AFFERENT CONNECTIONS OF THE THALAMIC REGION WITH THE LIMBIC CORTEX

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Continuing our investigations of the afferent connections of the internal organs with the various divisions of the central nervous system, we found that stimulation of the receptors of the stomach and urinary bladder evokes changes in the electrical activity in the ventral nuclei of the thalamus [4]. These findings are in agreement with the results obtained by recording the primary reactions in the thalamic nuclei in response to electrical stimulation of the corresponding visceral nerves [6, 11, 12, 21, 22]. On the other hand, studies of the thalamocortical connections have shown that the ventrobasal complex of thalamic nuclei is projected into both Areas 1 and 2 of the somatosensory cortex, the zones of cortical representation of the internal organs [14, 17, 19, 20, 25]. A closer investigation of the central link of the visceral analyzer, using both the conditioned reflex method [1-3, 13] and an electrophysiological method [5, 7], showed that the limbic region is also included in it.

The object of the present investigation was to ascertain whether a connection exists between the zones of afferent representation of the internal organs in the thalamus and the limbic cortex.

METHOD

Experiments were conducted on adult cats under intravenous thiopental sodium anesthesia (1% solution). To obtain a more convenient access to the limbic region one hemisphere was removed. The animal's head was fixed by means of a Horsley–Clark stereotaxic apparatus. The cortical potentials were picked up by silver button electrodes, the distance between the electrodes being 3-4 mm.

The electrocorticogram was recorded on a cathode-ray oscillograph with an amplifier, the frequency characteristic of which was expressed by a straight line in the range 10-1500 cps, and with a "Kaiser" ink-writing electroencephalograph. Stimulation of the thalamic nuclei was provided by means of a rectangular pulse generator through bipolar concentric electrodes. The parameters of stimulation were: voltage from 2 to 10 V, frequency from 2 to 20 pulses/sec, duration of pulse 0.1-1.0 msec; period of stimulation 15 sec. The electrodes were implanted into the thalamus by means of the stereotaxic apparatus in accordance with the coordinates of the atlas compiled by Jasper and Ajmone-Marsan. In individual experiments the position of the electrodes was verified histologically. The brain was fixed in Bouin's fluid. Serial paraffin-wax sections were cut to a thickness of 20 μ and stained with a 0.1% solution of toluidine blue.

RESULTS

In animals anesthetized with thiopental sodium the cortical electrical activity was composed of so-called barbiturate discharges or "spindles" and a between-discharge or background activity. The barbiturate discharges consisted of 10-14 waves varying in amplitude from 25 to 200 μV. In deep anesthesia the discharges in different areas of the cortex were synchronized, while in light anesthesia they were not. The background (between-discharge) activity was represented by low-voltage potentials (5-20 μV) with a frequency of 8-15/sec.

*Deceased.

