INFLUENCE OF THE SOMATOSENSORY CORTEX ON AFTER-INHIBITION IN THE POSTERIOR VENTRAL THALAMIC NUCLEUS

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The dynamics of the recovery curve of amplitude of the testing response in thalamocortical fibers to paired stimulation of the medial lemniscus (ML) during the action of various procedures on the somatosensory cortex was investigated in acute experiments on cats anesthetized with pentobarbital. The curve served as an indicator of corticofugal influences on after inhibition (AI) in the thalamic relay nucleus. Procedures directed toward one somatosensory cortical area blocked the transmission of afferent impulses in 70% of neurons of the thalamic relay nucleus. Correlation was found between the number of neurons participating in the response and the character of the initial phase of AI.
KEY WORDS: cerebral cortex; thalamic nuclei; regulation of the afferent flow; after-processes.

If a single afferent volley passes through the thalamic somatosensory relay – the posterior ventral nucleus (PVN) – of the barbiturate-anesthetized animal, after inhibition (AI) develops in the relay cells of the nucleus [3, 4, 5]. Since PVN has close two-way connections with the somatosensory cortex [1, 8, 9, 12] and since corticofugal modulation of afferent transmission is possible in the relay nucleus, it was decided to study the role of the somatic cortical projection areas in the formation of after-inhibition in PVN following the passage of an afferent volley.

The influence of the first (S_1) and second (S_2) somatosensory areas of the cortex on fast (phasic) effects in relay neurons of PVN triggered by the passage of an afferent volley was investigated in separate experiments.

EXPERIMENTAL METHOD

Acute experiments were performed on 34 cats under intravenous pentobarbital (40 mg/kg) anesthesia. After fixation in a stereotaxic apparatus and appropriate dissection the animal was immobilized with flaxedil and artificially ventilated.

To stimulate the medial lemniscus (ML) square pulses (100 μsec) were applied through bipolar needle electrodes (interelectrode distance 1 mm) in accordance with coordinates of a stereotaxic atlas [7].

Potentials evoked by stimulation of ML were recorded from the thalamocortical projection fibers in the white matter in the immediate vicinity of the somatosensory cortex. To alter the functional state of the somatosensory cortex, areas S_1 and S_2 were treated by application of penicillin solution (100,000 units/ml) or by thermocoagulation.

EXPERIMENTAL RESULTS AND DISCUSSION

The original curve of one experiment, showing the amplitude of the second (testing) response of the thalamocortical fibers in the region of S_1, as a percentage of the amplitude of the first (conditioning) response, as a function of the time interval between the two stimuli (in msec) applied to ML is shown in Fig. 1. Three main

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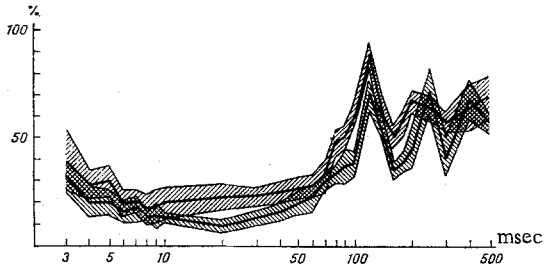

Fig. 1. Curve of recovery of amplitude of testing response of thalamocortical fibers running to area S_1 in response to stimulation of ML. Shading from right to left indicates background curves; shading from left to right indicates curve after coagulation of cortical areas S_1 and S_2 during paroxysmal activity in cortex. Abscissa, interval between conditioning and testing stimuli (in msec; logarithmic scale); ordinate, amplitude of testing response relative to amplitude of conditioning response (in %).

parts of the curve can be distinguished. There is an increase in AI until 30-35 msec after application of the conditioning stimulus, between 30 and 80-100 msec AI weakens, and in the period after 100 and until 500 msec phases of waxing and waning of AI alternates with a period of about 100 msec. Averaging the results of all the experiments smoothed out the individual cyclic variations in AI (Fig. 2A) on the curve between 100 and 500 msec caused by scatter of the times of occurrence of the peaks of waxing and waning of AI in the different experiments. The initial segments of this curve (until 10 msec) is well approximated by the exponential function $y = 87.2 \times 0.89^x$, as shown by the value of the coefficient of correlation $r = 0.99$ (Fig. 2B).

