EFFECT OF TRANSECTION OF AFFERENT PATHWAYS ON EVOKED POTENTIALS, THETA RHYTHM, AND NEURONAL ACTIVITY IN THE HIPPOCAMPUS

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The effect of destruction of septo-hippocampal and subiculo-hippocampal connections on the electrical activity in the hippocampus was studied in tubocurarized rabbits. The theta rhythm and the so-called "intracellular theta rhythm" [7] were found to disappear on destruction of the septo-hippocampal connections, other consequences being the loss of neuronal capacity for responding to sciatic nerve stimulation, loss of neuronal inhibitory responses, and total or partial suppression of the negative phase of the evoked potential (EP). Destruction of subiculo-hippocampal connections entails a decrease in amplitude of the theta rhythm recorded from the hippocampal surface, retention of the "intracellular theta rhythm," and a slight decrease in amplitude of both EP phases. The number of neurons failing to respond to sciatic stimulation is increased; the character of cellular response remains unchanged. It is hypothesized that hyperpolarization of hippocampal pyramidal neurons may be responsible for generating the negative phase of the EP, and that this phase and the hippocampal theta rhythm may be of a common origin.

INTRODUCTION

The afferent volley elicited by peripheral stimulation is conveyed to the hippocampus along two main routes: by way of the subiculum [6, 10] and by way of the septum [12]. Another possible route is by way of the fornix [9].

The route followed by septal afferents towards the pyramidal neurons of fields 1 and 2 has not been studied sufficiently. Some authors [8] are of the opinion that the septal afferents terminate on the cells of the fascia dentata, the mossy fibers of the latter forming contacts with the pyramidal cells of hippocampal fields 3 and 4, with Schaeffer's collaterals of these neurons being in contact with the pyramidal cells of fields 1 and 2. Other authors [5, 12] believe the septal afferents to terminate directly on the pyramids of hippocampal fields 3 and 4, implying that the pathway between the septum and the pyramids of fields 1 and 2 contains but one synaptic relay.

From the septum, an afferent volley arrives at the most proximal segments of the apical dendrites of pyramids in hippocampal fields 1 and 2, where the synaptic terminals of Schaeffer's collaterals are located. The afferents from the subiculum terminate on the most distal segments of the apical dendrites of the same pyramids. The discharges from the subiculum towards the basal dendrites of the pyramids (Cajal's alvear tract) and thence over the mossy fibers of the granule cells of the fascia dentata and over Schaeffer's collaterals of fields 3 and 4 [10] are much weaker.

Destruction of the medial nuclei of the septum is known to abolish hippocampal theta rhythm [11], whereas complete removal of the entorhinal cortex, connected with the hippocampus via the subiculum, does not produce this effect [3].

The purpose of this investigation was to study the effect of transection of the septal and subicular afferents - at the site where they enter the dorsal hippocampus - on hippocampal evoked potential, theta rhythm, and responses of fields CA₁ and CA₂ to sciatic nerve stimulation.


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Fig. 1. Effect of transection of septo-hippocampal connections on hippocampal electrical activity. Evoked potential (a), superficial hippocampal electrical activity (b), and intracellular recording of electrical activity of a pyramidal neuron (c) before (above) and after transection of the septum. Arrows indicate moments at which stimulation was applied to the sciatic nerve.

Fig. 2. Summated histograms of spike activity on the part of 50 hippocampal neurons during sciatic stimulation. a) Before transection of septo-hippocampal connections; b) after.

METHOD

The experiments were carried out on unanesthetized rabbits immobilized by tubocurarine. A trephined opening was drilled above the dorsal hippocampus, the dura mater was removed, and the neocortex above the hippocampus was drawn off by suction. The hippocampal surface was covered with 4% agar. The opening in the skull was covered with a Plexiglas stopper in which passages were made for macro- and microelectrodes.

In the experiments in which septo-hippocampal connections were destroyed, the septum was cut in its frontal plane by means of an eye scalpel inserted through the trephined opening into the appropriate segment of the brain.

The subiculum was transected within the boundaries of the dorsal hippocampal segment from which electrical activity was being recorded. In order to eliminate the influence of subicular discharges via the intrahippocampal connections, the control experiments involved additional transection of the hippocampus, done in such a way as to separate its dorsal part from the ventral. The quality of transection was checked histologically.

Single stimuli (1 msec in duration; 3-10 µV in amplitude) were applied to the sciatic nerve on the homolateral side by means of bipolar immersion electrodes. Silver macroelectrodes were used in recording the EP of the hippocampus; and neuronal activity was recorded with the aid of glass micropipettes filled with 2.5 M KCl and with a resistance of 5 to 30 MΩ.

RESULTS

Stimulation of the sciatic nerve activated the hippocampal theta rhythm 5 cps in frequency and 350 µV in amplitude (Fig. 1, b, upper tracing). Following complete transverse transection of the caudal septum, the theta rhythm disappeared completely; sciatic stimulation no longer produced its activation (Fig. 1, b, lower tracing). The rest of the slow electrical activity also decreased in amplitude.