Hypothalamic Motivational Processes as Reflected by their Hippocampal Electrical Correlates

Abstract. *Electrical stimulation of the same hypothalamic point with current of mild or strong intensity produces opposite behavioral effects; moreover, interruption of either kind of stimulation invariably results in the appearance of powerful antagonistic aftereffects. There is a strict correlation between approach behavior and hippocampal theta rhythm on the one hand and withdrawal behavior and desynchronization on the other. The importance of the antagonistic aftereffects in the organization of conditional processes and in the interpretation of the "drive reduction" hypothesis is emphasized.*

The existence of two basic and opposed behavioral mechanisms, sometimes referred to as "approach" and "withdrawal" (*1*) is now being strongly substantiated by extensive research into the neural substrate of motivation in mammals (*2*).

Recent experiments in which animals are stimulated in a dual conditional reflex situation have clearly shown that these basic processes are strictly interconnected and common elements of both approach and avoidance conditional reflexes (*3*). A closer understanding of their neural integration has not been possible, however, because of the lack of an adequate method to reveal the dynamic aspects of the whole motivational system.

In this report we describe some basic findings obtained with a brain stimulation technique called the "pedal switch-off method." By pressing a pedal the animal turns off brain stimulation started by the experimenter. We have found that stimulation of motivational neural representations is consistently followed by conspicuous effects which have the nature of a rebound. Simultaneous recordings from the hippocampus revealed a strict correlation between two characteristic electrical patterns and the overt motivational manifestations both during and after stimulation. These electrical indicators of basic motivational effects allowed the dynamics of motivational processes to be followed during different kinds of conditioning more successfully than before (*4*).

Twelve freely moving cats were used, each bearing stereotaxically implanted electrodes. Generally, four pairs of stimulating electrodes were implanted in different regions of the hypothalamus and four pairs of recording electrodes in the basal, intermediate, and dorsal parts of the hippocampus. When the cats had recovered from surgery they were subjected to the following experiments. A pedal with a surface of 15 by 30 cm, and 2 cm in height, was placed on the bottom of a soundproof cage 1.5 m long by 1.5 m wide. The function of this pedal was to interrupt stimulation through the animal's own action in the course of the locomotion induced by hypothalamic stimulation. The stimulation was consistently started by the experimenter when the animal had assumed a predetermined place in the cage. The location of the pedal was changed according to the requirements of the experiment. The locomotor reactions were recorded by photographing the light of a small lamp attached to the head of the animal. The electrical activities of the hippocampus were recorded with an eight-channel routine electroencephalograph and a two-channel automatic frequency analyzer.

The most important observation was that when the electrodes were implanted in certain locations, diametrically opposed direct effects and antagonistic aftereffects (indicated both by the behavior of the animal and by the electrical recordings) could be produced with two critical intensities of stimulation (*5*).

Repeated stimulation with current of moderate intensity, slightly above threshold, elicited behavioral manifestations characteristic of the orienting cat: sniffing and searching accompanied by progressively increasing locomotion and, simultaneously, a continuous and regular theta rhythm in the hippocam-