After application of penicillin solution to both somatosensory areas of the cortex in order to form paroxysmal activity therein [6, 10, 11], on the appearance of the so-called penicillin discharges changes in the testing response were again recorded. The curve of AI (Fig. 2C) differed from the preceding curve (Fig. 2A) in the absence of the maximal inhibitory effect 30 msec after application of the conditioning stimulus and in the generally low level of AI. The initial segment of the curve also was approximated by the exponential function $y = 114.7 \times 0.96^x$; $r = 0.98$ (Fig. 2D).

After removal of cortical areas S_1 and S_2 in a period of penicillin-induced paroxysmal activity the AI curve (Fig. 2E) assumed a character similar to that observed in the animals before penicillin application (Fig. 2A). The segment of the curve from 3 to 10 msec was approximated by the function $y = 106.8 \times 0.91^x$; $r = 0.99$ (Fig. 2F); periods of cyclic fluctuations in the intensity of AI appeared (as in Fig. 1).

After removal of only one cortical area (S_1) during a period of paroxysmal activity evoked in both areas (S_1 and S_2) significant deviations were observed in the curve of changes in the testing response (Fig. 2G). Only the initial segment of the curve resembled its previous experience and until 6 msec it was approximated well by the function $y = 112.05 \times 0.9^x$; $r = 0.99$ (Fig. 2H). By 30 msec, instead of a maximum of inhibition, a decrease in AI was observed.

Application of penicillin to the somatosensory projection areas (S_1 and S_2) caused paroxysmal activity in the coritical neurons (Fig. 3b, c, d), as a result of which the number of relay neurons in PVN responding to stimulation of ML was considerably reduced. For example, the amplitude of potentials in fibers of the relay cells of PVN recorded close to cortical area S_1 in response to conditioning stimulation of ML at a time of paroxysmal activity in the projection cortex (S_1 and S_2) was only 30% of the initial level (Fig. 3b), i e., of the level before penicillin application (Fig. 3a). After coagulation of area S_1 the amplitude of these potentials increased to 70% of the initial level (Fig. 3d), but after coagulation of area S_2 this was not observed (Fig. 3c).

Curves of recovery of the response of the thalamocortical fibers illustrated in Fig. 2 give information on the different numbers of relay neurons in PVN participating in the transmission of afferent impulses to the cortex. For example, the curve in Fig. 2C shows the recovery cycle of activity of 30% of the population of relay cells which, despite the development of paroxysmal activity in the cortex, remained capable of transmitting afferent impulses [2].

