DYNAMICS AND SPREAD OF PAROXYSMAL DISCHARGES AFTER STIMULATION OF DORSAL AND VENTRAL HIPPOCAMPUS

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Stimulation of the structures of the dorsal and ventral hippocampus causes complex behavioral or epileptiform responses. The most typical bioelectrical phenomena accompanying these responses are paroxysmal convulsive discharges of focal or generalized character.

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Among the limbic structures, an important position is occupied by the dorsal and ventral parts of the hippocampus [11]. Data in the literature show that the low convulsive threshold [10, 12, 13, 14-16], the manifestation of reflexes [4, 6, 8, 9, 17], aftereffects [18, 19], emotional responses [1, 14], and also inhibitory and excitatory influences [5,7] are connected with the hippocampus. However, this does not rule out the possibility of other functions being performed by the hippocampal structures.

The object of the present investigation was to examine the character of behavioral responses arising during threshold electrical stimulation of the structures of the dorsal and ventral hippocampus, to determine the characteristics of electrographic responses (after-discharges) after stimulation of these formations, and to study the nature of functional interaction between the hippocampus and other limbic formations and brain structures (using data of bioelectrical processes).

EXPERIMENTAL METHOD

Experiments were performed on 18 rabbits into each of which 7 monopolar steel electrodes (diameter 150 μ) were introduced into the ventral and dorsal parts of the hippocampus (20 electrodes), the medial and intralaminar nuclei of the thalamus and nuclei of the reticular formation (18 electrodes), the nuclei of the amygdaloid complex (28 electrodes), and into the septal region (18 electrodes) by means of a stereotaxic apparatus. The subcortical electrodes were used both for unipolar stimulation of the brain and for unipolar and bipolar recording of the potentials. Other details of the experimental method were described in our previous papers [2, 3].

EXPERIMENTAL RESULTS

During stimulation of the structures of the dorsal and ventral hippocampus with a minimal electric current (0.5 V, 100 cps, 1 msec), a group of motor manifestations was observed, which could be described as an arousal or preparatory response. With an increase in strength of the current, rapid movements to either side appeared, the rabbit struck the floor of its cage with its hind limbs, and periodically became fixed in one position. In other cases the response appeared immediately as a sudden cessation (inhibition) of preceding motor responses, possibly combined with adversion, opisthotonus, tremor, and clonic movements of one forelimb. Most characteristically these motor manifestations were dominated by influences of tonic type. A prolonged aftereffect (60-200 sec) was the rule after stimulation ended.

The most typical bioelectrical phenomena accompanying the motor responses described above were variants of paroxysmal discharges (Fig. 1). In contrast to discharges in the nuclei of the amygdaloid complex, after-discharges of the hippocampus as a rule were more intensive in both amplitude and frequency.

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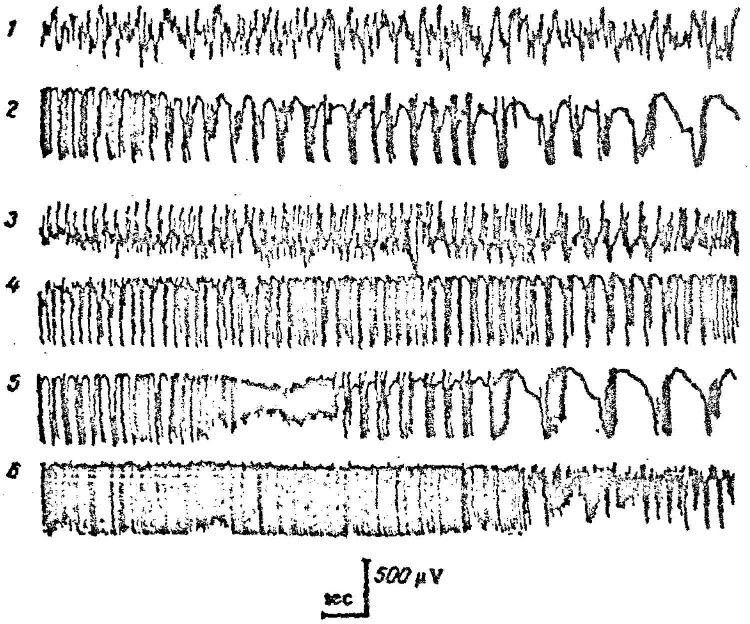

Fig. 1. Typical variants of after-discharges recorded in hippocampal structures. 1) Background electrical activity (Θ-rhythm) before stimulation; 2-6) variants of paroxysmal after-discharges. Explanation in text.

