Septal lesions enhance delay of responding on a free operant avoidance schedule[1]

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Rats with bilateral lesions of the septal nuclei demonstrated superior response inhibition relative to controls on a free operant avoidance task. They received fewer shocks but exhibited a lower response rate and thus longer pauses between responses. These findings are not consistent with the notion that septal lesions result in an inability to withhold responding.

The functional role played by the septal area of the brain has been frequently characterized as one of response inhibition (e.g., McCleary, 1966). Such an interpretation was advanced initially to account for the observation that Ss with lesions of the septal area were unable to withhold an appetitive response to food after receiving electric shocks for approaching the food (McCleary, 1961). Following septal lesions, rats will respond at a higher rate on both fixed interval and DRL schedules (Ellen & Powell, 1962; Ellen, Wilson, & Powell, 1964). These observations indicate that following septal lesions, Ss have a high probability of rapid responding even on tasks whose requirements demand the withholding or delay of that response. This study was designed to investigate the effects of septal lesions on the acquisition of responding on a free-operant avoidance task (Sidman, 1953) where a high response rate due to an inability to inhibit responding should facilitate performance.

SUBJECTS AND APPARATUS

Twelve male Long-Evans rats, approximately 125 days of age, served as Ss. They were housed in individual cages and maintained on ad lib food and water. Two Lehigh Valley Electronics (Model 1316) operant boxes, with the experimental space reduced to 19 x 11 x 18 cm, were used. All programming was automated, and data were collected on cumulative recorders and digital counters which provided interresponse time distributions (IRTs) in 10 successive, 2-sec class intervals. Shock was delivered from a Grason-Stadler E 1064GS scrambled shock source.

PROCEDURE

Six unoperated rats were used as control Ss and six rats received electrolytic lesions of the septal area. Lesions were created by passing 1.5-mA anodal dc for 20 sec through a 30-gauge stainless steel electrode, insulated except for a .5-mm bare tip. Measurements were made in millimeters from the bregma, midline, and top of the skull with the head at a 5-deg angle to the horizontal plane. Bilateral electrode insertions were at 1.7 A, .5 L, and 6.0 D. A 1-week postoperative period was allowed prior to training.

Subjects were then trained on a free-operant avoidance task in which the S received a 1.3-mA foot-shock for 0.5 sec at 5-sec intervals (S-S interval) if no response was made. A bar-press response delayed the shock for 20 sec (R-S interval) and, if no other response was made to postpone the shock for an additional 20 sec, the foot-shocks were resumed at the 5-sec S-S interval. In order to facilitate acquisition, the response bar was rendered inactive during the presentation of shocks to obviate escape responding, and a house light was turned on for 1 sec following each response to provide a distinct cue signaling an adequate response (Bolles & Popp, 1964). Ss were run for 25 4-h periods on alternate days and data were collected during the last 2 h of each experimental period in order to eliminate the variability commonly resulting from a warm-up effect.

At the completion of the experiment, Ss were sacrificed, perfused intracardially with saline and 10% formalin. The brains were embedded in celloidin and sectioned at 12 micra. Sections were stained with cresyl violet and examined for the locus and extent of the lesions.

RESULTS AND DISCUSSION

The septal lesions typically started anterior to the genu of the corpus callosum and extended posteriorly to the descending columns of the fornix and encroached upon these in some instances. The lesions extended ventrally to the level of the anterior commissure. Incidental damage to the anterior cingulate cortex, anterior commissure, and caudate nucleus was slight in all cases.

The rats with septal lesions learned the task faster and reached a higher level of performance than the control Ss. These differences were maintained throughout the 25 experimental days. Figure 1A shows that the experimental Ss decreased the rate of shocks received faster and maintained a lower shock rate than the control Ss. Contrary to what would be expected from earlier research and theorizing, the experimental Ss also decreased their response rates while the response rate of the control group increased (Fig. 1B). Figure 1C indicates that the median of the IRT distribution of the experimental group increased at a more rapid rate and stabilized at IRTs longer than those of the control group. A sign test revealed that the experimental and control groups were reliably different in rate of responding, rate of shocks received, and in median IRT (all $p < .001$).

Responding at a very high rate with very short pauses between responses, i.e., a low median IRT, is one response strategy available to the S on a free-operant avoidance task. Although shocks are avoided, this seems to be an inefficient mode of responding since a large output of work is demanded. All of the present Ss employed this strategy on the first few days of training. The most efficient strategy would be to delay approximately 18 to 19 sec between successive responses, thereby maximizing the length of time shock is delayed per response. No S ever attained this high degree of response inhibition but the experimental Ss lengthened the pause between successive responses sooner and for a longer duration than did the control Ss. Thus, the Ss with septal lesions were able to avoid more shocks with fewer responses than the control Ss. Therefore, it seems legitimate to conclude

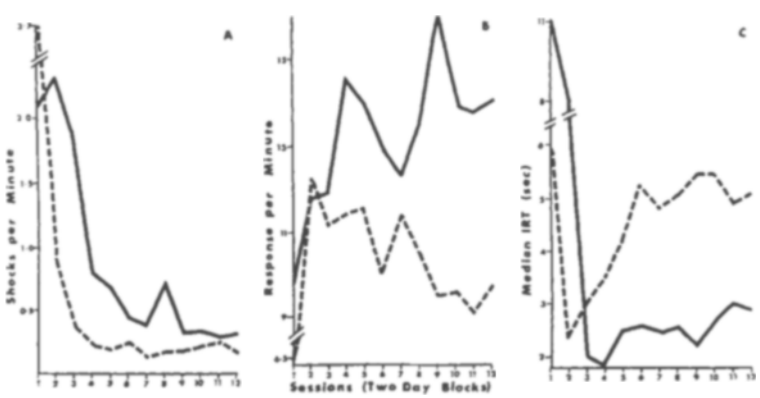

Fig. 1. Curves showing (A) the rate of shocks received, (B) the rate of responding, and (C) the median interresponse time (IRT) of the experimental (broken line) and control groups (solid line) as a function of experimental sessions. These values are averaged across 2-day blocks of sessions.