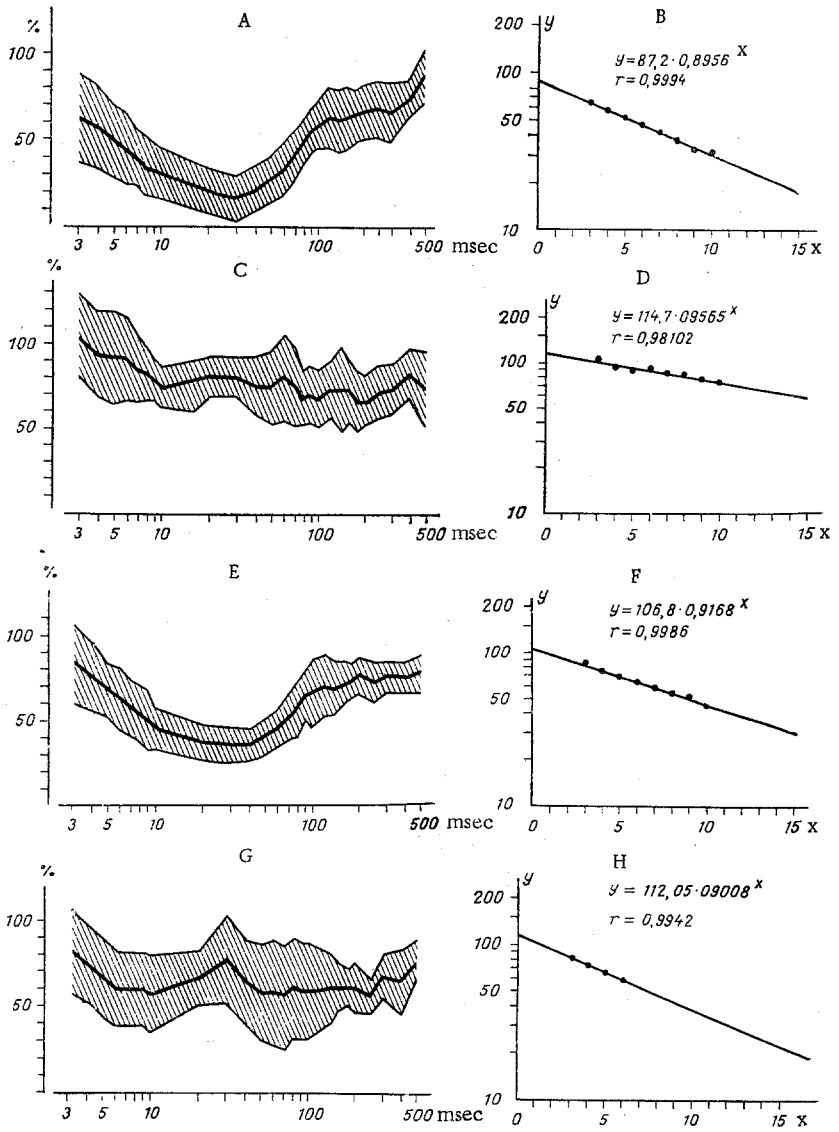

Fig. 2. Averaged curves of recovery of amplitude of testing responses of thalamocortical fibers (left) and approximating exponential functions of initial segments of these curves (right). A, B) Original curve; C, D) after application of penicillin to cortical areas S_1 and S_2; E, F) after coagulation of cortical areas S_1 and S_2 during a period of paroxysmal activity in both cortical areas; G, H) after coagulation of cortical area S_1 during a period of paroxysmal activity in both cortical areas. Remainder of legend as in Fig. 1.

The curves in Fig. 2, E, G characterize the behavior of 70% of the relay neuron population after coagulation of the cortex at a time of paroxysmal activity. AI developing in the relay cells until 10 msec after transmission of the afferent stimulus is considered to be independent of the cortex [3, 4, 5].

However, even the initial segment of these curves (until 3 msec), although it shows the same tendency, nevertheless lies at different levels (see Fig. 2: B, D, F, H). Assuming 100% participation of relay cells in transmission of the afferent stimulus, at 3 msec (x = 3) y_1 was 62.64 (Fig. 2A, B), with 30% participation (during paroxysmal activation) at the same time interval (x = 3) it was 100.37, and with 70% participation (after coagulation of the cortex) it was 82.29, i.e., intermediate in position between y_1 and y_2. These results indicate the presence of clear correlation between the number of relay cells transmitting the stimuli and the character of the developing AI. This correlation can be explained on the grounds that, after the application of penicillin, the distribution of probability of response of relay cells capable of transmitting the afferent stimulus differs from the distribution of probability of response of the whole cell population before penicillin application. The

