SOME NEURAL AND BEHAVIORAL CORRELATES OF ELECTRICAL SELF-STIMULATION OF THE LIMBIC SYSTEM

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Recent studies have demonstrated that behavior can be established and maintained in experimental animals using direct electrical stimulation of the brain as reinforcement (Delgado, Roberts, & Miller, 1954; Olds & Milner, 1954; Sidman, Brady, Boren, Conrad & Schulman, 1955). Following the original observations by Olds and Milner that localized brain stimulation could serve as a reward for lever pressing (Olds et al., 1954), several reports have described interaction effects involving electrical self-stimulation of selected brain areas and a wide variety of behavioral, physiological, and anatomical factors (Brady, 1957; Brady, 1956; Brady, 1958a; Brady, 1958b; Brady, Boren, Conrad & Sidman, 1957; Lilly, 1958; Miller, 1958; Olds, 1958a; Olds, 1955; Olds, 1956a; Olds, 1956b; Olds, 1958b; Olds, Killan & Bach-y-Rita, 1956). However, surprisingly little attention has been directed toward an analysis of the interrelationships between the physiological events associated with self-stimulation and the behavior of the self-stimulating animal. Toward this end the present study provides preliminary experimental observations correlating electroencephalographic and behavioral activity accompanying self-stimulation of several limbic system structures in monkeys.

METHOD

General Procedure

Nine rhesus monkeys served as experimental subjects. Animals were first operated surgically under pentobarbital anesthesia for the implantation of electrode arrays in the brain. Multiple bipolar electrodes were stereotaxically placed in various limbic system and related structures, and were rigidly fixed to the skull by means of a common socket pedestal to which stimulating and recording leads could be firmly attached according to the method described by Sheatz (1957). Following a 3-to-5-day postoperative recovery period, all animals were placed in restraining chairs and trained in lever pressing, first for sugar-pellet rewards and then for brain-shock reinforcement through selected electrode placements. Electroencephalographic (EEG) activity from the various electrode locations was recorded before, during, and after electrical self-stimulation on a Grass Model III electroencephalograph. Cumulative and numerical recordings of the lever-pressing behavior for brain-shock reward were correlated with EEG recordings of the electrical activity in the limbic system. Upon completion of the experimental observations, all animals were sacrificed and the electrode locations verified histologically. A total of 29 limbic-system electrode placements were identified, including locations in the hypothalamus, preoptic area, septum, median forebrain bundle, midbrain tegmentum, anterior thalamus, hippocampus, and amygdala.

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Behavioral Procedure

Behavioral observations on all animals were obtained in a specially constructed primate restraining chair previously described in some detail (Mason, 1958). Each chair was equipped with a lever (modified telegraph key), an automatic pellet feeder (Davis) and hopper, and a visual stimulus panel containing five different-colored lights. The monkeys were initially deprived of food for 24 hours and given a 3-hour magazine training session during which sugar pellets (48 milligrams each) were automatically delivered into the hopper on a variable-interval (average 60 seconds) schedule. Then they were trained in lever pressing on a continuous-reinforcement schedule (200 sugar pellets) followed by a series of 2-hour daily experimental sessions on a variable-interval reward schedule (average 60 seconds) for sugar pellets. When a relatively stable performance was obtained on this schedule, the reward for lever pressing was changed from sugar pellets to electrical stimuli to the brain through a pair of implanted electrodes on a continuous-reinforcement schedule. A change in the colored light from white to blue on the visual stimulus panel facing the monkey accompanied this switch from sugar-pellet to brain-shock reinforcement. Using this procedure, all electrode pairs were explored to determine whether the electrical stimulus (over a range of intensity values) was sufficiently reinforcing to maintain lever-pressing behavior in the absence of sugar pellets.

Throughout the course of each experimental session, both numerical and graphic records of lever responses and reinforcements were obtained. All recordings of the animal's behavior and programming of the experimental procedures were accomplished automatically by timers, magnetic counters, cumulative-work recorders, and associated relay circuits.

Electrical Stimulation Procedure

The electrical brain stimulus used to reinforce the lever-pressing response in the self-stimulation portions of these experiments was provided by a Tektronix stimulating unit modified to give a biphasic pulse similar to that described by Lilly, Hughes, Alvord, and Galkin (1955). The parameters of this intracranial electrical stimulus were usually kept constant for each animal throughout the course of a given set of experimental observations except on those occasions when an observed effect was explored as a function of the brain shock stimulus intensity. Each brain shock consisted of a 100-cycle-per-second, 5-to-20-milliampere electrical stimulus (pulse duration, 0.2 millisecond) applied for a train duration of 0.5 second after every lever press. Tissue-resistance values in the monkeys approximated 1500 to 2000 ohms.