Sometimes only rare paroxysmal discharges appeared. Different variants of paroxysmal after-discharges were observed in the hippocampus: periodic, multiple spikes (Fig. 1, 2), continuous spike discharges with an amplitude of more than 500 µV and a frequency of 12-15/sec (Fig. 1, 3,4), changes in paroxysmal activity characterized by periods of continuous spikes alternating with a period of rhythmic high-frequency synchronization, and a period of multiple spikes, superposed on high-amplitude slow waves (Fig. 1, 5), and finally, continuous high-amplitude and high-frequency (17-25/sec) spike discharges (Fig. 1, 6). According to the observations of Penfield and Jasper [20], all the above variants of after-discharges are local in origin and reflect maximal hypersynchronization of neuronal activity.

The results of our experiments show no strict correlation between the severity of the motor manifestations after stimulation of hippocampal structures and the intensity of paroxysmal convulsive activity. Often absence of visible motor manifestations was accompanied by high-amplitude, high-frequency paroxysmal discharges for a long period after the end of stimulation (150-200 sec). This fact confirms data indicating extremely high paroxysmal preparedness of the hippocampus by comparison with other brain structures, except for the nuclei of the amygdaloid complex.

One of the problems studied in this investigation was the dynamics of spread of hippocampal discharges to certain other limbic (septum, amygdala) and reticular (reticular nuclei of the cerebral peduncles, tegmentum, thalamus) structures. First, it is important to stress that in some cases the hippocampal discharges were limited, focal in character, i.e., they were manifested in one structure only. However, focal paroxysmal discharges could be observed not only in the stimulated structure, in this case in the hippocampus, but they could also arise secondarily in other structures. Examples of the focal appearance of after-discharges are shown in Fig. 2. The development of typical after-discharges in the hippocampal structures only can be seen in Fig. 2A (leads 6 and 5). It is clear from Fig. 2B, that stimulation of the ventral hippocampus led to the appearance of bioelectrical activity of paroxysmal type in the nuclei of the amygdaloid complex (lead 4). However, spread of after-discharges to other brain structures was more typical of the dynamics of paroxysmal activity. A regular feature was irradiation of the paroxysmal process in the first place within the limbic system.

The discharges most frequently and readily affected the nuclei of the amygdaloid complex and septum because of the presence of bilateral connections between these structures [15, 16, 21]. Characteristically, the relationship between the hippocampal and amygdalar paroxysmal process in the course of development