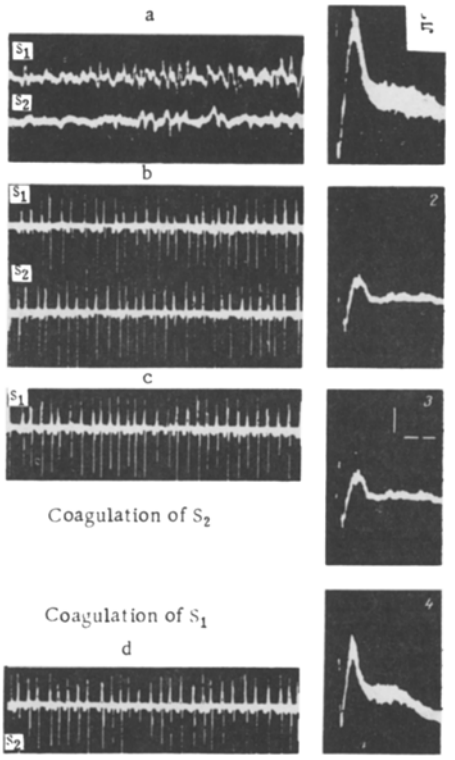

Fig. 3. Potentials recorded in cortical areas S_1 and S_2. Left: corticogram in S_1 and S_2; right – focal potentials of thalamocortical fibers in region of S_1 evoked by stimulation areas; C) after coagulation of area S_1 during a period of paroxysmal activity; D) after coagulation of area S_1 during a period of paroxysmal activity. Calibration: time 5 msec, amplitude 100 μV.

probability of response of a single cell is determined by the afferent input and modulating influences from outside. Since the density of the inputs is unequal, there is some inequality also in the distribution of the probabilities of response of single cells. It is natural to suggest that during procedures directed toward the cortex cells with the lowest probability of response will be inhibited first. For that reason, during application of penicillin to cortical area S_1, when the amplitude of response to the conditioning stimulus was only 30% of the initial value, cells with the highest probability of response did in fact respond. The possibility cannot be ruled out that the excitatory influence of cortical area S_2 masks the internal after-inhibition actually in the initial phase. The phasic excitatory influence from area S_2 may be either direct or mediated through the nonspecific system of the thalamus.

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AFFERENT IMPULSES FROM SKIN RECEPTORS IN RESPONSE TO A JET OF AIR

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The colliding impulse method was used to investigate afferent impulsation in different types of fibers of the cutaneous nerves innervating the hairy skin on the medial surface of a cat's paw. It was shown that a change in the intensity of the acting stimulus caused a change in the structure of the afferent flow. An increase in the strength of the jet of air caused an increase in the number of active fibers and in the frequency of the afferent impulsation and it led to the excitation of other types of fibers also.
KEY WORDS: cutaneous nerve; nerve fibers; stimulation of the skin; afferent impulsation.

The morphological and physiological properties of single skin receptors have now been studied detail [7-9]. The coding of information on stimulation is known to take place in them through changes in the frequency of impulsation [10-12]. Under natural conditions of excitation, however, many receptors of different types are excited simultaneously. Differentiation of the quality and intensity of the acting stimulus in this case is carried out through a code of nervous impulses travelling along the collection of nerve fibers with different conduction velocity and with different frequencies of impulses in the volley [18].

It is difficult to form any sufficiently true impression of the afferent flow from responses of single receptors, for, in the first place, when single fibers are tested the thickest of them are involuntarily chosen [8, 15] and, second, when fibers are separated from the nerve trunk the integrity of the ionic barrier surrounding the excitable membrane is disturbed. This leads to changes in the characteristics of the afferent responses [5]. The activity of a single receptor, moreover, depends not only on the parameters of the acting stimulus, but also on the influence of neighboring excited receptors on it [2, 13]. Ultimately all these factors modify the character of the global response of the receptors. To assess the afferent flow carrying information about stimulation correctly, it is essential to do more than analyze the activity of single nerve fibers.

In the course of the present investigation the method of recording from a whole nerve trunk was used. Changes in the afferent flow in the saphenous nerve were investigated during stimulation of the hairy skin by jets of air of different intensities.

EXPERIMENTAL METHOD

Experiments were carried out on 25 cats anesthetized with hexobarbital (250 mg/kg body weight, intramuscularly).

To determine the frequency spectrum of afferent impulsation and the distribution of the relative number of afferent fibers conducting impulses of particular frequencies, a modified colliding impulse method [4] was used.

For this purpose stimulating electrodes were applied in the region of the groin to a dissected length of the saphenous nerve, the central end of which was divided. The nerve was stimulated by square pulses whose

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