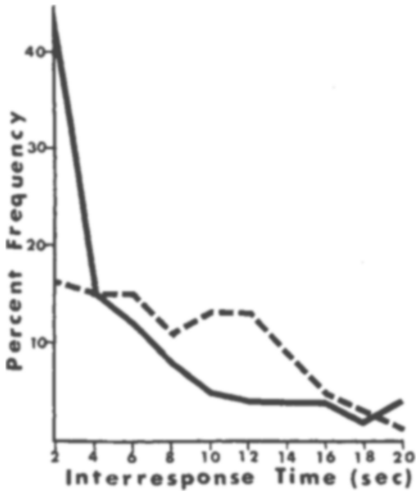

Fig. 2. The per cent frequency distributions of the time between successive responses (interresponse time) averaged over the last 5 days of training for a representative S with a septal lesion (broken line) and a control S (solid line). The frequencies are plotted at the upper limit of the 2-sec interval.

that the Ss with septal lesions performed the free-operant avoidance task more efficiently than did the control Ss by virtue of their enhanced ability to delay successive responses.

Figure 2 further demonstrates the enhanced response inhibition of the experimental Ss. This figure illustrates IRT distributions of the avoidance responses for a representative S from each group averaged over the last 5 days of training. The modal point of the distribution for the control S remained in the 0 to 2-sec IRT interval and constituted 42% of the avoidance responses. While the modal point for the experimental S was also in the 0 to 2-sec interval, it constituted only 16% of the avoidance responses. The median of the IRT distribution for the control S was 3.1 sec while the median for the experimental S was 6.7 sec. The IRT distribution of the experimental S in Fig. 2 shows the formation of a secondary peak in the 8- to 10-sec and 10- to 12-sec IRT intervals. The individual IRT distributions of the last 5 days which were averaged to form the distribution shown in Fig. 2 also indicated this secondary peak in the same intervals. The formation of the secondary peak in these intermediate intervals indicates a more rapid development of a temporal discrimination and, thus, more efficient performance in the experimental Ss than in the control Ss.

Boren, Herrnstein, & Sidman (1959) found that for individual Ss, increasing levels of shock lead to increased rates of responding on a reinforcement schedule similar to the one used in this study. This would indicate that the Ss with septal lesions are not responding with lower rates due to an increase in shock sensitivity.

Therefore, whether considering initial acquisition or long-term performance, the rats with lesions in the septal area learned the task faster and reached a higher level of performance than the control Ss. The experimental group received fewer shocks but demonstrated a lower response rate and enhanced response inhibition. It has been hypothesized that the septal area mediates response inhibition in the intact animal. In view of our results, it seems that this interpretation is not sufficient to cover the entire range of phenomena observed following damage to the septal area.

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NOTE

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A pheromone associated with social dominance among male rats[1]

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Forty male rats, living in 10 groups (N = 4 per group), with stable dominance hierarchies preferred the odor from submissive strange males over that from dominant strange males (p < .05). The response to the two odors was not significantly related to Ss' rank in their hierarchy. Fourteen males from four unstable hierarchies (N = 3-4 per group) preferred neither odor. The data suggest the existence of a releaser pheromone associated with social dominance in rats.

Olfaction is known to play an important role in the regulation of agonistic behavior among both wild and domestic rats (*Rattus norvegicus*). If reared from weaning in small groups, males of either variety live in reasonable harmony—the domestic rats by establishing a linear and transitive hierarchy (Baenninger, 1966) and the wild rats a stratified organization consisting of three classes, with members of each class treating each other approximately as equals (Barnett, 1964). In both varieties, high ranking residents readily attack adult male intruders, but not adult females or young (Grant & Chance, 1958; Runyon & Turner, 1964; Barnett, 1964). Attacks are preceded by olfactory investigation, especially of the intruder's genitalia. Males of lower rank are less likely to attack intruders, but the presence of an intruder causes an increase in "recognition sniffing" among residents (Barnett, 1964). If members of two isolated groups of wild rats can smell each other through a barrier, they do not fight when placed together (Barnett, 1967, p. 98). Thus, a "group" odor may inhibit aggression.

Runyon & Turner (1964, pp. 78-81) reported that adult male intruders usually are forced to the bottom of a hierarchy of domestic rats, but occasionally a particularly aggressive intruder may cause the residents to assume postures of defeat before fighting occurs. These workers suggested that the residents may respond to the appearance or the odor of the aggressive intruder. Therefore, the present experiment was performed to determine whether domestic rats react differentially to the odors from strange dominant vs submissive males and whether S's rank in its hierarchy influences its reactions to the two odors.

SUBJECTS
AND ODORANT ANIMALS

Seventy-two male rats of the Long-Evans strain were housed as weanlings in 18 groups of four rats each. Fourteen groups provided 54 Ss (2 died before testing) and the remaining four groups provided the domi-