Electrical self-stimulation and recording sessions usually lasted for approximately 45 minutes and were carried out 3 to 4 times a week over a 1-to-3-month period with each animal. Occasionally, however, an individual experimental session was continued for as long as 3 or 4 hours when the temporal course of some systematic observations seems to justify this procedural extension.

RESULTS

General Observations

A total of 29 electrode placements in various limbic-system structures of the nine monkeys was found to yield positively rewarding effects in response to electrical self-stimulation. The distribution of these locations and the relative rates of lever pressing maintained by self-stimulation of the different structures corresponded closely to the reported findings of Olds for the rat (Olds, 1956). With the monkeys in this study, the highest rates of lever pressing for brain shock on a continuous-reinforcement schedule were obtained through electrodes located in the posterior hypothalamic and midbrain tegmental regions. In fact, with five placements in these areas, response rates were so high (approximately 50 responses per minute) that the stimulation artifact precluded adequate interpretation of the EEG tracing. With the remaining 24 electrode placements in the more anterior and lateral portions of the limbic system, however, intermediate response rates of 25 to 30 lever presses per minute (anterior limbic-system structures) or lower response rates of 5 to 10 lever presses per minute (lateral limbic-system structures) permitted satisfactory EEG tracings to be obtained between periods of stimulation. Fifteen of the 24 placements from which satisfactory records of brain-wave activity were obtained consistently showed electroencephalographic patterns which could be correlated in systematic ways with characteristics of the self-stimulation lever-pressing behavior. The remaining 9 loci yielded good EEG tracings, but the brain-wave activity showed no consistent relationship to self-stimulation behavior. Significantly, the highest incidence of these "negative" placements was observed in the more lateral limbic-system structures where lever-pressing response rates for brain-shock reinforcement were lowest.

Anterior hypothalamus, preoptic area, ventral septum (median forebrain bundle). Eight monkeys with electrodes in this general area of the brain showed good lever-pressing rates (25-30 responses/minute) for a continuous brain-shock reward. Six of the 8 animals showed EEG patterns characterized by spike and slow-wave activity throughout the hypothalamus and septum during self-stimulation in the median forebrain bundle area. The septal-hypothalamic spike and slow-wave pattern developed 25 to 75 milliseconds after the start of each individual 0.5-second electrical stimulation train. When fully elaborated, the amplitude of this pattern reached 100/ microvolts and its duration, 400 milliseconds. With four of the six animals showing this spike and slow-wave response to median forebrain bundle stimulation, a definite relationship between the lever-pressing rate and the manifestation of the electrical activity could be discerned. Figure 1 shows sample cumulative-response curves and EEG tracings from one of these four monkeys during an extended experimental session involving median forebrain bundle self-stimulation, and illustrates this relationship between behavior and the electrical activity of the brain. The lettered segments of the EEG record represent sample tracings taken during the correspondingly lettered sections of the cumulative-response curve with the exception that EEG tracing "A" provides a normal base-line reference record taken from the same leads before self-stimulation. The "B" sections are representative samples taken during the first hour of self-stimulation, when the lever-pressing rate was highest and the spike and slow-wave complex most clearly formed in the septal lead. As the lever-pressing rate for electrical self-stimulation in the median forebrain bundle declined gradually during the second and third experimental hours (section "C" of the cumulative-response curve), and decreased sharply during the fourth hour (section "D" of the cumulative-response curve), the electrical-discharge pattern in the septum became correspondingly less distinct (segments "C" and "D"

