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Lateral Hypothalamus: Food Current Intensity in Maintaining Self-Stimulation of Hunger

Abstract. *Rats displaying stimulus-bound eating will press bars for currents slightly above eating threshold only when food is near the bar. At higher currents self-stimulation is maintained without food. Such currents may spread to activate consummatory feedback appropriate to the drive elicited; or, for more intensely stimulated drive mechanisms, wider ranges of sensory feedback may be reinforcing.*

In this study we examined the possibility that reinforcement in self-stimulation is dependent upon sensory feedback appropriate to a drive that is electrically elicited. The examination bears upon the proposition (*1*) that electrical intracranial stimulation is self-administered by an animal only if both a drive system and a reinforcement system are activated jointly. In the usual situation, activation is presumably accomplished by the current spreading to both systems in the brain. However, even if the current is somehow regulated to activate only one system, self-stimulation should still occur provided the other system is concurrently activated in some other way. For example, an animal may not self-administer current that stimulates a drive only, but, on the other hand, it may self-administer current if the reinforcement system is operated at the same time in some normal fashion, such as by making available sensory stimuli appropriate to the consummation of the drive.

To test this possibility, male albino rats, with permanently implanted monopolar electrodes (*2*, *3*), were allowed the opportunity of self-stimulating a known hunger-drive mechanism in the lateral hypothalamus (*4*, *5*) at current intensities just above the thresholds for eliciting stimulus-bound eating and yet, presumably, too weak to affect a reinforcement system also. The following questions were then asked: (i) Would a thoroughly satiated rat repeatedly press a bar to deliver such a current if food were absent? (ii) If the animal would not press, would it do so if food were continuously available immediately by the bar?

Three prerequisites were necessary in the selection of subjects. First, they should display clear stimulus-bound eating of wet mash to electrical stimulation of the lateral hypothalamus (ESLH). [Screening procedures (*4*, *5*) and threshold measurements (*6*) for stimulus-bound eating have been described.] Second, at currents well above eating threshold, they should press a bar at moderate rates to self-administer 2-second trains of ESLH delivered through the same electrode that elicits eating. Third, if a dish of wet mash were by the bar, they should readily eat in response to each self-delivery of the stimulation. In our study, seven rats met the first criterion and these also met the latter two criteria. This high coincidence of stimulus-bound eating and self-stimulation by way of the same electrode has been noted before (*7*).

Two experiments comprised the study. The second, a modification of the first, was to control for some possible procedural artifacts. Accordingly, experiment 1 and only those features of experiment 2 that were different will be described.

The slightly suprathreshold current employed for each of four animals used in experiment 1 is indicated in the upper right of Fig. 1a by an open circle below the bar showing the eating threshold. At that current each animal's bar-pressing was measured as a joint function of whether bar-pressing delivered stimulation and whether food was by the bar. At least 20 minutes before all tests, animals were satiated by putting a dish of wet mash in their home cage. Four conditions were presented to each rat in the following order: (i) stimulation plus no food (S-NF); (ii) stimulation plus food (S-F); (iii) no stimulation plus no food (NS-NF); and (iv) no stimulation plus food (NS-F). Seven blocks of these four conditions comprised each animal's test, and each condition lasted 2 minutes. The order of conditions was chosen to keep the initially high extinction rates that might follow the S-F condition from falsely elevating the S-NF or NS-F rates.

Tests were administered in two Plexiglas boxes that were identical except that one always contained a dish of wet mash by the bar and the other did not. The animal and the manipulandum were rotated from box to box every 2 minutes, and the animal was placed in the middle of the box facing the bar. On every other trial within a given box, pressing the bar did not deliver ESLH.

In experiment 1, if an animal failed to press within 10 seconds after being placed in a box, it was reminded of what a lever press on that trial would deliver by being primed with a free sample (2 seconds) of such stimulation. If the animal still did not press, this priming was repeated up to twice more on the 15th and 20th second of the trial. Thus all priming occurred within the first quarter of each 2-minute period and without regard to the animal's orientation in the box. Priming in the no-stimulation periods (NS-NF and NS-F) consisted of the noise of the stimulator, but no current was passed.

New rats were employed for experiment 2. The slightly suprathreshold current used for each is shown in the upper right of Fig. 1b by an open circle below the bar indicating the eating threshold. The design was the same as for experiment 1 with the following exceptions: Each press delivered 3 seconds of stimulation instead of 2, and the response measure was the number of reinforcements obtained rather than the absolute number of presses. Eight instead of seven blocks of four conditions were used. The order of the four

conditions from block to block was not fixed but was varied in a Latin-square design to control for order effects. Most importantly, no priming was administered. This checked the possibility, in experiment 1, that some inadvertently differential use of priming in the four conditions accounted for the results.

