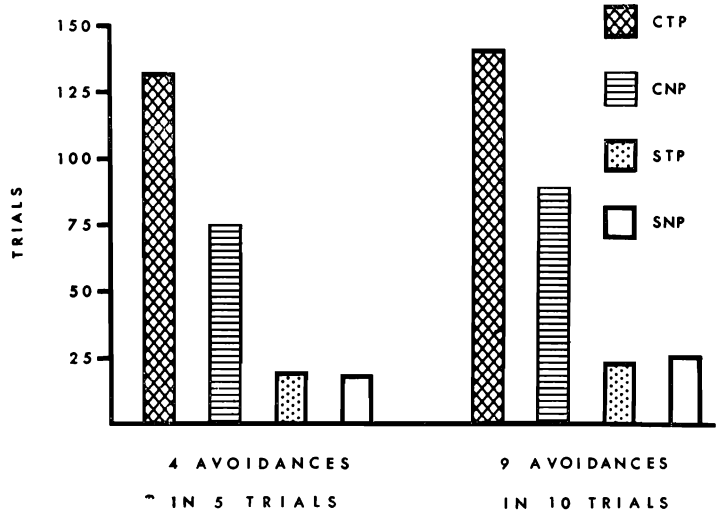

Fig. 3. Mean number of trials required by control non-preexposed (CNP), control preexposed (CTP), septal non-preexposed (SNP) and septal preexposed (STP) subjects to reach a criterion of four avoidances in five consecutive trials and a criterion of nine avoidances in 10 consecutive trials.

Individual comparisons showed that the interaction was due to a significant difference between tone preexposed and non-preexposed control rats ($p < 0.05$) and a lack of such a difference between preexposed and non-preexposed (septal rats ($p > 0.2$).

Analysis of avoidance learning to the criterion for four avoidances in five consecutive trials confirmed the results of the above analysis.

Discussion

The increased exploratory activity exhibited by the septal rats confirms several previous reports (7, 17, 32). The finding that tone preexposure did not differentially affect the exploratory activity of control and septal rats is consistent with reports of no changes in sensitivity to auditory stimulation as a result of septal lesions (18, 20). However, this absence of differentiation is inconsistent with Gotsick's (15) findings of increased spontaneous activity of septal rats induced by auditory stimulation. Gotsick evaluated the effect of auditory stimulation against the background of habituated exploratory behavior, whereas in the present study,

auditory stimulation was presented during the habituation process. This procedural difference may be responsible for the discrepancy.

The markedly faster acquisition of the two-way avoidance response by septal rats is consistent with data previously reported by several researchers (21, 24, 30, 36, 41). The impaired avoidance learning of control rats following stimulus preexposure confirms the occurrence of the latent inhibition effect within the avoidance paradigm (1, 29). However, unlike control subjects, septal rats were unaffected by repeated nonreinforced stimulus presentations; i.e., they failed to exhibit the latent inhibition effect. Since septal rats demonstrated superior avoidance learning, the absence of latent inhibition cannot be explained by a "ceiling" effect or by interference, either of which could conceivably be responsible only if septal rats had exhibited slower learning.

Since empirical findings (33, 34) indicate that latent inhibition is not a result of acquisition of a competing motor response during preexposure, the absence of latent inhibition in septal rats cannot be ascribed, contrary to the majority of other septal deficits, to response perseveration or to a response inhibition deficit. Furthermore, if the hypothesis that septal lesions produce response perseveration and the hypothesis that the latent inhibition effect is due to the acquisition of a response which competes with the response to be learned are both assumed correct, then preexposed septal rats should persist in this competing response longer than preexposed controls and would therefore exhibit a relatively greater retardation of avoidance acquisition. The results, however, are in the opposite direction.

