Situational control over electrically induced ingestive behavior: A comparison of hippocampal and hypothalamic feeding

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Either hippocampal or hypothalamic stimulation was used to induce feeding in rats during five $\frac{1}{2}$ -h conditioning sessions. Subsequently, the animals were tested for feeding in the same situation, but without brain stimulation. During the no-stimulation condition, the hippocampal animals ate more than the hypothalamic animals and unstimulated control animals. The hypothalamic animals did not differ from controls on the no-stimulation days. These findings indicate that ingestive behavior induced by brain stimulation can come under situational control but that this phenomenon is dependent upon electrode placement.

Masserman (1941) was the first to question the correspondence between electrically elicited behaviors and similar behavioral sequences under more natural conditions. He raised this issue because he could not condition hypothalamic rage in cats using a classical conditioning paradigm. More recent attempts to condition electrically elicited ingestive behaviors have also been unsuccessful. Andersson and Larsson (1956) were unable to condition thirst induced by lateral hypothalamic stimulation in goats. Huston and Brozek (1972) were unsuccessful in conditioning feeding and drinking elicited by hypothalamic stimulation in rats.

These findings may indicate a fundamental difference between electrically induced behaviors and natural behaviors. Alternatively, this evidence may reflect a general constraint on conditioning; namely, certain behavioral sequences require specific organismic conditions which cannot be triggered by external stimuli (Bindra, 1969). In support of this argument, it is generally conceded that normal ingestive behavior cannot be conditioned (Cravens & Renner, 1970). On the other hand, some consequences of electrical brain stimulation have been conditioned (Bindra & Campbell, 1967; Huston & Brozek, 1972; Thomas & Basbaum, 1972). Thus the constraints on stimulation-induced behaviors may simply be those imposed on normal behavioral sequences.

The belief that normal ingestive behavior cannot be conditioned has been challenged by a series of recent experiments. Persistent and vigorous drinking can be conditioned to an environmental complex (Seligman, Ives, Ames, & Mineka, 1970). Feeding can also be conditioned to an environmental complex (Grant &

Milgram, 1973) or to specific conditioned stimuli (Mineka, Note 1). These findings call for a re-examination of the conditionability of electrically induced ingestive behavior. The present experiment examined whether feeding elicited by brain stimulation could be conditioned to an environmental complex. Two neural regions were studied: the lateral hypothalamic area and the dorso-lateral hippocampus. Although stimulation of both regions facilitates feeding, they differ in that hippocampal feeding starts at the offset of brain stimulation (Milgram, 1969a), while hypothalamic feeding is stimulation-bound and stops at the termination of the stimulation.

METHODS

Twenty-eight male hooded rats, weighing 275-325 g, were used. Eight animals had hippocampal electrodes, 6 animals had hypothalamic electrodes, and 14 were unoperated controls. The animals were selected from a group of 64 rats, including 16 hippocampal animals, 16 hypothalamic animals, and 32 unoperated controls. Prior to any experimental testing, each control animal had been paired with one experimental animal on the basis of body weight. Thus, there were four groups of animals: hypothalamic animals (N = 6), hippocampal animals (N = 8), hypothalamic controls (N = 6), and hippocampal controls (N = 8).

Surgical and Histological Techniques

Electrode implantation was performed under sodium pentobarbital anesthesia (54 mg/kg). The monopolar electrodes were made from .09-in.-diam 80% platinum, 20% iridium wire which was insulated to about .5 mm of the sharpened tip. Standard stereotaxic procedures were used with the surface of the skull parallel to the base of the stereotaxic instrument. The coordinates used for the hippocampal electrodes were: 4.0 mm anterior to the earbars; 4.0 mm lateral to the midline, and 3.3 mm down from the dural surface. The hypothalamic electrodes were aimed at a point 6.0 mm anterior to the earbars, 1.7 mm lateral to the midline, and 7.5 mm below the dural surface. A stainless steel wire wrapped around jewelers screws in the skull was used as the indifferent electrode.

At the end of the experiment, the animals were sacrificed and perfused intercardially with physiological saline followed by 10%

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Figure 1. Feeding during conditioning and testing sessions of hypothalamic and hippocampal animals and their matched controls.

Formalin. Frozen sections of 40-micron thickness were cut and stained with cresyl violet to verify the electrode placements.

Testing Procedures

The animals were tested in 12 x 8 x 24 in. clear Plexiglas boxes with grid floors. A metal bar 1.5 in. from the grid floor was located at one end of each box. Water was available in a graduated cylinder immediately to the right of the bar, and Purina laboratory pellets were scattered over the floor of the box. Each box was located within a sound-isolated white chamber with fluorescent lighting, a one-way mirror at the front of the chamber, and an exhaust fan at the rear of the chamber, which provided a constant noise level.

The experiment was divided into pretraining, conditioning, and testing phases. Pretraining began at least 7 days following surgery. The animals were first trained to barpress for 60 Hz sine wave stimulation. The current intensity was individually adjusted. The duration used for the hippocampal animals was 1.0 sec. The hypothalamic animals were trained to press for 20-sec-duration stimulation.