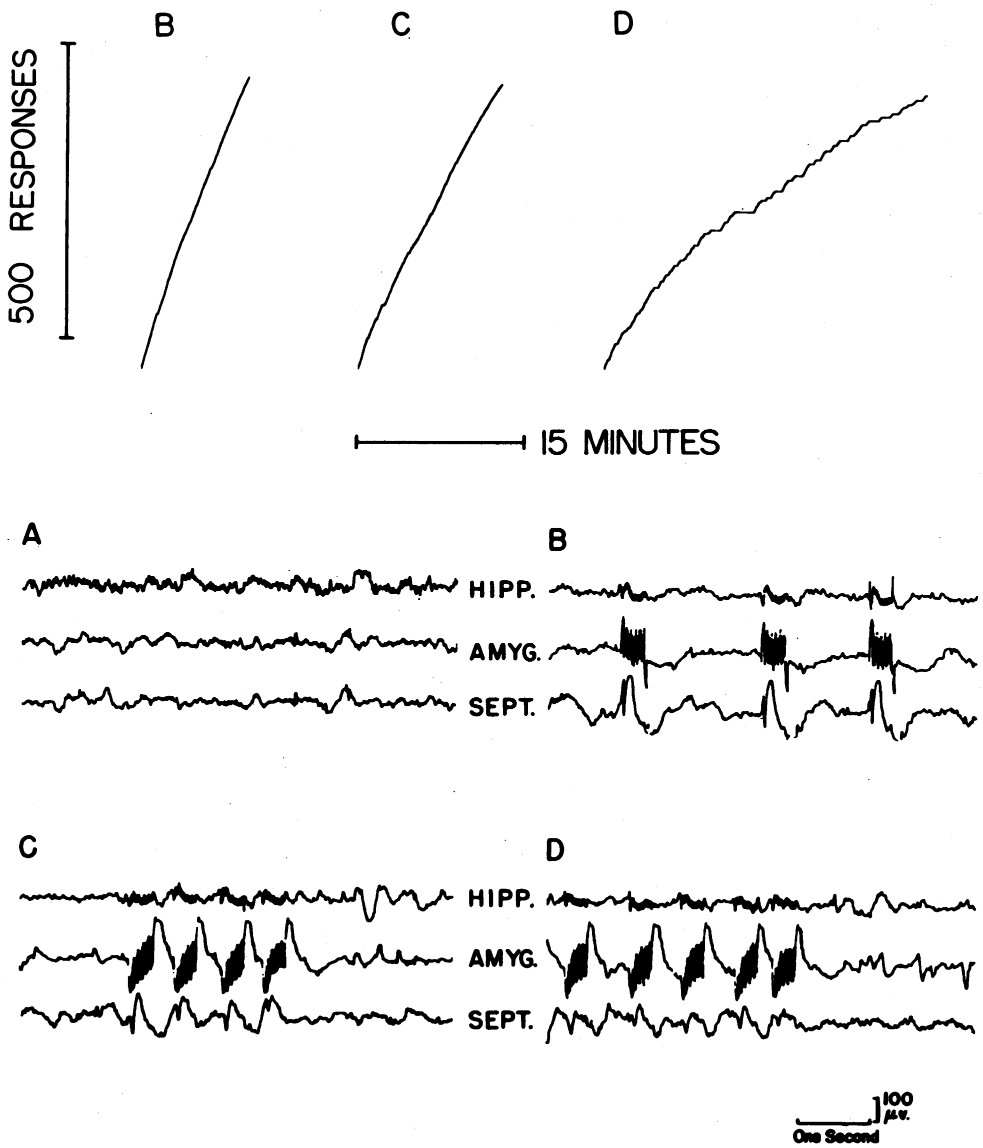

Figure 1. Lever-pressing response curve (above) and coincident EEG record (below) for self-stimulation of the median forebrain bundle area at the preoptic level during first (B), second (C) and fourth (D) hours of the experimental session. The EEG tracing labeled A was taken before stimulation was begun.
Abbreviations for this and subsequent figures: HIPP–hippocampus; AMYG–amygdala; SEPT–septum; HYPO–hypothalamus.

of the EEG tracing). In contrast, little or no change in the electrical activity of the hippocampus is apparent throughout the course of this experimental session, and little more than the stimulation artifact appears in the amygdala lead. During subsequent experimental sessions with this same animal and with the other three monkeys of this group, similar electrical activity in the septal region was apparent whenever the lever-pressing rate was optimal (25-30 responses per minute) for median forebrain bundle self-stimulation. In the remaining two monkeys showing similar electrical activity in the septal region in response to self-stimulation of the medial forebrain bundle, the spike and slow-wave complex did not change consistently with variations in the lever-pressing rate. Two of the eight monkeys with good self-stimulation lever-pressing rates in the area of the median forebrain bundle showed no electrical activity changes in the septal region or hypothalamus.