The finding that septal rats do not exhibit the latent inhibition effect may help elucidate results that until now remained unclear. Harvey, Lints, Jacobson and Hunt (18) reported that septal rats were impaired in the acquisition of conditioned suppression to a light associated with a 1-ma shock. However, later in the same study, they found no deficit in septal rats trained under similar conditions. Since stimulus habituation preceded CER training in the latter case, the lack of difference between septal and normal rats could have been due to selective impairment of conditioning in normal, but not in septal rats as a result of stimulus preexposure. Unlike the majority of previous studies (9, 18, 41), Duncan (10) found no difference in conditioned suppression learning between normal and septal rats. His experimental procedure involved stimulus habituation prior to conditioning and therefore his results like the ones just discussed, might have been due to learning impairment in control but not septal subjects.

The abolition of latent inhibition in septal-lesioned rats introduces an important design principle for experiments comparing learning processes

in normal and septal rats. No stimulus preexposure should be given in such experiments since this will bias the results against normal animals. Since the abolition of latent inhibition in hippocampal-lesioned rats has also been reported (2), this principle may be extended to studies involving hippocampal lesions. In fact, until the effects of lesions of other brain structures on latent inhibition are examined, caution should be exerted in interpreting results of research involving stimulus exposure prior to conditioning.

EXPERIMENT II

Several investigators (38, 40, 44) have suggested that latent inhibition may result from habituation of the orienting response. They contend that the orienting response must be reestablished before subsequent learning can proceed. The number of trials required to reestablish the orienting response reflects the magnitude of the latent inhibition effect. Previous demonstrations (14, 37) indicate that habituated responses are extremely susceptible to dishabituation, which leads to the prediction of small differences between preexposed and non-preexposed subjects, consequently, the large difference found in Experiment I argues against explanation of latent inhibition in terms of orienting response habituation. Although tenuous, the orienting response habituation hypothesis might still account for the latent inhibition difference between septal and control rats if there were an impairment of response habituation in septal rats. If this explanation were correct in its general form, septal rats would be expected to demonstrate poorer habituation of exploratory activity as well. Although septal rats displayed no impairment in the rate of habituation of exploratory activity, they still exhibited an enhanced level of exploration at the end of the preexposure phase. Therefore, it was decided to compare orienting response habituation in control and septal rats, to the tone stimulus which served as the conditioned stimulus in Experiment I.

Methods

Subjects were 16 male Long–Evans rats weighing between 250 and 300 g at the beginning of the experiment. Eight rats received septal lesions and eight served as operated controls. Surgical and histological procedures as well as the recovery period were the same as in Experiment I.

The apparatus consisted of four identical plexiglass boxes located in a larger sound attenuating chamber. Drinking spouts protruded inside

the boxes. To obtain a stable baseline of drinking over the entire half-hour sessions, spouts with 1-mm diameter were used. Background noise and the tone stimulus were identical to those used in Experiment I and were delivered through an overhead loudspeaker. Licks were recorded by electromechanical equipment, which was also used to control experimental contingencies.

Twenty-four hours prior to the first experimental day, subjects were water deprived and for the remainder of the experiment were allowed access to water only during experimental sessions.

This experiment consisted of two phases. During Phase I, which lasted 7 days, subjects were given daily 30-min sessions of drinking in the apparatus. These sessions were intended to produce a reliably stable drinking rate over the whole test period. Phase II was the test session given on the eight experimental day. While the subjects were drinking, the tone stimulus was delivered 30 times for the last 10 sec of each minute. Licks were recorded during the 40th, 50th, and 60th sec of each minute. When a subject made fewer licks during tone presentation than during the preceding 10 sec, this was considered to reflect the occurrence of an orienting response.

Results

A two-way analysis of variance with lesion and days as main factors was performed on the number of licks during the seven days of acquisition. The main effect of days was significant ($F = 26.35$, $df = 6,84$, $p < 0.001$) but neither the main effect of lesion ($F = 2.73$, $df = 1,14$, n.s.) nor lesion by days interaction ($F = 1.56$, $df = 6,84$, n.s.) was significant. The main effect of days reflected an increase in drinking over successive days. The lack of a significant effect of lesion and lesion by days interaction suggests that septal and control rats did not differ with respect to amount of drinking nor did they acquire the drinking response at different rates.