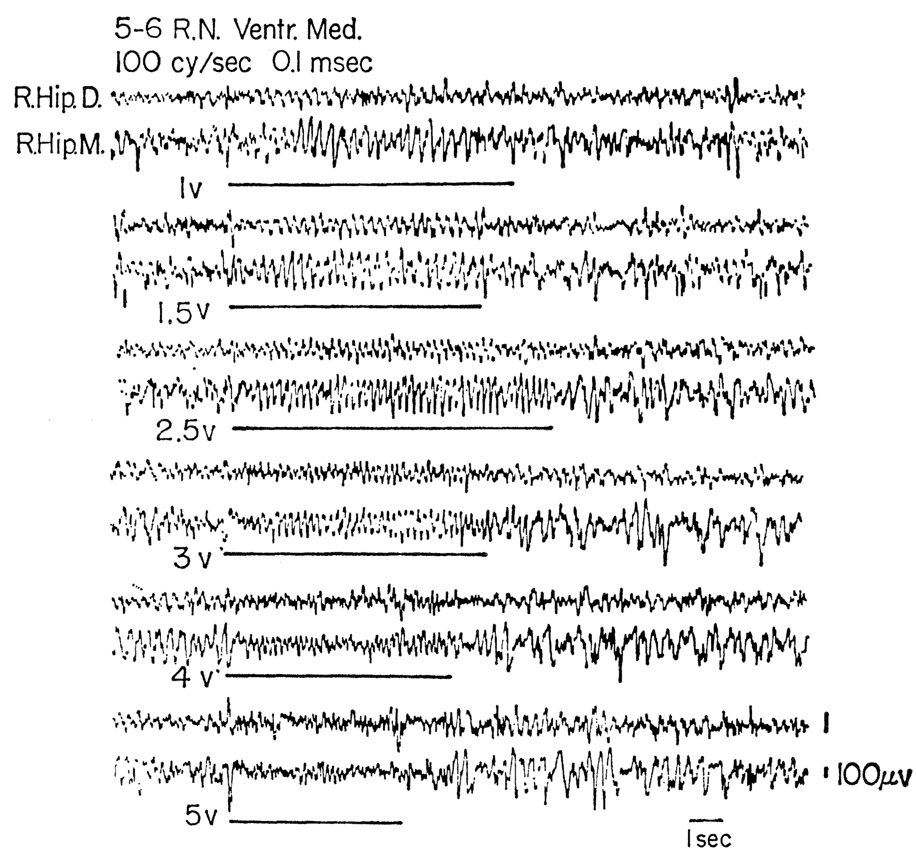

Fig. 1. Progressive reversal of the hippocampal theta response to desynchronization in the course of a step-by-step increase of intensity of hypothalamic stimulation. The behavioral consequences of interruption of stimulation with current intensities of 1 to 1.5 v were in striking contrast to those observed when the intensity was 5 v. The stimulations at more than 2.5 v were followed by arrest-reactions of progressively increasing duration. Note the character of the electrical aftereffects. Here and in the other figures the continuous line marks duration of stimulation. *R.Hip.D.*, right dorsal region of the hippocampus; *R.Hip.M.*, right intermediate region.

pus. Interruption of the stimulation resulted in a sudden withdrawal or jumping off the pedal, the behavior having a definite aversive character; simultaneously, there was a rebound-like desynchronization in the hippocampus.

In response to a stepwise increase in the intensity of the current, both the behavioral and electrical manifestations of stimulation gradually changed until, on reaching a critical intensity, they were in sharp contrast with the primary manifestations. Orientation movements were replaced by ever-increasing, flight-like running and the former theta rhythm was gradually displaced by desynchronization in the hippocampus (Fig. 1).