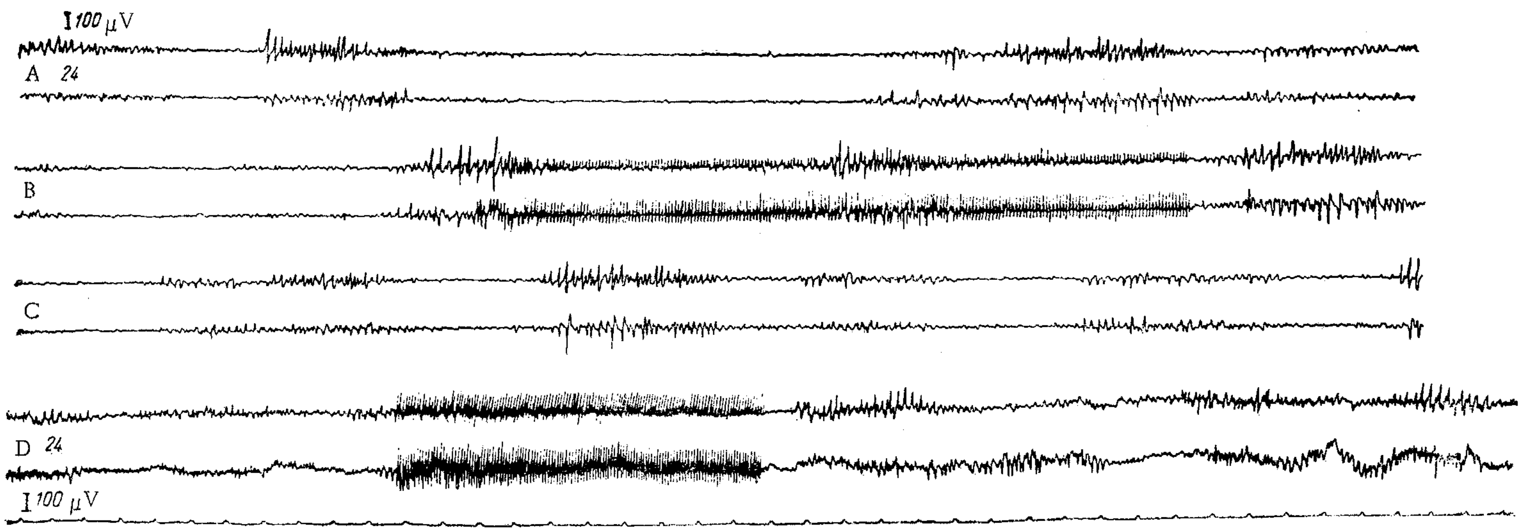

Fig. 1. Intensification of electrical activity in Area 24 during stimulation of n. VPL. In this and the other figures the period of stimulation is denoted by an artefact of stimulation; time marker 1 sec.

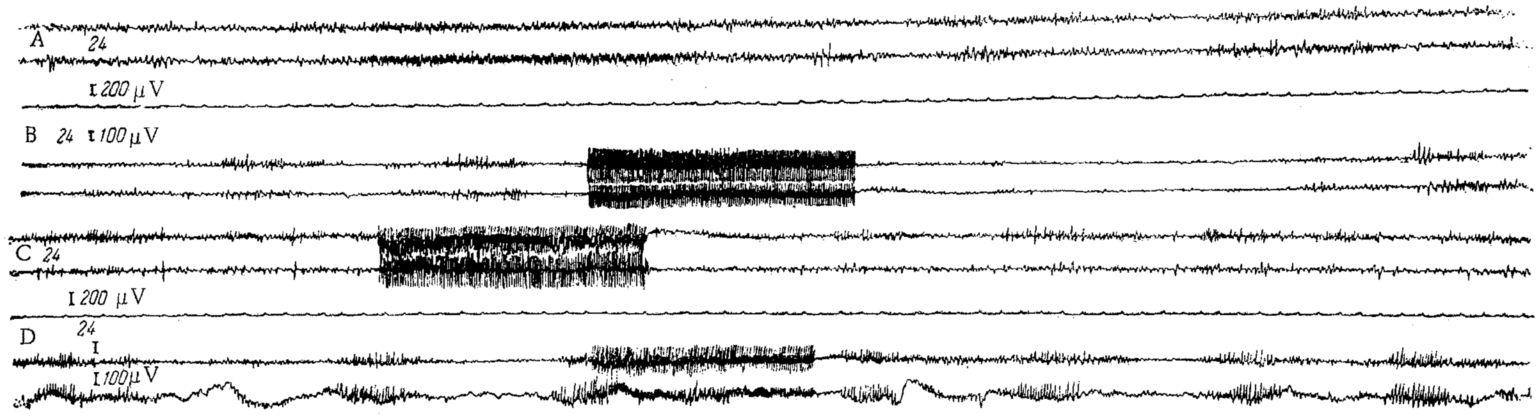

Fig. 2. Changes in electrical activity in Area 24 during stimulation of n. VPL (A, B) and n. AV (C, D).

During electrical stimulation of the thalamic nuclei, definite changes were observed in the electrocorticogram of the limbic region. In our experiments the stimuli were applied to the ventral nuclei of the thalamus: the posterolateral ventral nucleus (n. VPL), the posteromedial ventral nucleus (n. VPM), and the anterior ventral nucleus (n. VA), the nuclei of the anterior and lateral groups: the anteroventral nucleus (n. AV), the anterodorsal nucleus (n. AD), the dorsal lateral nucleus (n. LD), and the posterior lateral nucleus (n. LP), and the nuclei of the reticular complex of the thalamus: the reticular nucleus (n. R) and the nucleus of the centrum medianum (n. CM).

