

Lateral Hypothalamus: Learning of Food-Seeking Response Motivated by Electrical Stimulation

Abstract. *Stimulation of the lateral hypothalamus, which induces eating, resembles hunger in that it motivates rats to learn, for food reward, a response of pressing a bar. The response is discriminatively confined to only a bar that delivers food on either a 100-percent or a partial schedule of reinforcement. This discriminative responding can be transferred to hunger that is normally induced by deprivation of food.*

Electrical stimulation of the lateral hypothalamus (ESLH), which causes satiated animals to eat, resembles in effect the hunger normally produced by deprivation of food in that it also motivates them to perform a response that they previously had learned as a way of getting food (1). Grastyan, Lissak, and Kekesi (2), however, have suggested that the elicitation by ESLH of an already learned response is due not to the specific arousal of the hunger mechanism but to the nonspecific facilitation of a dominant habit. If ESLH can motivate the trial-and-error learning of a new response that is rewarded by food, this alternative interpretation is ruled out because the response to be learned is not dominant at the beginning of training. Furthermore, if the effects of ESLH resemble normal hunger, shifting the reward of food to another response, after one response has been learned and has become dominant, should cause the first response to be extinguished and a new response to be learned. It is clearly impossible for the hypothesis of nonspecific facilitation to account for such reversal learning.

An experiment by Wyrwicka *et al.* (3) strongly suggests that ESLH functions like normal hunger in motivating learning, but their experiment is not completely conclusive for two reasons: (i) they developed the response that they were seeking by themselves moving the leg of the goat upon presentation of the conditioned stimulus, a procedure that may have increased the dominance of that response—for example, by establishing an association similar to that involved in cortical conditioning (4); and (ii) because lifting of the leg was always followed after a few seconds by the termination of ESLH, acquisition of the response may have been caused by the reinforcing effect of this termination (5)

rather than by administration of food.

These objections were met in a previous experiment by Coons (6), in which learning during continuous ESLH was demonstrated by decreased latency of panel pushing, and also in an experiment on maze learning in which Mendelson and Chorover (7) turned off the ESLH immediately when they had removed the rat from either goal box. Our experiment provides additional evidence by testing a satiated rat's ability to learn, during continuous ESLH, to press the one of two bars that delivers food and to reverse this learning when the function of food delivery is shifted to the other bar. Our experiment also tests for (i) reversal learning when the reinforcement is scheduled so that not every press of a bar delivers food, and (ii) transfer of such learning from the motivation aroused by ESLH to that of hunger normally produced by deprivation of food; such transfer is demanded if the motivation artificially aroused by ESLH in fact involves the same drive mechanism as does normal hunger.

Three male albino rats that displayed good stimulus-bound eating when electrically stimulated by way of a permanently implanted indwelling electrode aimed at the lateral hypothalamus were used. Stimulation was by a continuously monitored 60-cy/sec alternating current, of constant intensity, that could be accurately adjusted to a level (50 to 56 μ a) capable of maintaining vigorous eating for sustained periods if food was available. Described in stereotaxic coordinates used to aim the electrodes, the hypothalamic point that was stimulated lay 0.8 mm posterior to Bregma, either 1.3 mm to the left or 1.7 mm to the right of Bregma, and 8.5 mm ventral to the top of the skull; these coordinates apply only to an animal positioned in a stereotaxic instrument in which the top of the incisor bar lies 3.2 mm above the plane of the interaural line. The operative techniques have been detailed (6, 8).

The three rats used were selected from a number of thus-treated animals by screening tests designed to determine by way of which electrodes and at what current intensity reliable stimulus-bound eating could be electrically induced. Beginning an hour before both these tests and the subsequent daily learning periods, each rat's home-cage diet of lab chow *ad libitum* was liberally supplemented with Noyes food pellets to satiate it thoroughly. When many screening tests or learning periods were given per day, they were occasionally separated

by additional exposure of the rat to lab chow and pellets.

