Discrimination of response feedback following septal lesions*†

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In a two-bar operant task, rats were required to make five consecutive responses on one bar (count bar) and then press the food bar once for reinforcement. Shifts to the food bar before the required count had been completed on the count bar did not lead to reinforcement but reset the counter such that the required sequence had to be started again. Septal animals were deficient in learning when to shift to the food bar. The results were interpreted in terms of a deficiency in the discrimination of response-produced feedback.

The overresponding by animals with septal lesions on a DRL (differential reinforcement of low rates of response) reinforcement schedule is a well-documented phenomenon (Ellen, Wilson & Powell, 1964; Burkett & Bunnell, 1966; Carey, 1967, 1968). However, despite the ample body of evidence describing the behavioral effect, the basis of this overresponding by septal animals is still obscure. This is more paradoxical in view of the fact that although septal animals fail to obtain reinforcement on the schedule, nonetheless, they do show a significant reduction in overall response rate from the beginning to the end of training on the schedule.

Two possibilities present themselves. The overresponding may reflect a breakdown in inhibitory mechanisms, i.e., perseveration of an ongoing or prepotent response (McCleary, 1966), or it may reflect a failure in the discrimination of when to barpress (Ellen & Butter, 1969). Which of these possibilities is the more likely, however, cannot be determined within the context of the DRL schedule, since typically, when animals are run on this schedule, only a single lever is available in the operant chamber and nonbarpressing behavior is not brought under explicit experimental control.

However, a recent study by Wagman (1968) offers a methodology that has the potential for resolving this issue. In Wagman's study the effects of frontal lobe damage in cats were assessed by a reinforcement schedule in which the animals were required to make a series of responses on one lever (count bar) in an operant chamber, and then indicate when this series of responses

was completed by shifting to another lever (food bar) which delivered reinforcement. Failure to inhibit a prepotent response on this schedule is evidenced by the animal's persisting in a response to either lever. Failure to discriminate when to barpress is evidenced by the animal's shifting to the food bar prior to the completion of the required number of responses on the count bar. Wagman found that frontal damage caused the cats to shift prematurely. Since no external stimuli were programmed to signal the animals when to shift, Wagman interpreted the behavioral effect in terms of a deficit in the discrimination of response-produced feedback stimulation. In view of the fact that we have previously described the effect of septal damage on performance in operant tasks (Ellen & Butter, 1969) and in the Dashiell maze (Ellen & Bate, 1969, 1970) as resulting from a failure to discriminate response-feedback stimulation, it seemed reasonable to expect that septal damage in rats might lead to the same kind of behavioral effect on the count schedule that Wagman reports for frontal cats. The present experiment was designed to explore this possibility.

SUBJECTS

Ten experimentally naive male Long-Evans hooded rats, approximately 100 days old and weighing 320-374 g at the beginning of the experiment, were used. The animals were housed in individual cages with ad lib food and water. On the fourth day after arrival at the laboratory, they were deprived of food for 23 h. The following day, all animals were trained to barpress for a 45-mg pellet of food. They were trained in the same chamber used for the experiment, but with only one bar present. Each animal was left in the experimental chamber for 30 min or until they obtained 150 reinforcements, whichever came first. They were then returned to their cages and given a dish of 15 g of wet mash as a daily sustaining ration. This

preoperative training under continuous reinforcement (CRF) lasted for 7 days, by which time the criterion set for 150 reinforcements per 15 min was reached. Subsequently, the animals were divided into two groups: five normals and five septally lesioned animals.

PROCEDURE

On the first postoperative day, all animals were individually carried to the experimental room in their home cages and placed in the operant conditioning chamber, and training on a 1:1 two-bar fixed-ratio counting schedule was begun. Under this schedule, the animals were required to press one time on the left bar (count bar) and one time on the right bar (food bar) to obtain reinforcement. Training on this schedule continued for 5 days. On the sixth postoperative day, the ratio was increased, and the animals were required to barpress five times on the count bar and one time on the food bar to obtain reinforcement. Shifts to the food bar before the requisite count on the count bar had been completed did not produce reinforcement but did reset the counter, requiring that the sequence be restarted. Each daily session lasted 30 min. At the end of each session, the animals were returned to their home cages, and a dish of 15 g of mash and water was given as a sustaining diet. Training on the 5:1 ratio was continued for 22 days.