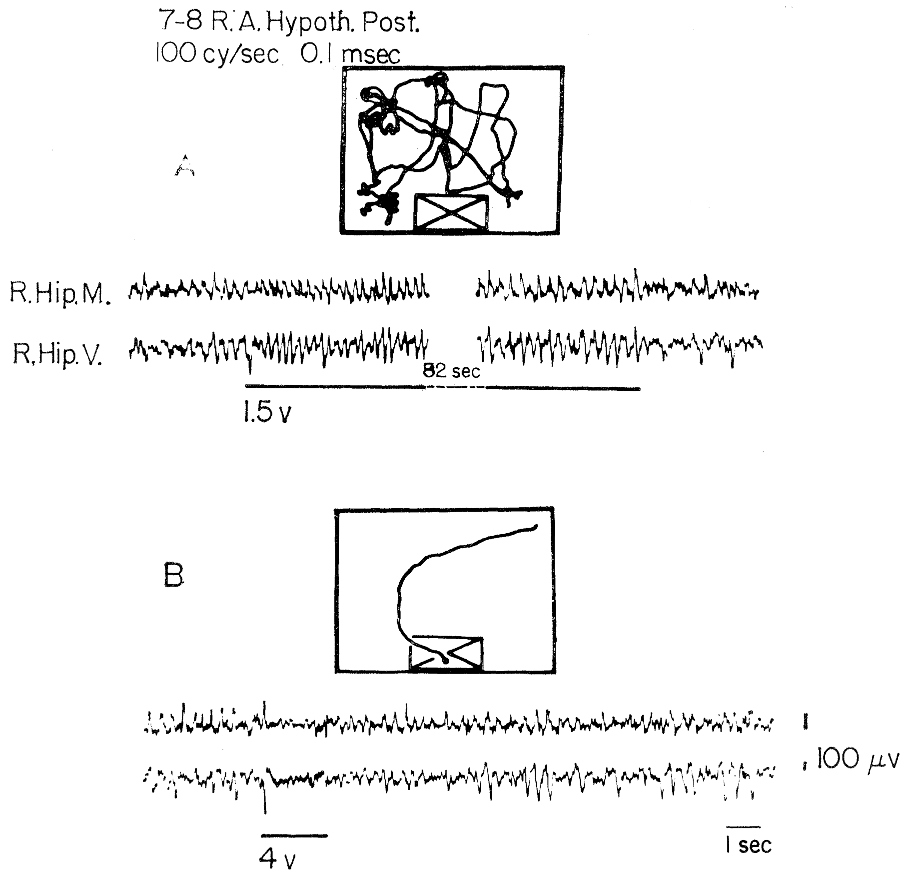

Fig. 2. The final outcome of mild (*A*) and strong (*B*) stimulation of the same hypothalamic point producing continuous theta activity and desynchronization respectively. (*A*) Avoidance conditional reaction, (*B*) approach conditional reaction. The enclosed area represents the "pedal switch off" experimental situation; the crossed rectangle in it represents the pedal and the irregular lines represent the recorded locomotor reactions. *R.Hip.M.*, right intermediate hippocampus. *R.Hip.V.*, right ventral hippocampus.

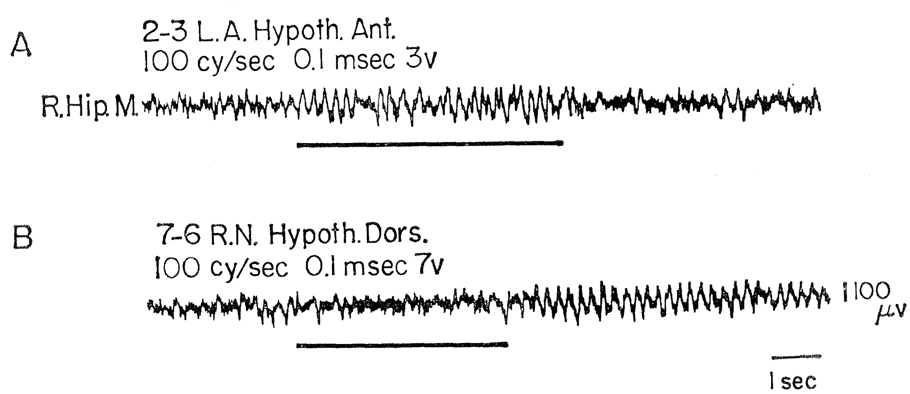

Fig. 3. Stimulation of hypothalamic points producing exclusively approach or withdrawal reactions are also characterized by conspicuous aftereffects. Upper trace: rebound desynchronization appearing at termination of an approach effect elicited by near-threshold intensity. Lower trace: rebound theta activity appearing on interruption of a withdrawal effect. Both reactions were elicited in the same animal and recorded with the same hippocampal electrode. *R.Hip.M.*, right intermediate hippocampus.

Upon termination of stimulation the cat suddenly stopped running and adhered to the pedal. Stimultaneously, a continuous train of high-amplitude theta activity of a rebound character was recorded from the hippocampus.

The functional significance of the aftereffects was revealed by the following observations. After repeated stimulation with current of moderate and high intensity, conditional reactions corresponding to the character of the aftereffects, approach or avoidance, occurred. When mild stimulation was interrupted several times, the cat, instead of approaching the pedal, walked around it or leapt over it —that is, it showed avoidance behavior (Fig. 2*A*). After repeated interruption of a strong stimulation the cat showed a conditional approach behavior. In the course of that process the animal approached the pedal with successively decreasing latencies, then sat on it steadily (Fig. 2*B*). If only one kind of stimulation (either mild or strong) was repeated for a longer time, then in the inter-trial periods the animal showed the same tendency to avoid or approach the pedal as it did during stimulation. The spontaneous behavior was unaffected by the position of the pedal. It should be mentioned that stabilization of one of the conditional reactions always counteracted elicitability of the stimulation effect responsible for the antagonistic reaction. This influence manifested itself in a definite shift of the critical intensity value at which, prior to conditioning, the reaction reversal had occurred.

