Temporal patterns in the facilitation of Sidman avoidance by lateral hypothalamic stimulation¹

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Rats were trained to run in a wheel to avoid electric shock on a Sidman schedule. Lateral hypothalamic stimulation facilitated avoidance responding. The aftereffect of lateral hypothalamic stimulation was a depression of avoidance responding if the stimulation had mixed rewarding and aversive properties.

Presentation of noncontingent rewarding lateral hypothalamic (LH) stimulation while rats are performing a well-learned Sidman avoidance task enhances avoidance responding (Margules & Stein, 1968; Carder, 1969). The present experiment involved a close observation of the temporal characteristics of this enhancement.

METHOD

Seven male Sprague-Dawley rats, weighing from 300 to 450 g, were implanted with monopolar electrodes aimed at the LH region.

After recovery from surgery, Ss were trained to run in a running wheel to avoid electric shock on a Sidman schedule. The wheel was of low inertia, with a diameter of 24 in., and it rotated in only one direction. The wheel was supported in a wooden enclosure. An electrode was placed in the skin of the S's back at the beginning of each session. An ac shock of 1.3 mA RMS could be passed between this electrode and the floor of the wheel for 0.5 sec. Animals receiving these shocks jumped from the floor as though the shock had its main effect on the feet. The Sidman avoidance schedule had a shock-shock interval of 1 sec. Running terminated the shock-shock interval and initiated the response-shock interval of 5 sec. The response-shock interval did not begin to time out until running ceased and could be reset if running began again. Avoidance training was carried out for 5-10 1/2-h sessions, at which time performance was stable and efficient, with Ss taking an average of less than one shock per minute.

Following this training, lateral hypothalamic stimulation was introduced.

The stimulation was given daily in 12 periods, 40 sec long and 2.5 min apart, in the course of the avoidance session. The stimulation was 60-cycle ac delivered twice each second in 0.1-sec pulses at levels of 40-80 microamps RMS for the several Ss.

RESULTS

LH stimulation produced a marked facilitation of avoidance responding in all seven Ss. Ss fell into two groups, however, regarding the transient characteristics of their behavior in the stimulation tests. Figure 1 presents a representative cumulative record for one S in each group. Ss in the pause-enhancement group paused at the onset of stimulation, then showed facilitation. In addition, the offset of stimulation produced a further enhancement of responding. Ss in the no-pause depression group showed an immediate enhancement during stimulation and a marked depression of responding after the offset of stimulation. Three Ss showed pause enhancement behavior; the other four exhibited no-pause depression behavior. Pause depression and no-pause enhancement configurations were not observed.

Figure 2 presents averaged data for the two groups. The initial pause in the pause-enhancement group is obscured by enhanced running after the pause when the data are averaged over 10-sec periods, since a shock followed a pause of 5 sec. The other features described in the cumulative records are evident in the figure. All pause-enhancement Ss responded more in the first 10 sec following stimulation than in the last 10 sec during stimulation. The no-pause depression group showed greater facilitation during stimulation and a depression of responding following the stimulation period. Although the prestimulation baseline of the no-pause depression group was higher, there was overlap between the groups.

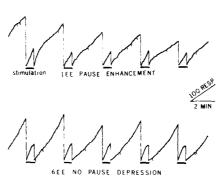


Fig. 1. Sample cumulative records for one S in each group. Each response indicates about 6 in. of running; diagonal marks indicate shocks. Following testing in the avoidance situation, Ss were tested in a lever-press apparatus for self-stimulation. Each lever press produced a 0.5-sec pulse of the current used in the first experiment. Two of the three pause-enhancement Ss self-stimulated. Although one S in the no-pause depression group had died before this test could be run, the other three self-stimulated. Self-stimulation rates were 1,500-2,500 responses per hour with no apparent difference between the two groups.

Because an experiment by Williams & Carder³ with rewarding stimulation and aversive brain shock had produced no-pause depression results, and because of the casual observation that at very high current levels, no-pause depression Ss began to show pause-enhancement behavior, it seemed that the pause-enhancement behavior might be a result of mixed rewarding and aversive properties of the stimulation in these Ss.

To test this hypothesis, the six remaining Ss were placed in a shuttlebox, in order to observe the latency of appearance of aversive effects of the brain stimulation. A continuous current at the level used previously was turned on and terminated when the S moved to the other side of the shuttlebox. Consistent performance appeared in a very few trials. Pause-enhancement Ss terminated the stimulation sooner (p < .01), suggesting that aversive effects were stronger in pause-enhancement Ss.

