Facilitation of passive avoidance acquisition in rats with septal lesions¹

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The effects of septal lesions were investigated on a passive-avoidance type of task where quinine, rather than electric shock, was the aversive stimulus. Contrary to typical results with shock, rats with gross septal lesions were superior to controls in inhibiting their approach to, and consumption of, quinine. The results indicate the presence of at least two dissociable effects associated with septal lesions, one mediating response perseveration and the other more dominant one mediating quinine rejection.

Septal lesions have typically been reported to impair an animal's ability to inhibit a previously established somatomotor cued response. Schwartzbaum & Donovanick (1968) found that while septal lesions did not effect the acquisition of a spatial or brightness discrimination, they selectively impaired the reversal of the spatial discrimination and blocked the acquisition of a spatial-alternation problem. Similarly, Gittelson & Donovanick (1968) found that septal lesions impaired the reversal, though not the original learning, of a kinesthetically cued discrimination problem. The increased response perseveration of animals with septal lesions has further been demonstrated by the poor performance of such animals on passive-avoidance problems (e.g., McCleary, 1961; Zucker, 1965). For instance, Kaada, Rasmussen, & Kveim (1962) found that rats with septal lesions accepted more shocks than did control animals when the rats were exposed to an electrified water dish for 20 min following a 48-h deprivation period.

Paradoxically, however, in certain instances, septal-lesioned animals are superior to controls in inhibiting a previously learned response (Morgan & Mitchell, 1969). For instance, Fallon and Donovanick² found that when rats were trained under food deprivation, and extinguished under water deprivation, septal-lesioned animals responded

significantly less than did controls during extinction. Further evidence for enhanced response inhibition in septal-lesioned animals can be inferred from the data of palatability studies. When an aversive-tasting substance like quinine hydrochloride is added to the animals' drinking water, the suppression of intake is much more marked in septal-lesioned animals than in controls (Beatty & Schwartzbaum, 1967).³ The present study examined the effect of septal lesions on a passive-avoidance task where quinine, rather than electric shock, was the aversive stimulus pitted against deprivation.

METHOD

The Ss were 20 male albino rats which had previously served as Ss in a saccharine vs water consumption study (Zuromski, Burright, & Donovanick, 1969), concluded 5 weeks prior to the beginning of this investigation. The rats, however, had no experience with either quinine or deprivation (and were individually housed in a vivarium, with a 12-h light-dark cycle and with temperatures between 21 and 23 deg C). Surgery was performed under nembutal anesthesia, using normal stereotaxic techniques 14 weeks prior to this study. Half of the rats (N = 10) had received bilateral electrolytic lesions of the septal area, while the remaining animals had undergone sham operations. Lesion

placement was histologically verified at the end of testing.

Following the 5-week interim between studies, during which food and water were available ad lib, the rats were placed on a 23-h water-deprivation schedule for 12 days, and the amount of water consumed during the hour of water availability was measured to the nearest milliliter with 100-ml Richter tubes. On Days 13 and 14, the rats were given a single tube of a .025% solution of quinine hydrochloride for 1 h, followed by an additional hour of water with the HCl tube still present on Day 14. On Day 15, the rats again received an hour of water. From Day 11 until the termination of the study, the amounts of liquid consumed during the 1- or 2-h periods of fluid availability were cumulatively recorded after 5, 10, 20, 30, 45, and 60 min. During the course of this investigation, food was always available.

RESULTS

Histological verification of the lesion placement typically revealed near total destruction of the septum from the region of the hippocampus pars anterior to a point just posterior to crossing of the anterior commissure. Occasionally, slight damage to the nucleus accumbens and to the anterior commissure was sustained, but damage to other adjacent structures was essentially nonexistent.

In confirmation of previous investigations (e.g., Harvey & Hunt, 1965; Donovanick, Burright, & Gittelson, 1968), septal-lesioned animals consumed significantly more water than controls. For the 5 days prior to the introduction of quinine, the controls

Fig. 1. Fluid consumed in quinine passive-avoidance problem. Panels A and B, base-level days and pre- and post-quinine passive-avoidance days, respectively; Panel C, 1 h of QHCl intake; Panel D, water intake hour post-QHCl.

averaged 18.4 ml/day, while the septals averaged 21.6 ml/day ($U = 21.5$, $N_1 = N_2 = 10$, $p < .05$). As can be seen from Panel A in Fig. 1, the course of water consumption for septals and controls over the hour is very similar.