Anterior thalamus. Six monkeys with electrode placements primarily located in the antero-medial nucleus of the thalamus in close proximity to the medial intralaminar structures showed positively reinforcing effects from self-stimulation. Characteristically, however, the lever-pressing responses for the continuous brain-shock reward in this area occurred in bursts of 3 to 5 followed by a period of no responding, often for as long as several seconds. The rather "ragged" appearance of the cumulative curve in Fig. 2 reflects this "burst-break" response pattern, as illustrated by a sample record taken from one of the monkeys during a portion of an experimental session involving self-stimulation of the anterior thalamus. Four of the six monkeys showing intermediate lever-pressing rates (15–20 responses per minute) for a continuous brain-shock reward in this region also showed related changes in electrical activity as illustrated by the EEG tracings in Fig. 2. Again, the "A" segment of the tracing represents a normal prestimulation base-line control record from the three leads (hippocampus, septum, hypothalamus) studied in these animals. In the "B" portion of the EEG record, however, taken during a self-stimulation session in the anterior thalamus, a spike and slow-wave complex is seen to extend into the septum and a slow wave into the hypothalamus during each self-stimulation train, although partially occluded by stimulation artifact. In addition, stimulation of this area induced a train of such complexes in the septum and hypothalamus which continued with a frequency of about 1 per second, often for a period of several seconds after a burst of self-stimulation lever presses had been completed. These after-discharges were consistently correlated in time with the "break" periods which followed a "burst" of lever pressing for self-stimulation in this region of the brain. Observations of gross behavior during this time revealed that the monkeys invariably remained quiet and immobile, staring straight ahead in a manner similar to the "arrest" reaction described by Hunter and Jasper (1949), with the exception that they could be aroused by intense visual or auditory stimuli. Following the cessation of this after-discharge, however, animals again resumed lever pressing for electrical stimulation.

Continued observations of the electroencephalogram during extended experimental sessions for self-stimulation in the anterior thalamus revealed the development of an additional feature of the brain-wave activity. Varying between 5 and 15 minutes after the start of such a self-stimulation session, the characteristic spike and slow-wave pattern in the septum and hypothalamus was frequently followed by a burst of repetitive fast waves at a frequency of 12 to 15 cycles per second, as illustrated by the "C" segment of the EEG tracing in Fig. 2. The duration of this fast-wave discharge varied from a fraction of a second to as long as one-half minute, usually showing a gradual increase in length as the experimental session continued. Significantly, however, this fast activity was also evoked by the spike and