In screening tests, the animal was stimulated in the test apparatus with a current intensity that was slowly increased from zero until the rat either ate the liberally scattered Noyes pellets or showed bizarre motor movements or excited behavior incompatible with eating. For rats that did no eating, this procedure was repeated until the negative results were thoroughly convincing; but, if an animal did eat, increase in current intensity was halted and a series of 12 30-second trials of stimulation at the attained level of current was administered. To qualify for inclusion in the study, the rat had to eat at least one pellet during each of these trials and eat no pellet during the last 30 seconds of each 1-minute rest that separated trials; failure to eat on every trial was followed by repetition of the trials at higher intensities of stimulation. If the animal ate between trials, tests were recommenced 5 minutes after the last eating.

A learning period for animals that qualified for the study consisted of 10 minutes of continuous ESLH in a transparent Skinner box containing a food cup placed between a reinforcement and a nonreinforcement bar located 10 cm to each side; a counter recorded the number of presses of each bar during each period. A 10-minute rest without ESLH separated learning periods. The reinforcement was a single Noyes pellet delivered initially every time the bar was pressed (100-percent schedule) and later only on the first press after a variable interval (that averaged 15 seconds, VI 15 sec) following the previous rewarded press. There were minor variations in the conditions for different rats (Fig. 1).

The initial learning and subsequent reversal curves for each rat (Fig. 1) show that the rats not only acquired the reinforced response of bar pressing but also learned to confine their presses chiefly to the one bar that caused food to be delivered. Thus the effects of ESLH do indeed resemble normal hunger in that they can function as a drive for new learning. Reversal learning eliminates the possibility that the differential responding in initial acquisition was either a fortuitous preference for position or facilitation of a dominant habit. Furthermore, the fact that the learning occurred during long periods of continuous ESLH rules out the possibility that it was reinforced by termination of ESLH. Finally, it should be

noted that learning and performance motivated by the effects of ESLH can occur with a variable-interval schedule as well as with a 100-percent schedule of reinforcement—another respect in which the effects of ESLH resemble normal hunger. These findings substantiate other reports that learning of a food-seeking response was elicited by ESLH (3, 6, 8) and agree with the results of various other experiments by Coons and Miller on the motivational correlates of eating that is induced by electric stimulation of the lateral hypothalamus of the rat (6, 9).

Previous experiments have shown that a food-seeking response learned in a state of hunger from deprivation can transfer to an ESLH-induced "hunger" state. The conditions of our experiment, like those of the study by Wyrwicka *et al.* (3) that we have criticized on other grounds, made it possible to test the converse: whether a food-seeking response learned only in an ESLH-induced "hunger" state can transfer to

a deprivation-hunger state. Rats I and III, having learned to press preferentially the reinforcement bar, were starved for 48 hours and then tested during several completely unreinforced trials to see whether they still pressed bars, and with the same preference. Subsequently, the rats were resatiated and given partially reinforced reversal training during ESLH, after which the same deprivation procedures and tests were repeated. For rat III these transfer tests followed the test shown in Fig. 1; for rat I they occupied interim periods during which the unrewarded response was being extinguished.

The learned preferences for bars and their reversals were transferred, in confirmation of the findings of Wyrwicka *et al.* (3). For the total of eight transfer trials the average numbers of presses on the bar that formerly delivered reinforcement and on the nonreinforcement bar were, respectively, 13.9 and 5.5 for rat I and 10.6 and 2.5 for rat III. A correlated *t*-test of the trial dif-

ferences on these bars yielded a $p < .05$ (7 degrees of freedom, two-tailed) for each rat. The complete absence of pressing on either bar during rest periods (no stimulation) that were given to these rats while satiated indicates that the differences in pressing were relevant to the drive and not simply to the strength of the habit.