The rate of habituation of the orienting response was statistically analyzed for three criteria: the number of trials to the first tone presentation which failed to result in an orienting response, the number of trials required to reach a criterion of four tone presentations without an orienting response out of five consecutive trials, and the number of trials required to reach a criterion of nine tone presentations without an orienting response out of 10 consecutive trials. Table I presents the number of trials required to reach each of these criteria by septal and control subjects. Individual comparisons for each of the measures revealed no significant differences ($p > 0.2$) between groups.

TABLE I

Mean number of trials required by control and septal subjects to meet successive criteria

Mean number of trials to:	Control	Septal	Significance level
First tone presentation without an orienting response	2.5	2.0	$p > 0.2$
Four out of five tone presentations without an orienting response	9.0	9.5	$p > 0.2$
Nine out of 10 tone presentations without an orienting response	16.9	21.7	$p > 0.2$

Discussion

No differences between control and septal lesioned rats in the rate of habituation were found in this experiment. Therefore, it seems unlikely that the abolition of the latent inhibition effect in septal rats resulted from impaired habituation. Hypotheses which reduce latent inhibition to orienting response habituation (38, 40, 44) seem less tenable in view of the finding that septal lesions abolish the former without affecting the latter.

Another explanation of latent inhibition implicates the reduction of attention or reduction of the functional impact of the stimulus which results from repeated nonreinforced stimulus presentation (4). This explanation, or any other explanation of latent inhibition in terms of a decremental rather than a learning process, encounters difficulties similar to the orienting response habituation hypothesis. Decremental processes are extremely prone to disinhibition by any stimulus or environmental change (14). Latent inhibition on the other hand seems to be a robust effect which persists in spite of such changes. Furthermore, decremental explanations require specific assumptions to explain the faster extinction of preexposed subjects when compared to non-preexposed subjects. Contrary to decremental hypotheses, a learning hypothesis does not rely upon dishabituation and regards the retardation of response acquisition as being the result of an active process whereby the subject must, after nonreinforced exposure to a stimulus, unlearn that there is no contingency between that stimulus and his responses nor between that stimulus and other environmental events. Only after this unlearning has taken place may the acquisition of the CS–US contingency proceed. Viewing latent inhibition in this way also provides a reasonable explanation for the faster extinction of preexposed subjects. After unlearning the initial lack of contingencies during the preexposure phase, and then learning the CS–

US relationship during the response acquisition phase, preexposed subjects, during extinction, may be expected to reacquire the lack of contingencies more rapidly in accordance with the "principle of the primacy of first training" (23).

The failure of septal rats to exhibit the latent inhibition effect in Experiment I is not easily explained by a response inhibition hypothesis. However, the observations of septal deficits which have led to this hypothesis have usually been based on learning tasks which share one common characteristic with the latent inhibition paradigm. These learning tasks involved a temporal discontinuity between response and reinforcement. Latent inhibition may be considered the extreme case of such a discontinuity since reinforcement during preexposure is eliminated. It is reasonable to hypothesize then, that situations involving discontinuity between response and reinforcement are more difficult for septal rats and therefore are responsible, both for the deficits previously ascribed to impaired response inhibition and for the absence of latent inhibition. Accordingly, septal rats would be expected to exhibit impaired extinction (3) and reversal learning (35) since they would be poorer at learning that responding no longer results in reinforcement. Additionally, septal rats should be impaired in developing the nonreinforced collateral behaviors (42) required to perform efficiently in DRL tasks (25). This hypothesis may also explain why the magnitude of the partial reinforcement effect; i.e., greater resistance to extinction after intermittent reinforcement during acquisition, is attenuated in septal rats (16). This attenuation may be due to the impaired ability of septal rats to learn, during acquisition, that some responses are not reinforced. Similarly, in a spontaneous alternation task, septal rats will be impaired in learning that their responses to maze cues are not reinforced and therefore would be expected to alternate less (5).

Further experimentation is needed to substantiate the tentative hypothesis that septal lesions disrupt the learning process when either response–reinforcement continuity is disrupted or when learning occurs in the absence of reinforcement. The sensory preconditioning paradigm, among others, seems to provide such a testing opportunity.

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