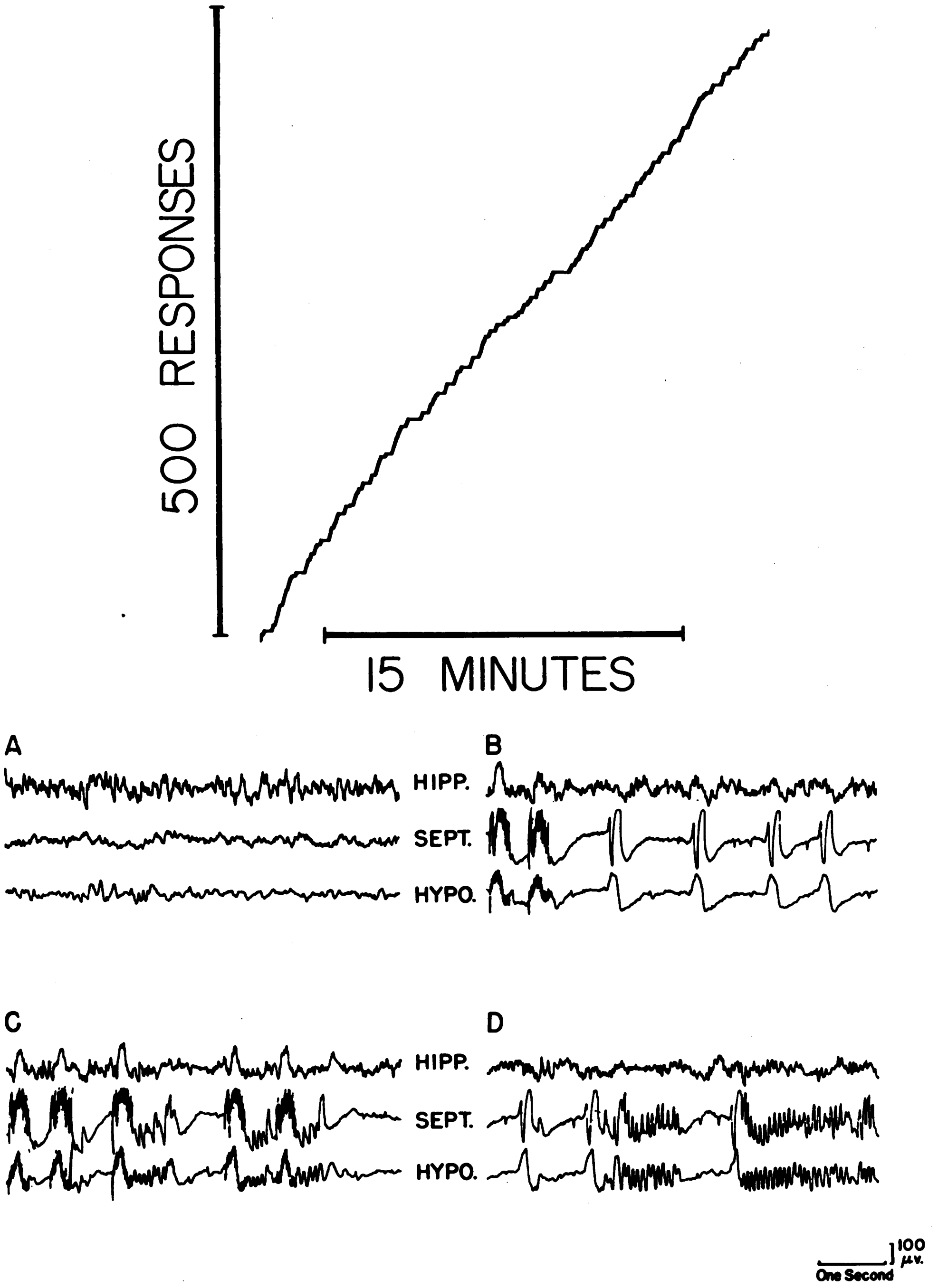

Figure 2. Lever-pressing response curve (above) and EEG record (below) for self-stimulation of anterior thalamic nucleus. EEG tracing taken before (A), during first 5 minutes (B), and after 10 minutes (C and D) of stimulation. Periods of stimulation can be detected by the heavy black line superimposed on the EEG tracing, most pronounced in the septal lead.

wave complexes which occurred as after-discharges following self-stimulation of the anterior thalamus, as illustrated in the "D" segment of the Fig. 2 EEG tracing. As effective stimulation sites were located in the anteromedial nucleus of the anterior group, the possibility exists that the stimulus spread to the closely proximate medial intralaminar structures which have figured prominently in the study of induced spike and slow-wave discharge and petit mal epilepsy (Jasper & Droogleever-Fortuyn, 1947).

Hippocampus. Six hippocampal electrode placements provided positively reinforcing effects for the maintenance of self-stimulation lever pressing in the present study. For the most part, however, the lever-pressing response patterns were erratic and frequently punctuated with long breaks and rapid bursts. Correspondingly, all six monkeys in this group showed frank seizure discharges similar in character to that described by Liberson (1955) as a frequent response to the hippocampal stimulation. The seizure activity was often restricted to the hippocampus, although some spread to related structures was occasionally observed. Generally, there were no grossly overt behavioral signs of convulsive seizure activity, and the animals remained quiet and immobile during the electrical discharge. In at least three of these monkeys with electrode placements in the more posterior aspects of the hippocampus, a close relationship between the electrical-seizure activity and the lever-pressing response pattern could be discerned. Figure 3 illustrates this relationship between the cumulative-response record and the electroencephalographic tracing for one of the monkeys during a portion of a typical experimental session. The cross-lined bars superimposed upon the "breaks" in the cumulative-response curve indicate the temporal distribution and duration of each electrical-seizure discharge during the sample lever-pressing period. The hippocampal-seizure activity illustrated by the "B," "C," and "D" segments of the EEG tracing in Fig. 3 can be seen to follow immediately upon each burst of self-stimulation lever presses in the early portions of the cumulative record. As the session continued, however, the duration of each seizure discharge gradually decreased so that after 4 or 5 minutes had elapsed, the seizure pattern could no longer be elicited and lever pressing stopped for periods of 15 to 30 minutes or more. Characteristically, self-stimulation lever pressing following such an extended interval would again elicit the hippocampal seizure activity and a similar alternating cycle of response "bursts" and seizure "breaks" would develop.

Self-stimulation of the three more anteriorly placed hippocampal electrode sites occasionally induced seizure discharges in the region of stimulation and related areas, but the electrical stimulus intensity required to elicit such effects was usually well above the threshold values required to maintain the lever-pressing response, and the appearance of the seizure activity could not be systematically related to the behavioral pattern.