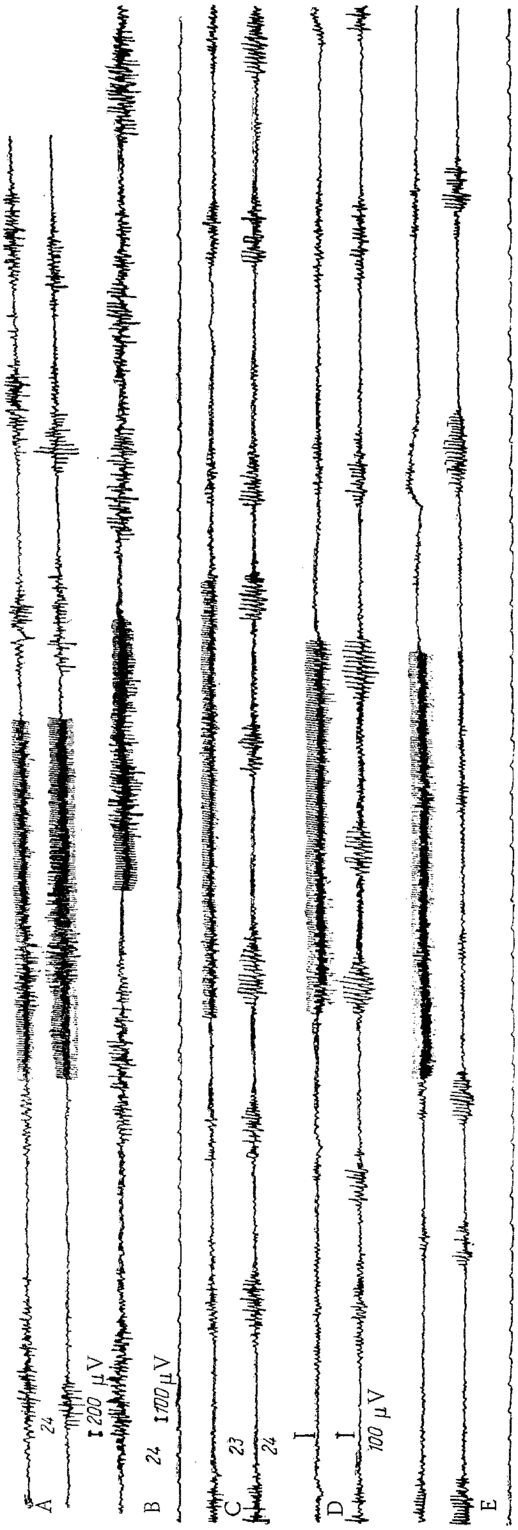

Fig. 3. Changes in electrical activity in Areas 23 and 24 during stimulation of n. R.

Changes in the Electrical Activity of the Limbic Region During Stimulation of the Ventral Group of Nuclei of the Thalamus (n. VPL, n. VPM, n. VA, n. VM)

These changes were most clearly and constantly expressed during electrical stimulation of the n. VPL and n. VPM. Only 7 of 55 stimuli produced no effect. In the remaining cases either a shortening of the intervals between the barbiturate discharges (quickening of the barbiturate rhythm), an increase in the amplitude of the waves in the discharge, or the appearance and intensification of the background activity was observed. These changes in the biopotentials in the limbic gyrus were recorded most frequently in Area 24, less often in Area 29, and only occasionally in Area 23. It should be noted that the application of "weak" stimuli (voltage 2 V, frequency 10 pulses/sec, duration of pulse 0.8 msec) usually caused quickening of the barbiturate rhythm. For example, the interval between the discharges was shortened from 10 sec (Fig. 1A) to 4-5 sec (Fig. 1B, C). In individual cases, during the action of weak stimuli an increase in the amplitude of the barbiturate "spindles" took place. For example, the amplitude of the waves in the discharges after stimulation of the n. VPL rose by 50% compared with the initial activity (Fig. 1D).

The effect of "strong" stimulation (voltage 6-7 V, frequency 10-16 pulses/sec, duration 0.8 msec) was dependent to some extent on the character of the original electrocorticogram. In the presence of a well defined barbiturate rhythm and in a state of deep anesthesia, electrical stimulation of the n. VPL and n. VPM evoked a shortening of the intervals between the discharges of barbiturate activity and a very slight increase in the amplitude of the waves. This effect of stimulation of the n. VPL and n. VPM, amounting to an increase in the frequency and amplitude of the barbiturate discharges, and also an increase in the between-discharge (background) electrical activity of the limbic cortex, was assessed as excitation in agreement with the reports given in the literature.

However, in some experiments stimulation of the ventral nuclei evoked an inhibitory effect. This took place in cases in which stimuli were applied against the background of high cortical activity, leading to the appearance of a more clearly defined barbiturate rhythm (Fig. 2A). The application of repeated stimuli, especially with a frequency of 16/sec, usually caused inhibition of the cortical activity, in the form of a sharp decrease in the amplitude of the barbiturate discharges (Fig. 2B).