However, as Panel C shows, when quinine is introduced, the septal animals very clearly inhibit their drinking, with seven of the lesioned animals failing to consume a measurable amount of solution over the course of the hour on both days, despite the fact that E did observe sampling by all animals. The very slight rise that the curve exhibits is primarily due to the data of one animal. All controls, on the other hand, while clearly suppressed (re Panel A), consumed measurable amounts of solution on both days (median-mean daily control intake of QHCl over both days = 4.75 ml; septal = 0.00; $U = 6$, $N_1 = N_2 = 10$, $p < .002$). Further, when the last half-hour of quinine presentation is considered, the same picture emerges. That is, all controls were observed to sample the solution at least once and typically many times during the last half-hour on either of the 2 days, while five septals on the first day and six on the second failed to do so. From Panel D, it can be seen that when water was made available after the hour's exposure to quinine, the septals (with one exception) immediately returned to drinking and soon surpassed the controls on total liquid intake. Since the quinine tube was still present, the inhibitory cue was apparently taste and not smell. No Ss (either septal or control) drank any QHCl once water was available. Finally, as Panel B shows, the experience with quinine on Days 13 and 14 apparently had very little effect on the following days, 15 and 16, of water consumption for either septals or controls.

DISCUSSION

It has become increasingly clear that any single unifying concept of the effects of septal lesions, such as hyperemotionality (Brady & Nauta, 1955) or somatomotor disinhibition (e.g., McCleary, 1961), is inadequate to account for the behavior following such lesions. Thus, in the present experiment, we found that septal lesions facilitated, rather than impaired, the acquisition of a passive-avoidance task when quinine was used instead of shock.² These somewhat paradoxical effects may be related to the anatomical complexity of the septum and the consequent disruption of several circuits when large septal lesions are produced.

We now know that the response-inhibition deficit normally found following septal lesions may be localized to the anteriomedial septum (e.g., Carey, 1967; Donovanick, 1968), while the active-avoidance phenomenon is found following lesions throughout the septum (Donovick, 1968).

On the other hand, only lesions which destroy the posterior-supracommissural septum increase the rejection of quinine.³

In the present experiment, large septal lesions were produced, thus destroying both the anteriomedial "response-inhibition" circuit and the posterior-supracommissural "negativity" pathway. It is apparent that quinine, in contrast to shock, when pitted against deprivation, is sufficient to override the disinhibition commonly associated with septal lesions. Such an effect may be related to the balance of the anteriomedial and posterior-supracommissural pathways. In light of the fact that a considerable number of rats with septal, posterior-septal, or habenular lesions would rather die than drink 0.025% quinine,³ it is not too surprising that the rejection of quinine should override the perseverative response tendencies.

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NOTES

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2. Fallon, D., & Donovanick, P. J. Septal lesions, motivation, and secondary reinforcement: Lesion-induced somatomotor inhibition. Submitted for publication.
3. Donovanick, P. J., Burright, R. G., & Zuromski, E. Septal, habenular, and interpeduncular influences on water and quinine consumption. In preparation.

Copulation in rats: Relations among intromission duration, frequency, and pacing¹

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Thirty-eight male rats copulated in ad lib and enforced intercopulatory interval sessions; more than 1,200 intromission durations were electrically recorded. Intromission duration grew roughly linearly with increased intercopulatory intervals to 5 min, while intromission frequency

reached a minimum at intercopulatory intervals of 2 min.

The copulatory behavior of laboratory rats and of some other rodent species consists of a series of penetrating contacts (intromissions) of less than 0.5-sec duration, separated by periods of copulatory inactivity (intercopulatory intervals) lasting usually from 20-60 sec. Little or no seminal emission occurs during intromissions; the ejaculatory response occurs at the end of the series of intromissions and is characterized, among