Amygdala. Four monkeys showed relatively low lever-pressing rates (10-20 responses per minute) for self-stimulation in the amygdala. When the behavior was maintained by electrical stimulus intensities at or near threshold (5 to 10 milliamperes), no consistent electroencephalographic changes accompanied the self-stimulation pattern. When the intensity of stimulation was increased to 15 to 20 milliamperes, however, two of the animals showed seizure discharges after several

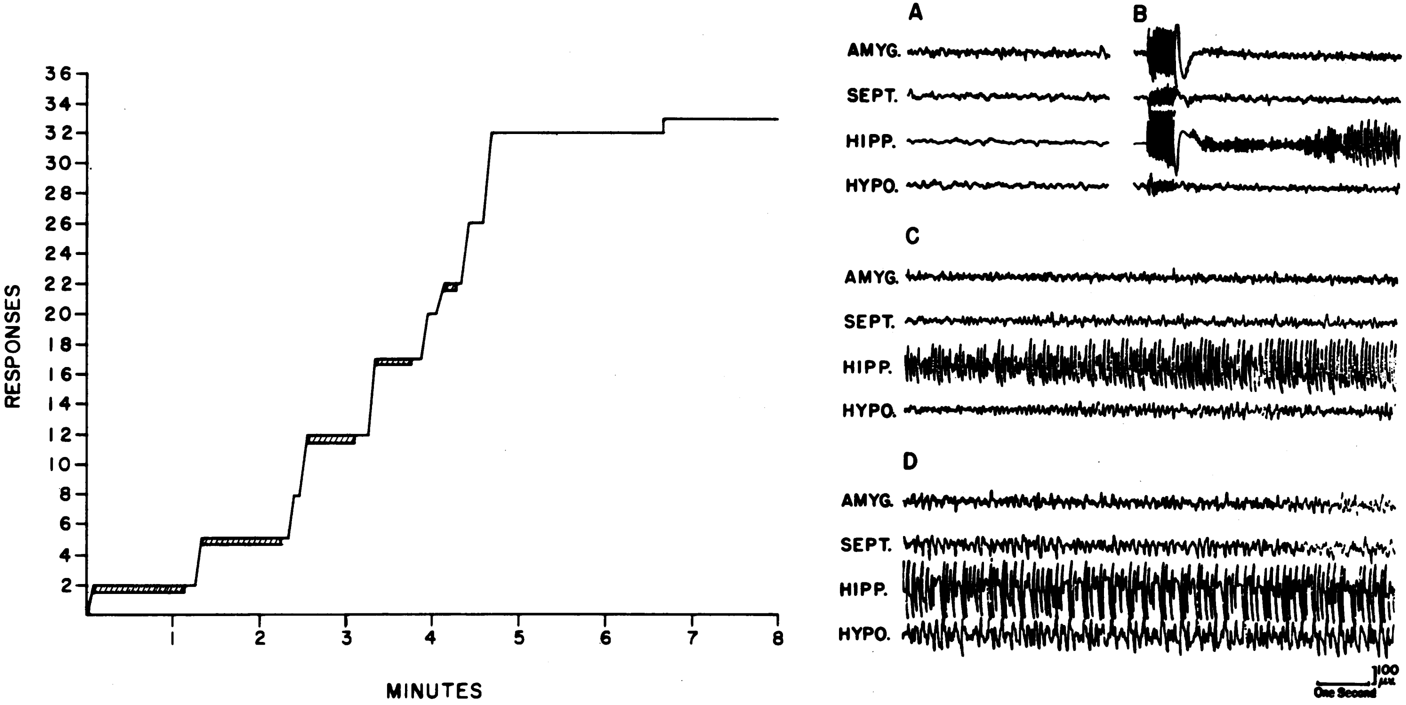

Figure 3. Lever-pressing response curve (left) and sample EEG tracing (right) taken during self-stimulation of posterior hippocampus. The cross-lined bars on the response curve represent periods when seizure discharge, as illustrated in EEG tracing (B–D), was manifest. Record A was taken prior to stimulation.

minutes of self-stimulation in the amygdala. The appearance of this electrical activity was invariably accompanied by a complete cessation of lever pressing for the remainder of an experimental session, and rest periods of as long as 24 hours were frequently required before self-stimulation lever pressing could be resumed. Figure 4 illustrates this suppressing effect of the seizure induced by amygdala self-stimulation upon the lever-pressing rate recorded for one of the monkeys showing this response during a typical experimental session. Again, the cross-lined bar superimposed upon the cumulative-response curve indicates the duration of the seizure discharge and illustrates the continued suppression of lever pressing after termination of the brain-wave pattern. Significantly, the two monkeys showing this response to amygdala self-stimulation developed the seizure pattern earlier in succeeding experimental sessions, and after several sessions failed to make any lever presses for electrical self-stimulation at these electrode placements.