A comparison of the lower portions of Fig. 1, a and b, clearly indicates that the same pattern of results was obtained for both experiments 1 and 2. Hence the results cannot be due to artifacts of priming or order of presentation. In both experiments bar-pressing to self-stimulate the lateral hypothalamic feeding area for currents only slightly above eating threshold was mainly dependent upon the presence of food by the bar (S-F greater than S-NF: in experiment 1, t of 7.79 at 3 df $= P < .005$; in experiment 2, t of 20.63 at 2 df $= P < .005$). Furthermore, the rates enhanced by food were inversely proportional to the eating thresholds (in experiment 1, r of $-.987$ at 2 df $= P < .05$; in experiment 2, r of $-.998$ at 1 df $= P < .05$). Evidently, the more successful the electrode placement in the feeding area, as judged by the lowness of a threshold, the more effective the food in elevating self-stimulation of that area. Although stimulation by itself also had a significant effect in elevating bar-pressing as evidenced by greater rates in the S-NF than in the NS-NF condition, the effect was small and atypical of accepted rates of self-reward.

Comparison of the NS-NF and NS-F conditions shows that, in six out of the seven rats in the combined experiments, the presence of food by the bar, even in the absence of current, evoked a slight increase in rate of pressing despite the fact that the animals never ate the food. Perhaps incentives learned to the cue values of food in the S-F condition motivated this increment.

In the S-F conditions each animal always ate and it generally pressed only once per stimulation train. In the other conditions eating did not occur and in the S-NF conditions bursts of several presses per train were much more frequent. Consummatory measures taken in experiment 2 indicated that each animal gained on an average of 22 grams over an entire test session.

In a later stimulation test without food present, an increment of from 2.8 to 4.8 μa was found necessary to reproduce bar-pressing rates at least as great and as stable as those in the S-F condition. At these intensities the rat would excitedly sniff over and under the bar and occasionally bite at it as if, under the increased drive, the bar now possessed some food-like qualities.

This study clearly indicates that a satiated animal will repeatedly press a bar delivering ESLH slightly greater than the hunger threshold when food is immediately available next to the bar, but not otherwise. At higher currents the presence of food is not essential. Both Mogenson and Mendelson (*8*), using rats that would self-stimulate by way of the same electrodes that elicited drinking, have reported results that point in the same direction as ours.

Although we predicted these results when using Deutsch's two-system hypothesis (*1*) as a model, there are other explanations that require that only one system be electrically activated. MacDonnell and Flynn (*9*) report that the hypothalamic stimulation in the cat that elicits attack also established sensory fields in the area of the muzzle from which head orientation and biting, that form the terminal components of attack, can be tactually triggered. The size of these fields is larger the more intense is the central stimulation that elicits attack. Similarly for self-stimulation, increasing the current may expand the peripheral sensory field from which feedback reinforcing to the drive being elicited may be obtained. Also, increasing the current may widen the sensory field by activating other drives as well as hunger, each with its own separate field. In either case this should expand the type and range of naturally occurring stimuli that are reinforcing to responses instrumental for self-stimulation. Since a variety of these stimuli (for example, proprioceptive stimuli, such as those that may function as subgoals in food-seeking activities) are likely to be present in any self-stimulation situation, self-stimulation at high intensities should be relatively independent of the presence or absence of any single type of stimulus.

Finally, it is possible that self-stimulation arises from a system entirely independent of hunger or thirst drive. Conceivably, the animals might have normally self-stimulated for low levels of current without the presence of food except that the unsatisfied hunger that was concurrently induced was so aversive as to mask reward. At higher currents the increased reinforcement obtained from self-stimulation may have outweighed this aversion. Alternately, in the present experiment the self-stimulation system at low currents reinforced bar-pressing only by summating with

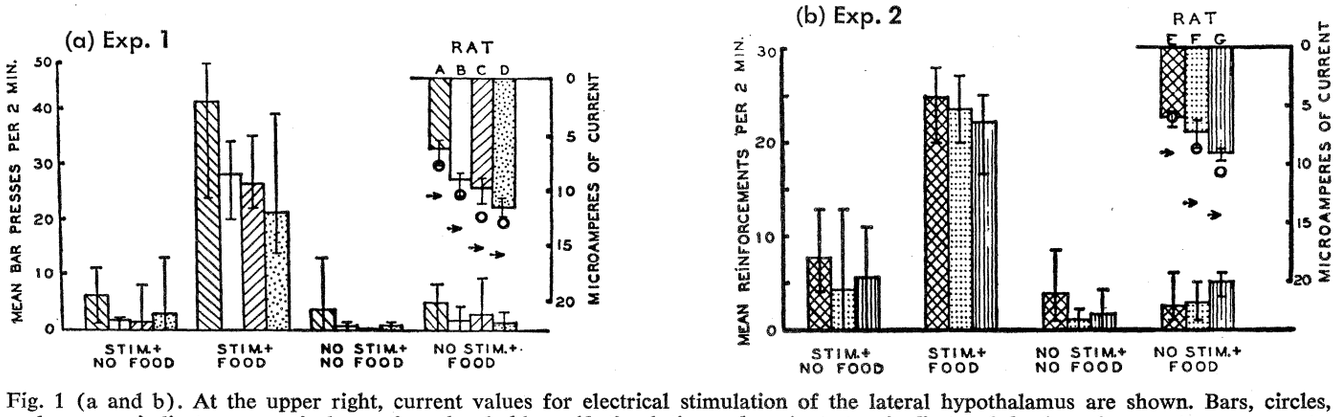

Fig. 1 (a and b). At the upper right, current values for electrical stimulation of the lateral hypothalamus are shown. Bars, circles, and arrows indicate, respectively, eating thresholds, self-stimulation values in tests of effects of food, and currents necessary to maintain self-stimulation in the absence of food. Vertical lines show the range of variability about the thresholds. At the bottom are bar presses or reinforcements for each animal in each condition. Individuals are identified by the markings of the bars that are the same for each rat as at the upper right. Vertical lines indicate the range of bar-press frequencies about the average.