For the last 7 days of the training, alternate groups of Ss were preloaded with their daily ration of 15 g of wet mash $\frac{1}{2}$ h before being taken into the experimental room, e.g., septals on Monday, normals on Tuesday, etc. Animals not fed prior to running were given their daily ration upon completion of the task.

APPARATUS

The apparatus was a Scientific Prototype operant chamber, Model D700, with double bars, enclosed in a Scientific Prototype sound-attenuated chamber, Model SPC-300. The houselight was provided by a 7-W bulb within the chamber. Standard BRS digital logic modules were used to program the reinforcement schedule and to record the Ss' responses.

SURGERY AND HISTOLOGY

Septal rats sustained electrolytic lesions, using a stereotaxic instrument under Nembutal anesthesia (40 mg/kg). Atropine sulfate, 0.4 cc (0.4 mg/cc), was given as prophylaxis for respiratory distress. The electrode was inserted 2.0 mm anterior to bregma on the midline (longitudinal sinus) and was lowered 5.5 mm below the surface of the brain. Lesions were produced by passing 2 mA for 15 sec

*Supported in part by NSF Grant GB 7184.

†A version of this paper was read at the 11th Annual Meeting of the Psychonomic Society, November 1970, San Antonio, Texas.

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†††We wish to acknowledge the technical assistance of William C. Aitken, Jr., and Edward A. DeGross, Jr., in the preparation of this paper.

Fig. 1. Food-bar and count-bar responding during various phases of the experiment. (A) Acquisition of count-bar responding on 1:1 ratio. (B) Responding on count and food bars during 5:1 ratio on count bar. (C) Preloading effects on food- and count-bar responding. Preloading done on alternate days for each group.

between the anodal electrode in the brain and the probe at the wound margin. Following surgery, all animals were given 0.2 cc Duracillin and were returned to their cages.

On completion of the experiment, septally lesioned Ss were sacrificed with a lethal dose of Nembutal and perfused intracardially with isotonic saline, followed by 10% formalin. After fixation of tissues in 10% formalin, frozen tissue technique was used and brains were cut 50 microns thick. Every fifth wet section was placed on a slide, and black-and-white photographs were taken of each individual section for histological analysis.

RESULTS AND DISCUSSION

The septal lesions had their maximal extent at A-P 7.6 of the Pellegrino & Cushman (1967) atlas. Maximum damage occurred to the medial septal nucleus with unilateral destruction of the lateral septal nucleus. Posteriorly, the lesion incriminated fornix longus and the hippocampal commissure. Ventrally, the lesions did not invade the anterior commissure.

The barpressing behavior on each of the two bars during the various phases of the experiment is illustrated in Fig. 1. Figure 1A shows the acquisition of the count-bar responding during the 1:1 phase. It will be noted that responding on the count bar increases during the 5 days that this contingency was in effect ($F = 4.48$, $df = 4/32$, $p < .01$). Although there was no difference between the groups in the overall acquisition of the count-bar responding ($F = .69$), there was a

significant Lesion by Days interaction effect ($F = 4.06$, $df = 4/32$, $p < .01$). That is, the septal animals initially tend to overrespond and then gradually decrease their count-bar responding to the schedule requirement, while the normal animals show a steady buildup to the schedule requirement. During the acquisition of the count-bar responding, the food-bar responding remained constant over the 5 days of training ($F = 1.60$), with no

significant group ($F = .05$) or interaction effects ($F = .57$) present.