DISCUSSION

The results confirm other observations of an enhancement of Sidman avoidance by rewarding LH stimulation. The no-pause depression effect seems to result from a relatively "pure" rewarding electrode. The poststimulation depression of responding is similar to contrast effects produced by a reduction in intensity (Trowill, Panksepp, & Gandleman, 1969) or frequency (Williams, 1965) of rewarding brain stimulation. The fact that this depression phenomenon extends to aversively motivated behavior supports Olds & Olds's (1964) and Stein's (1964) contention that both appetitive and aversive behavior are ultimately controlled by the positive incentive system.

The pause-enhancement configuration appears to result from stimulation having mixed rewarding and aversive properties. The poststimulation enhancement may then be a result of the termination of stimulation that has become increasingly aversive. Such an enhancement is predicted by the Olds and Olds and the Stein theories of avoidance behavior that propose that the termination of aversive stimulation produces a temporary enhancement of activity in the positive incentive system.

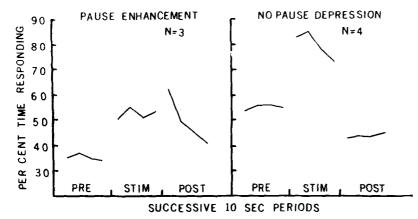


Fig. 2. Mean per cent time responding for each group before, during, and after stimulation.

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NOTES

1. This research was supported by Grant GB-2475 from the National Science Foundation to David R. Williams, while the author was a PHS predoctoral fellow.

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3. Williams, D. R., & Carder, B. Interaction of rewarding and aversive brain stimulation. Manuscript in preparation.

Variations in secondary reinforcers as a function of temporal relationship to UCS and UCS intensity

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Two predictions were tested: (1) that stimuli paired with shock termination become positive reinforcers, and (2) that the attractiveness of the reinforcer will be proportional to the aversiveness of shock preceding it. Two experiments carried out various tone-shock pairings; speed in a runway was subsequently observed when the tone was presented as a reward. Both predictions were confirmed.

Mowrer's behavior theory (1961) suggests that stimuli preceding aversive stimulation acquire negative reinforcing properties, while stimuli paired with the termination of such aversive stimulation become positive reinforcers through their contiguity with drive reduction. Mowrer & Aiken (1954) have shown that stimuli preceding shock are effective negative reinforcers, but they did not conclusively demonstrate that stimuli paired with shock termination were positive reinforcers. Goodson (1954), Smith & Buchanan (1954), and Murray & Strandberg (1965) have been able to demonstrate under several conditions that stimuli contiguous with shock offset are positive reinforcers.

It is claimed by Mowrer that the stimuli paired with the termination of noxious stimulation develop into positive reinforcers through their contiguity with "relief" resulting from the termination of discomfort or drive. This position implies that the amount of relief (and hence the attractiveness of stimuli paired with the relief) is proportional to the intensity of

aversive stimulation preceding the relief. Variations in the length or intensity of the UCS should produce differences in the reinforcing effectiveness of stimuli paired with the termination of aversive stimulation. Murray & Strandberg (1965) observed no relationship between shock length and the reinforcing properties of the stimulus paired with the termination of the shock; however, length of shock was not controlled and was allowed to vary between Ss.

The purpose of this study was to confirm the previous findings that stimuli paired with shock termination become positive reinforcers. The second and major purpose of the study was to test an associated hypothesis that the attractiveness of stimuli accompanying UCS termination is proportional to the aversiveness of the UCS. Both hypotheses were tested by the pairing of a tone with shock termination and subsequently observing the effect of the tone as a reward on speed of running in a runway.

EXPERIMENT 1 Subjects

Fifty male albino rats, 90-130 days old, were assigned randomly to five groups. All Ss were housed in pairs, with unlimited access to food and water except during training sessions.

Apparatus

Shock-tone conditioning was carried out in a sound-deadened ventilated compartment (Grason-Stadler E3125AA). Shock was administered through the grid floor by means of a shock-generator scrambler (Grason-Stadler E1064GS, set at 0.6 mA for all groups). The tone was presented in the chamber at -20 dB according to a General Radio sound-level meter. Performance in the 3 ft x 4 in. x 4 in. Hunter runway was measured by timers controlled by photocells placed 3 in. outside the start and goal boxes. Handling of each S between trials was eliminated by exchanging start and goal boxes at the completion of each trial. The sides of the runway were covered with black cardboard and the top was covered with glass.

Procedure

Group 1: Twenty Ss received 20 shocks of 3-sec duration, spaced at intervals ranging randomly from 40-80 sec at an average of 60 sec. A 1,000-Hz tone overlapped the termination of each UCS for 0.5 sec and continued for 2.5 sec after the termination of the UCS. After 10 min rest, each S was then placed in the runway start box. Half of the Ss received the CS as reward upon reaching the goal (Group 1A). The remaining Ss did not receive any tone in the goal (Group 1B). This procedure was