Changes in the Electrical Activity of the Limbic Region During Stimulation of the Anterior Group of Nuclei of the Thalamus (n. AV, n. AM, n. AD, n. JAM)

Stimulation of the anterior groups of thalamic nuclei also affected the electrical activity of the limbic cortex, although the effect was less constant and was observed in only 16 of 35 cases. Stimulation of the n. AV was most effective. The changes in the biopotentials of the limbic gyrus mainly took place in Area 24 and were almost absent in Area 23. The spontaneous electrical activity of the limbic zone in this case changed either in the direction of excitation, if the stimulus was applied against the background of a well defined barbiturate rhythm, or in the direction of inhibition, if it was against the background of an intensified between-discharge activity. Weakening of this latter is demonstrated in Fig. 2C, as a result of which the barbiturate discharges were seen more clearly. After stimulation of the n. AV a marked increase in the frequency of the barbiturate rhythm and in the intensity of between-discharge activity was observed (Fig. 2D).

Changes in the Electrical Activity of the Limbic Region During Stimulation of the Nuclei of the Reticular Complex of the Thalamus (n. R, CM)

In 15 of 25 cases, stimulation of the reticular nuclei led to intensification of the spontaneous activity in the cortex of the limbic zone. This took the form of either an increase in the amplitude of the barbiturate "spindles" during stimulation and in the after-period, or a shortening of the intervals between individual barbiturate discharges and an increase in between-discharge activity, or a combination of both these changes. The quickening of the barbiturate rhythm after stimulation of the n. R can clearly be seen in Fig. 3A. In Fig. 3B, besides the increase in the frequency of the discharges, a slight increase in the amplitude of their waves and a growth of background activity are observed. In a series of experiments an increase in the amplitude of the potentials in the discharges was observed at the moment of stimulation. Under these circumstances the character of the response reaction was related to the strength and frequency of the applied stimulus. If the voltage of the stimulating current was 2 V and its frequency 10 pulses/sec, a very slight increase in the amplitude of the discharge and background activities took place (see Fig. 3C). With an increase in the voltage to 6 V the amplitude of the discharges at the moment of stimulation rose by 50-100% (see Fig. 3D). Application of the same stimulus with a frequency of 16 pulses/sec caused inhibition of the discharges throughout the period of stimulation (Fig. 3E). Comparison of the changes in activity in the various areas of the limbic gyrus shows that they were weaker in Area 23 (see Fig. 3, the top line of each oscillogram).

So far as the nuclei of the lateral group of the thalamus (n. LD, n. LP) are concerned, stimulation of these nuclei had no significant effect on the electrical activity of the limbic cortex.

The changes in the spontaneous bioelectrical activity in Areas 24 and 29 of the limbic cortex observed in these experiments during electrical stimulation of the n. VPL and n. VPM suggest the presence of afferent connections between these structures. This conclusion is made more probable by the fact that the limbic cortex, one of the central links of the visceral analyzer, must be connected with the thalamic nuclei, which constitute the subcortical projection of the internal organs. However, recent histological investigations have established connections only between the anterior group of thalamic nuclei and the limbic gyrus [15, 16, 23, 24], a result which our experiments confirmed. Data indicating direct connections between the ventral thalamic nuclei and the limbic region, on the other hand, could not be found in the literature. Since from the morphological point of view the pathways of influences from the thalamus to the limbic gyrus are uncertain, it may be supposed that these influences are mediated through somatosensory Area 1, more especially since the existence of bilateral connections between the latter and the limbic cortex has been demonstrated [10, 25]. However, the predominance of limbico-motor connections, the absence of effects in the motor cortex after extirpation of the limbic zone, and the coarser and more undifferentiated structure of the limbic gyrus [8], suggest rather that indirect thalamo-limbic pathways are present.

It should be noted that stimulation of the reticular nucleus of the thalamus also modified the electrical activity of the limbic gyrus. The most marked changes took place in the discharge activity. Reports of changes in the cortical electrical activity in response to stimulation of the nonspecific nuclei have been given by a number of authors [18, 26]. It has been concluded from these results that the thalamic reticular formation has a regulatory influence on the cortical electrical activity. These views have subsequently been confirmed by the work of Soviet authors [9].

However, the results described above show that stimulation of the specific nuclei of the thalamus also modifies the pattern of the electrical activity in the areas of the limbic cortex. Hence, besides the nonspecific nuclei of the thalamus, its specific structures also participate in the regulation of the bioelectrical activity of the cortex.

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