Besides the above effects, which represent our most typical observations, we also found hypothalamic points from which no reaction reversal in the above sense could be elicited—that is, stimulation of these points with widely different parameters produced effects that varied in intensity but were always of the same type. Points producing pure approach reactions were found particularly in the lateral hypothalamic area. In these cases stimulation with current of either mild or strong intensity produced only theta activity and locomotion of an orientative character. Interruption of these stimulations was followed by a period of marked desynchronization in the hippocampus, accompanied by a flight-like behavior (Fig. 3*A*). In striking contrast, certain regions, in particular the medial hypothalamic and perifornical area, produced exclusively crouching, withdrawing movements simultaneously with pure hippocampal desynchronization. Termination of such stimulation resulted in a marked rebound-like train of theta rhythm accompanied by approach behavior (Fig. 3*B*).

The correspondence that existed between the electrical and the behavioral effects in any combination of events left no doubt that they were strictly correlated manifestations, the theta activity reflecting approach mechanisms and the desynchronization withdrawal mechanisms.

Strong withdrawal effects were often followed by a marked arrest reaction. This reaction was characterized by a special hippocampal electrical pattern, namely high-amplitude slow waves, sometimes slower than theta, interspersed with desynchronized periods (Fig. 1; aftereffect in the lowermost record). This pattern, essentially a mixture of the already-described pure electrical patterns, suggested that the arrest reaction might be an interference product of two antagonistic motor effects of the withdrawal and approach mechanisms.

Our results seem to warrant the following general conclusions.

1) In a manner similar to many other functions of the organism, the regulation of motivation seems to be homeostatic. This means that by a reciprocal neural organization of the basic motivational mechanisms the long persistence of motivational excitement at a definite intensity is ensured. This limiting mechanism works in such a way that, in response to an abrupt decrease in motivational excitement, the aftereffects establish conditional reactions which, on the one hand, hinder the animal from approaching environmental objects able to terminate a moderate excitement, and, on the other hand, compel it to approach objects able to decrease excitement exceeding a critical level. This interpretation, according to which, upon abrupt termination of motivational excitement, two different conditional (approach or avoidance) connections can develop—depending on the intensity of excitement—supports the importance of the so-called "drive reduction" hypothesis (*6*), but puts its role in a different light. From the existence of rebound effects it follows that the significance of drive reduction lies in its capacity for inducing an antagonistic drive.

2) Hippocampal theta rhythm and desynchronization seem to suggest two characteristically different functional states of the hippocampus. Their existence and dependence on stimulation intensity is supported by several recent findings (*7*). The earlier view of Grastyán *et al.* (*8*) that desynchronization rather than theta rhythm corresponds to an activated state of the hippocampus is further supported by the present findings and by those obtained with microelectrode recordings from the hippocampus (*9*).

Hippocampal ablation showed (*10*) that the hippocampus not only reflects but is implicated in the regulation of approach and withdrawal functions. Desynchronization would correspond to the active phase of a negative feedback control which, according to several authors manifests itself in an inhibition of brainstem and hypothalamic neural events (*11*). If it is considered that this selective hippocampal regulation of basic motivational forces necessarily depends on the discrimination of critical intensities, the assumption of McLardy (*12*), that one of the aspects of hippocampal function is represented by a detector-coder mechanism of intensity gradients, seems strongly substantiated.

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References and Notes

1. The terms "approach" and "withdrawal" (also referred to as rewarding-punishing, positively-negatively reinforcing, start-stop) are used here to denote two basic behavioral patterns during which the animal moves toward (approach) or away from (withdrawal) a given environmental object or stimulus. They do not refer to conditional processes, to which the term approach is often applied.
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5. For the sake of brevity the effects of changing other stimulation parameters (duration, frequency) are disregarded here. In the course of a systematic study it was found that by an appropriate combination of these parameters changes identical with those observed with different intensities could be reproduced.
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