The rate of bar pressing markedly decreased, however, with change from the ESLH state to the state of normal hunger. For the four trials preceding each transfer test, the average numbers of presses on the reinforcement bar and on the nonreinforcement bar were, respectively, 47.4 and 2.3 for rat I and 109.6 and 15.9 for rat III. Hence, although the transfer of preference again emphasizes resemblance between the effects of ESLH and normal hunger, the lack of complete transfer of rate suggests that differences may exist. One or both of the following factors may explain this reduction of pressing. First, because the animals were tested without reinforcement, bar pressing was undoubtedly being extinguished. Second, there may be a great stimulus-generalization decrement from the effects of ESLH to normal hunger, since the ESLH state to which learning was presumably conditioned probably involves many cues other than those of hunger, such as cues associated with sexual drive, sleep, thirst, temperature, and other functions that the lateral hypothalamus may also subserve.

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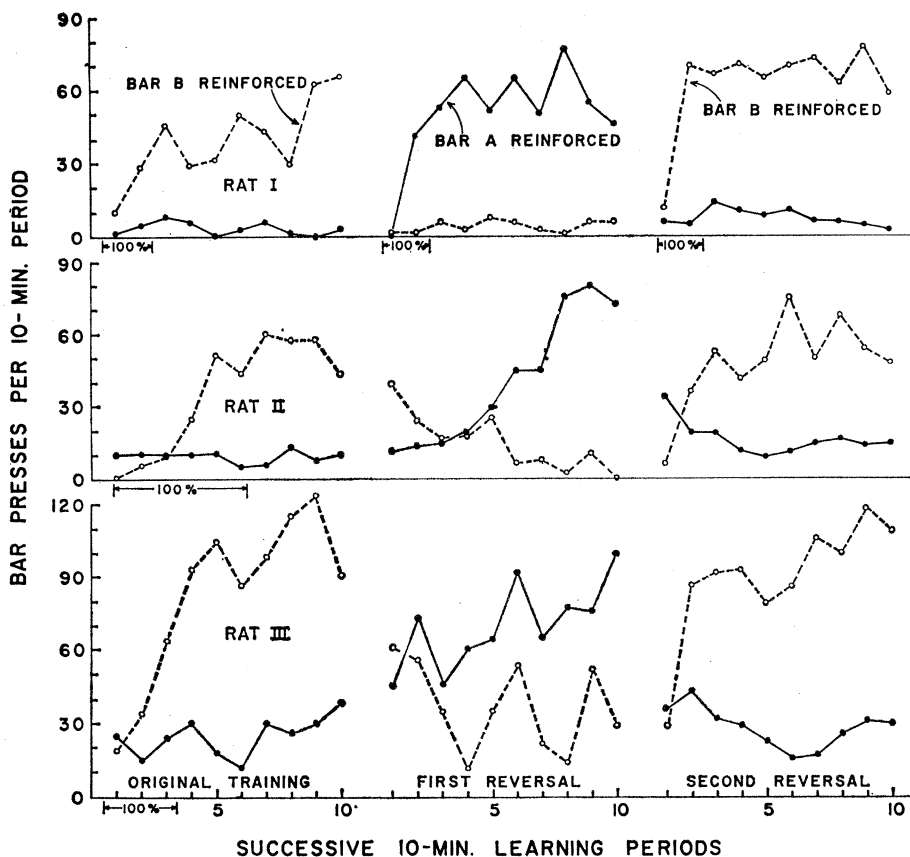


Fig. 1. Original and reversal learnings of discriminative bar pressing that was reinforced by food during continuous electrical stimulation of lateral hypothalamuses of satiated rats. Rats I and II were the first shaped by reinforcements to approach the food cup at the magazine sound of food delivery, before they were given access to the bars. Rat III received no magazine training, but for a few periods it was rewarded for pressing either bar. Except where the base line is marked 100 percent to indicate that every response was reinforced, reinforcement was on a VI-15-sec schedule. For rat I each period of reversal training was preceded by unrewarded extinction; for rats II and III there was no such extinction.

References and Notes

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