other reinforcements, such as that produced by eating. As a general explanation, however, this does not seem to be the case. Two of our eaters (not stimulus-bound drinkers), when deprived of water for 48 hours and presented with water instead of food by the bar in a stimulation condition, never pressed once while they were drinking as they might have been expected to do if summation of two types of reinforcement, in this instance water and subthreshold intracranial stimulation, could account for the results of this study.

EDGAR E. COONS
J. A. F. CRUCE
Department of Psychology,
New York University,
New York 10003

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Modification of Motivated Behavior Elicited by Electrical Stimulation of the Hypothalamus

Abstract. *Previous reports demonstrated that hypothalamic stimulation may elicit either eating, drinking, or gnawing and emphasized both the specificity of the neural circuits mediating these behaviors and the similarity to behavior during natural-drive states such as hunger and thirst. We find that, after a period of very consistent elicitation of one of these behaviors, the animal may exhibit an equally consistent alternate behavior. A learning component is implicated in the association of hypothalamic stimulation with a particular behavior pattern.*

Hypothalamic stimulation in the rat may elicit behaviors such as eating, drinking, and gnawing (*1, 2*); previous reports have emphasized both specificity of the neural structures activated and similarity of the behavior to that occurring during natural-drive states. As satiated animals exhibit the behavior only during the period of stimulation, the term "stimulus-bound" behavior has been applied. From the fact that animals that exhibit such behavior will perform some learned task (instrumental behavior) to obtain a relevant goal, it has been concluded that the stimulation does not trigger a stereotyped motor act, but activates a motivational state such as hunger or thirst.

We studied the development of "stimulus-bound" behavior and the possibility of modifying the elicited behavior in the absence of any change in stimulation site or stimulation parameters. Our results indicate that there is a learning component involved in the association of hypothalamic stimulation with such behavior as eating, drinking, or gnawing. Hence, we question those theoretical positions based on the conclusion that electrical (and perhaps chemical) stimulation activates fixed neural circuits mediating natural-drive states.

Bipolar electrodes (*3*) were implanted in the lateral hypothalamus of mature Holtzman albino rats of both sexes. With the dorsal surface of the skull level between bregma and lambda, the electrodes were positioned 2.50 to 3.50 mm posterior to bregma, 1.25 to 1.50 mm lateral, and 8.25 to 8.50 mm below the top of the skull (*4*). Animals were stimulated with either 30-second trains of 60-cycle sine waves or biphasic rectangular pulses (frequency, 100 pulses per second; pulse duration, 0.2 msec). The stimulus parameters used with each animal are provided in Table 1. All stimulation was programmed by automatic equipment and was not delivered under the experimenter's control.

After surgery but before any stimulation, the animals were placed individually in Plexiglas cages which served as living quarters and testing chambers. Light in the room was on from 7:00 a.m. to 7:00 p.m. each day. The cages contained three goal objects: pellets (Purina Lab Chow), a water bottle with a metal drinking tube, and a pine wedge mounted either on the wire-mesh floor or one of the walls. During preliminary screening to determine an appropriate stimulus intensity, animals were stimulated for a 30-second period followed by a 60-second interstimulus interval. The intensity was adjusted until the stimulus elicited a forward-moving "searching" behavior. If, after a period of time, the animal did not exhibit either eating, drinking, or gnawing in response to stimulation, the intensity was raised or lowered to what appeared to be a more promising level. If no specific behavior pattern emerged, the animal was stimulated throughout the night for 30 seconds every 5 minutes (night schedule). If no "stimulus-bound" behavior was evident, the sequence was repeated during at least one additional night before the animal was rejected. With this procedure, approximately 25 percent of the animals exhibited "stimulus-bound" eating, drinking, or gnawing on the pine wedges.

The animals that exhibited "stimulus-bound" behavior were then given a series of three standard tests (30 minutes in duration, with twenty 30-second stimulation periods, each separated by a 60-second interstimulus period). There was a minimum of 30 minutes between each test. During these tests, the three goal objects were present. After this first series of tests, the goal object to which the rat oriented was removed, and the animal was left overnight with the other two goal objects and stimulated on the night schedule. If, for example, the rat exhibited "stimulus-bound" drinking during the first series of tests, the water bottle was removed during the night, and only the wood and food pellets were left in the cage. *The stimulus pa-*