DISCUSSION

The results of this study indicate quite clearly that lever-pressing behavior maintained by electrical self-stimulation of selected limbic-system structures in monkeys can be shown to bear a direct relationship to the neurophysiological processes associated with the brain stimulation. Although precise and consistent correlations between these behavioral and electroencephalographic processes could be demonstrated in only slightly more than half of the electrode placements investigated, unavoidable technological problems associated with such factors as brain-shock-reinforcement intensity, stimulation artifacts, and the like can be seen to have constituted a major deterrent to a more complete experimental analysis at the present stage of these exploratory efforts.

Admittedly, the findings of this investigation provide little basis for an elaborate theoretical discussion of the "motivational" problems associated with electrical self-stimulation. Available evidence (Brady, 1957; Brady, 1956; Brady, 1958a; Brady, 1958b; Brady et al, 1957; Delgado et al, 1954; Miller, 1958; Olds, 1958a; Olds, 1958b; Olds, 1955; Olds, 1956a; Olds, 1956b; Olds, 1958c; Olds et al., 1956; Olds et al., 1954; Sidman et al., 1955), would seem to indicate that a wide range of conditions can affect the reinforcing properties of an intracranial electrical stimulus and that the locus of the stimulated area contributes prominently to the observed behavioral effects. The present study, however, suggests that a careful analysis of the electrophysiological events consequent upon brain stimulation may provide important additional leads to the necessary and sufficient conditions for the maintenance of such electrical self-stimulation behavior. Of particular interest in this regard are the findings correlating the manifestation of specific electrical patterns with changes in the self-stimulation lever-pressing rate. Those findings illustrated in Fig. 1 and 3 tend to suggest the possibility that the electrical activity induced by self-stimulation may actually play some role in maintaining the lever-pressing behavior. With stimulation of the median forebrain bundle at the preoptic level, the manifestation of spike and slow-wave activity can be seen to correlate in a general way with the lever-pressing rate. An even better illustration is seen with hippocampal stimulation. In this instance, during the early portions of an experimental session when a burst of responses was frequently followed by a relatively long