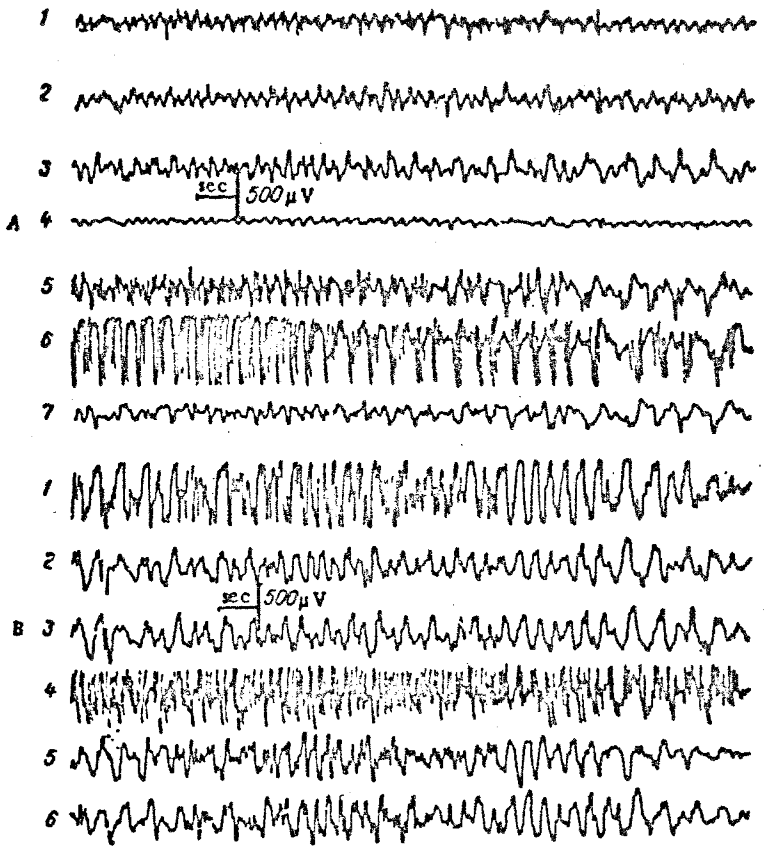

Fig. 2. Focal manifestation of convulsuve discharges after stimulation of the right ventral hippocampus (unipolar leads). A) Development of paroxysmal discharges in hippocampal structures only (leads 5 and 6); parameters of current: 2 V, 20 cps, 1 msec, duration of stimulation 15 sec. Leads: 1) right septal, 2) left septal, 3) central amygdaloid nucleus on the right, 4) basal amygdaloid nucleus on the left, 5) right ventral hippocampus, 6) left ventral hippocampus, 7) reticular pediculopontile nucleus; B) development of paroxysmal discharges only in amygdaloid nuclei (lead 4); parameters of current: 1.5 V, 100 cps, 1 msec, duration of stimulation 15 sec. Leads: 1) right parietal cortex, 2) right septal, 3) left septal, 4) central amygdaloid nucleus on the right, 5) basal amygdaloid nucleus on the left, 6) right ventral hippocampus. Explanation in text.

of the responses differed in character. The amygdaloid complex gradually became involved in the process arising in the hippocampus, after which this process became weaker (in amplitude and frequency of discharges) in the stimulated hippocampus and stronger in the amygdaloid complex, so that ultimately the total duration of the paroxysmal electrical activity was increased. By multiple insertion of electrodes, the dynamics of spread of paroxysmal electrical activity could be observed from the hippocampus to other brain structures and, in particular, to structures of the reticular formation. The results of these experiments show that a paroxysmal process arising in the hippocampus spreads to the structures of the reticular formation and takes place synchronously. It will be clear from Fig. 3 that at the 15th and 30th seconds of development of the activity structures such as the hippocampus, the amygdaloid complex, the parietal cortex, and also the reticular nuclei of the cerebral peduncles and tegmentum participate in paroxysmal electrical activity as a single functional system. Simultaneous recording of potentials from several limbic structures, followed by quantitative analysis (appearance and duration of after-discharges), reveal the general pattern of spread of the paroxysmal process arising from the hippocampus. These results are summarized in Table 1.

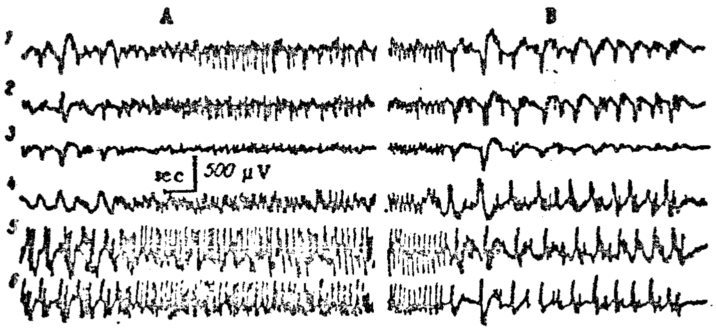

Fig. 3. Dynamics of paroxysmal electrical activity of limbic and reticular structures after stimulation of the right ventral hippocampus for 15 sec with a current of 2.5 V, 100 cps, 1 msec. A) 15th second of development of process; B) 30th second of process. Leads (unipolar): 1) left parietal cortex; 2) central amygdaloid nucleus on the right; 3) basal amygdaloid nucleus on the right; 4) right ventral hippocampus; 5) reticulotegmental nucleus; 6) reticular pediculopontile nucleus. Explanation in text.

TABLE 1. Dynamics of After-Discharges Arising after Stimulation of the Hippocampus

Leads	No. of appearances (in %)		Duration (in sec)		Remarks
	n	M±m	n	M±m	
Cortical areas	298	55±3.8	165	50±4.7	Process arises in hippocampus, in nonspecific nuclei of thalamus, irradiates, and is sustained by hippocampus-thalamus–cortex system
Thalamus	103	83±4.7	68	53±4.9	
Septum	80	74±5.8	59	46±5.1	
Amygdaloid complex	74	71±3.7	53	36±3.0	
Hippocampus	142	85±3.0	121	55±3.9	
Mean value	74		48		

Our results show that the hippocampus (ventral and dorsal parts), besides being in a state of high epileptogenic preparedness, also takes part in the regulation of behavioral responses. The dynamics of spread of paroxysmal discharges of hippocampal origin demonstrates that the limbic structures (amygdala, medial thalamus, septum) function in principle as a single system and interact closely with the structures of the reticular formation. A further study of these problems is necessary to elucidate the mechanisms by which these systems participate in integrative activity of the brain.

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