When the 5:1 contingency was introduced (Fig. 1B), both septal and normal animals showed a progressive increase in count-bar responding as training continued ($F = 11.09$, $df = 14/112$, $p < .01$). Septal animals tended to emit more count-bar responses throughout the entire course of training on this contingency; however, this difference was not reliable ($F = 3.48$, $df = 1/8$, $p \approx .10$). Once again, it will be noted that despite the increase in count-bar behavior, responding on the food bar remained constant for both groups over the course of training ($F = 1.36$), with no group differences present ($F = 1.66$). However, despite the consistency in the overall amount of food-bar responding, there was a progressive increase in the number of reinforcements obtained by the two groups ($F = 14.78$, $df = 14/112$, $p < .01$), with no group ($F = 1.48$) or interaction effects present ($F = 1.44$).

Figure 1C illustrates the effects of preloading the animals with their daily ration $\frac{1}{2}$ h before testing. On days in which the animals were preloaded, responding to both the count and food bars sharply decreased. On nonpreloaded days, responding remained at levels previously established. Of particular interest is the suggestion of a differential effect of the preloading on the septal animals. The septal animals essentially extinguished all responding to the count bar by the third day of

Fig. 2. Relative frequency of food-bar responses after 0-4, 5-9, and 10+ count-bar responses had been emitted on days on which animals were not preloaded.

Fig. 3. Effects of preloading on relative frequency of shifts to the food bar after 0-4, 5-9, and 10+ count-bar responses had been emitted.

preloading. In contrast, the normals, although showing a major reduction in count-bar responding from nonpreloading conditions, nonetheless continued to respond to the count bar at a consistent low level. This interaction was statistically significant ($F = 3.91$, $df = 2/16$, $p < .05$). A similar, though not as reliable, effect was found for the food-bar responding ($F = 2.79$, $df = 2/16$, $p = .09$).

Figure 2 shows the distribution of food-bar responses after 0-4, 5-9, or more than 10 count-bar responses had been emitted. It is evident that by the 15th day of training on the 5:1 contingency, normal animals have begun to make the majority of their food-bar responses after the required ratio of 5 responses on the count bar had been completed. In contrast, the septal animals tended to shift to the food bar before the required ratio had been completed. Even by the end of the experiment, septal animals still were just as likely to make food-bar responses before completing the required ratio on the count bar as after.

The premature shifting to the food bar by the septal animals is of particular interest. Since no exteroceptive stimulation was available to signal to the animals that they had completed the required ratio on the count bar, this premature shifting would suggest that the lesion prevented stimuli arising from the animals' own behavior from becoming discriminative cues for shifting to the food bar. This conclusion is thus consistent with those derived from previous studies in which the required behavior depended for its appearance on the discrimination of stimuli arising from ongoing movement patterns (Ellen & Bate, 1969, 1970).

In addition, it would appear that the failure to shift appropriately is not the result of differences resulting from motivational changes produced by the lesion. Such motivational changes might be inferred from the fact the preloading had a differential effect on the count-bar behavior of the septal animals, and also from results of previous studies which show enhanced response rates on operant schedules (Ellen & Powell, 1962a, b). In addition, response rate differences in the present study (Fig. 1B), although not reaching statistical significance, nonetheless were in a direction consistent with the inference of a lesion-induced motivational change. However, when the distribution of shifts to the food bar was examined for those days in which the animals were preloaded, we find that shifts to the food bar after 0-4 count-bar responses had been emitted are predominant (Fig. 3). In addition, Mechner & Guevrekian (1962) have shown that increasing deprivation in animals running on this kind of count schedule does not affect when the animals shift from the count bar to the food bar, but only the time from the beginning of a count sequence to the shift. In other words, animals with higher motivation merely run through the required ratio faster. They do not have difficulty in completing the required ratio. In the present study, shifts to the food bar by septal animals occurred before the required count-bar ratio was

completed, even when motivational levels had been decreased by the preloading. Thus, the failure to shift correctly reflects a primary failure in response differentiation mechanisms rather than a secondary consequence of a motivational increase resulting from the lesion.

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