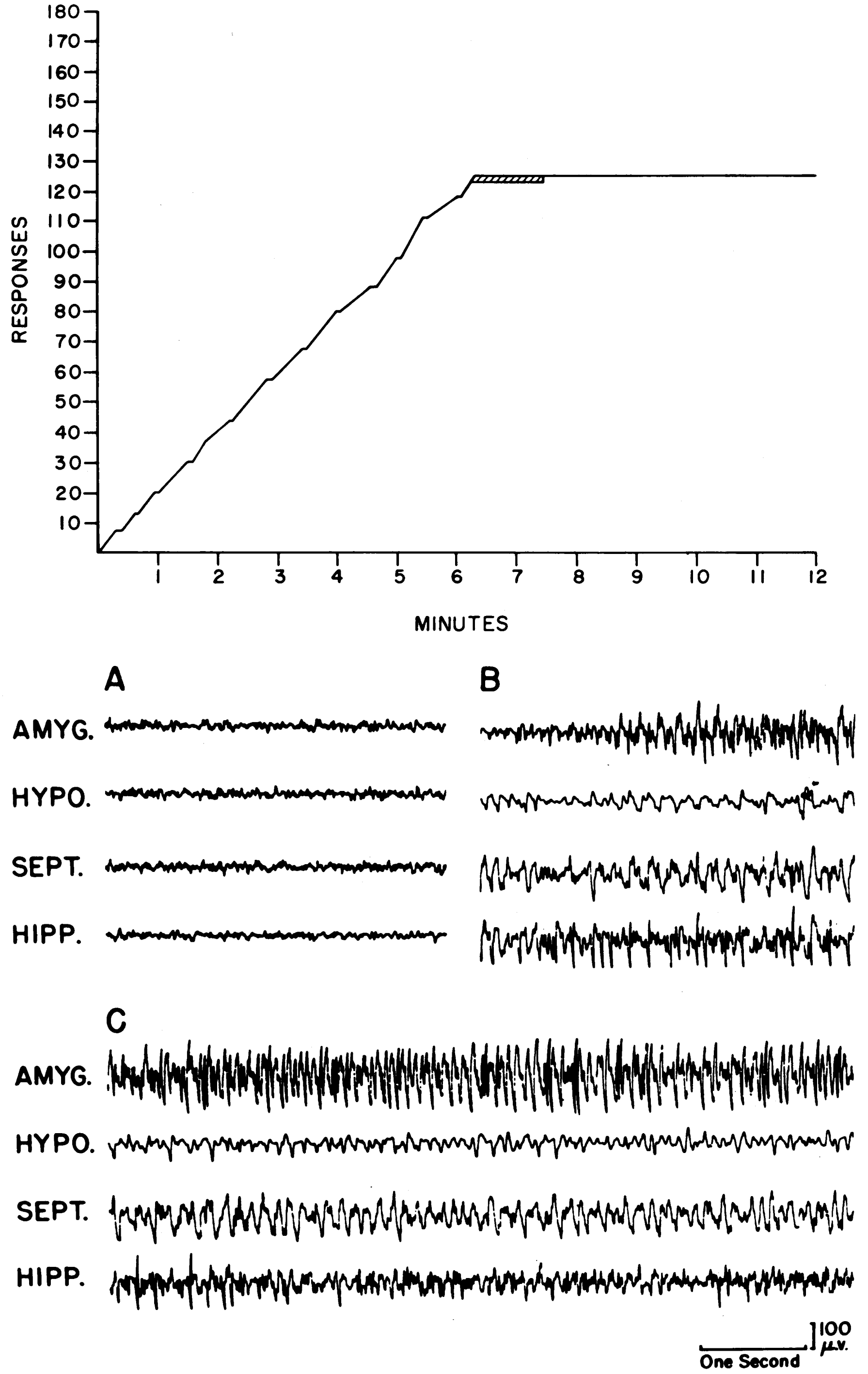

Figure 4. Lever-pressing response curve (above) and sample EEG record (below) taken during self-stimulation of the amygdala. The cross-lined area superimposed on the response curve indicates the time during which seizure discharge could be seen on the EEG record as illustrated (B and C). The A record represents a pre-stimulation control.

seizure discharge, the resumed lever-pressing rate was maintained at consistently high rates. As the duration of the seizure discharge decreased and eventually disappeared later in the session, the lever-pressing rate declined practically to zero for periods of up to 30 minutes or more until electrical self-stimulation again produced hippocampal seizure activity and bursts of high-rate lever-pressing reappeared.

It is of some interest in this connection to recall reports of self-induced seizures in some epileptic children whose attacks appeared to be induced by waving the hand before the eyes to interrupt visual stimulation from the sun or other light source until loss of consciousness occurred (Bickford, 1953; Penfield & Jasper, 1954). In a few of these children, at least, such seizure-producing activity has even been related to verbal reports of pleasure.

The finding in the present study involving seizure discharge following amygdala self-stimulation, however, suggests a somewhat different relationship between the seizure activity and maintenance of the lever-pressing behavior. Certainly, the consequences of a single self-stimulation-induced seizure in this case, as illustrated by the complete and prolonged suppression of the lever-pressing rate shown in Fig. 4, are in marked contrast to the repetition pattern observed following hippocampal seizures.

The behavioral aspects of spontaneous convulsive seizures in humans recently reviewed by Williams (1956) suggests a relationship between the structural locus of the electrical discharge pattern and the phenomenological report of the patient. When a feeling of fear was a subjective manifestation of the seizure, the epileptogenic focus appeared in the anterior temporal regions of the brain. When the patient reported a feeling of pleasure during the convulsion, the posterior portion of the temporal region was found to be the site of the electrical discharge, although other patients with lesions in this same general area described unpleasant reactions in relation to seizures. The present findings of repeated self-induced seizure activity in the posterior temporal region and avoidance of such activity in the anterior would not seem to be at variance with this clinical report.

Certainly, much remains to be learned from future investigative efforts concerning specific loci for such electrophysiological processes, spread of current effects, and the like, before an adequate analysis of the motivational aspects of such self-stimulation behavior can be expected.

SUMMARY

Experimental observations have been reported correlating electrophysiological and behavioral changes accompanying electrical self-stimulation of the limbic system through chronically implanted electrodes in nine rhesus monkeys. Changes in lever-pressing rates for intracranial electrical-stimulus reward were correlated with electroencephalographic changes as a consequence of such stimulation in many of the limbic-system structures studied in these experiments. Self-stimulation of the septal region, anterior hypothalamus, and anterior thalamic nucleus was most consistently associated with a spike and slow-wave complex in the septal nuclei. Frank seizure activity was found to accompany self-stimulation of the hippocampus in certain animals, and the maintenance of high lever-pressing rates appeared to be positively correlated with the incidence and duration of these seizure

patterns. In contrast, seizure discharges following self-stimulation of the amygdala produced suppression of the lever-pressing rate for extended periods of time.

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