The conditioning sessions were instituted once an animal had acquired the barpressing response. A self-induced eating technique was used. The animals were given daily ½-h barpressing sessions with a weighed quantity of food scattered over the floor of the box. The animals were tested at approximately the same time each day, with each animal receiving a minimum of six such sessions. Animals were discarded from the experiment if the average intake over the last five conditioning sessions was less than 1.5 g. Thus, selection of animals was based on two criteria: first, the animals had to learn to barpress; and, second, they had to demonstrate facilitated feeding.

The control animals received identical amounts of experience in the testing chambers as the experimental animals. Every time an experimental animal was placed in the testing situation, its matched control was placed in an identical testing box for the same length of time. The control animals received no stimulation and were maintained on ad-lib food and water.

The testing sessions were on 5 consecutive days, beginning on the day following the last conditioning session. The procedure was the same as during conditioning except that the bar was disconnected from the stimulator.

RESULTS

Figure 1 summarizes the food intake for the four groups of animals during the conditioning and the testing sessions. The data were analyzed by a two-factor mixed design analysis of variance, treating each of the four groups as independent. The main effect during the conditioning trials was significant ($F = 15.16$, $p < .001$). Orthogonal comparisons indicated that both the hippocampal and the hypothalamic animals ate significantly more than the control group but did not differ significantly from each other.

During the testing sessions, the main effect for groups was also significant ($F = 5.08$, $p < .01$). Orthogonal comparisons indicated that the hippocampal animals ate significantly more than each of the other groups. The other three groups did not differ significantly from each other. The analysis of variance also revealed a significant Trials by Groups interaction ($F = 2.28$, $p < .025$). Figure 1 indicates that this interaction is partly due to a decrease in feeding during the course of the testing trials in the hippocampal animals. The hippocampal animals ate significantly less over the testing sessions than they did during conditioning ($F = 20.17$, $p < .005$).

Five hypothalamic animals were classified as stimulus-bound drinkers. Their average water intake over the conditioning trials was 7.08 ml. During testing, however, the water intake decreased to an average of .16 ml, which was less than the control animals which drank an average of .64 ml of water.

DISCUSSION

The most important finding of this experiment was the facilitated feeding of the hippocampal animals during the testing sessions. This result is attributable to the prior conditioning experience. The feeding is not a consequence of hunger or other organismic conditions associated with prior food deprivation, as the animals were maintained on ad-lib feeding throughout the experiment. It is also unlikely that the results are a consequence of the procedure to select hippocampal eaters. Eight of the 16 animals implanted with hippocampal electrodes met the criteria for selection as subjects, and all of these animals ate more than any of the hippocampal controls. Moreover, the hippocampal animals ate significantly more during the conditioning sessions than they did during the testing sessions, indicating that the feeding during conditioning was a consequence of the stimulation. This is consistent with other data indicating that hippocampal eating is determined by the electrode placement rather than the specific animal stimulated (Milgram, 1969a). Finally, the facilitated feeding is not attributable to the prior experience with positive reinforcing stimulation. The hypothalamic animals also had prior experience receiving positively reinforcing stimulation but did not show facilitated feeding during the testing sessions.

To the extent that the facilitation of feeding was a consequence of the prior conditioning experience, the present data suggests that electrically induced ingestive behavior can come under control of an environmental complex.

As previously mentioned, attempts to condition feeding induced by brain stimulation have been unsuccessful. The present results suggest that electrode placement is a critical variable. The other relevant studies all used hypothalamic stimulation to induce ingestive behavior; in the present experiment, the hypothalamic animals ate vigorously during the conditioning sessions but ate virtually nothing during the testing sessions. The unsuccessful attempts to condition hypothalamic feeding may simply be attributable to procedural variables such as the limited number of conditioning sessions provided. Although such possibilities cannot be ruled out, they do not account for the differences between hippocampal and hypothalamic animals. The conditioning experience provided the two groups was equated in so far as it was possible. In fact, the hypothalamic animals did not differ significantly from the hippocampal animals during the conditioning sessions. Thus, if it were possible to condition hypothalamic feeding, different or more extensive procedures would be required than were successful for hippocampal feeding.

The difference between hippocampal feeding and hypothalamic feeding may reflect different underlying neural systems. Other evidence is consistent with this suggestion. Ingestive behavior induced by hypothalamic stimulation is relatively plastic insofar as it can be modified to other behavioral sequences (Valenstein, Cox, & Kakolewski, 1970). Hippocampal feeding shows greater specificity (Milgram, 1969b). Milgram and Stockman (unpublished) found that hippocampal feeding often recovered prior to normal feeding following lateral hypothalamic lesions, which suggests that hippocampal feeding may be partially independent of the lateral hypothalamic region.

The apparent plasticity of hypothalamic eating may be attributable to the simultaneous activation of motivational systems other than those which control normal feeding (Milgram, Devor, & Sever, 1971). This suggests an alternative explanation for the failure to condition hypothalamic feeding. Possibly other consequences of hypothalamic stimulation are conditioned to the testing situation which are incompatible with feeding. Wise and Erdman (1973), for example, have suggested that many of the anomalous aspects of hypothalamic feeding are a consequence of a corresponding increase in emotional reactivity produced

by the stimulation. It is more difficult to condition normal feeding in emotionally reactive animals than in less emotional animals (Grant & Milgram, 1973).

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