SECHENOV INHIBITION OF CHEMORECEPTOR ACTIVITY IN THE FROG'S TONGUE

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Descending inhibitory influences from the thalamus on chemoreceptor activity in the frog's tongue are demonstrated. Efferent impulses arising during stimulation of the thalamus and disappearing after division of the central end of the lingual nerve were recorded in single fibers of that nerve. The role of lingual nerve fibers in conduction of descending inhibitory influences is established.

Many facts concerned with the influence of the reticular formation on the somatic afferent flow at all levels of the relay system have now been obtained [5-7, 10, 11]. The reticular formation can also influence the afferent flow from peripheral receptors themselves. Such influences were first described for muscle receptors [3] and later for the hair receptors of the cochlea [2]. The reticular formation can also regulate visual and olfactory reception, but its influence is exerted not on receptors but on the ganglionic cells of the retina in the first case [4] and on the granular cells in the second [9].

The object of this investigation was to study the character of chemoreceptor activity of the tongue and the effect of descending influences from the reticular formation upon it.

EXPERIMENTAL METHOD

Activity of the chemoreceptors of the tongue were studied in relation to indices of afferent impulse activity in thin branches of the lingual nerve in response to adequate stimulation. Experiments were carried out on thalamic preparations of frogs (Rana temporaria). An incision was made in the brain at the level of the lamina terminalis, and the hemispheres were removed. The section through the brain was stimulated by application of a crystal of rock salt or of filter paper soaked in 1% adrenalin solution. The experiments were carried out 30 min after dissection. To begin with, the initial level of receptor activity during adequate stimulation was established; responses of the receptors to taste stimulation were then recorded 1, 3, 5, 7, and 9 min after application of the stimulus to the brain section. The character of recovery of the responses was investigated after removal of the stimulus and washing the brain section with Ringer's solution. Activity was recorded by a pair of silver electrodes on an "Alvar" myocathograph. The test stimuli for the chemoreceptors of the tongue were standard solutions of sodium chloride and glucose and tap water. Animals used in the experiments were immobilized by injection of a solution of succinylcholine or flaxedil into the lymph sac.

RESULTS AND DISCUSSION

Stimulation of the thalamus caused a definite decrease in the flow of afferent impulses evoked by adequate stimulation of chemoreceptors of the tongue. Not only a decrease in the level of sensitivity of the chemoreceptors was observed, as reflected in changes in the responses to stimuli of threshold intensity, but also marked inhibition of responses to stimuli of above-threshold strength. The decrease in response

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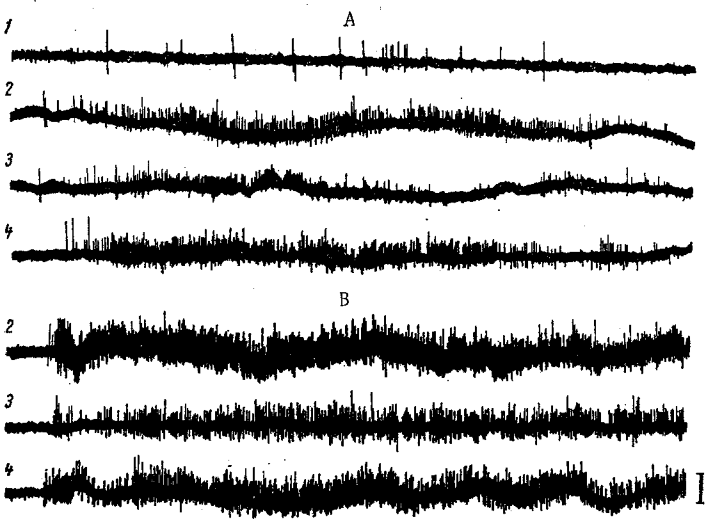

Fig. 1. Changes in chemoreceptor activity of the tongue in response to stimuli of low intensity during thalamic stimulation. A) Character of impulse activity in lingual nerve in response to action of 0.5% NaCl solution; B) the same during the action of 1.5% NaCl solution. 1) Background activity; 2) initial response to salt; 3) 5 min after beginning of stimulation of thalamus; 4) 5 min after stopping thalamic stimulation. Amplitude calibration 100 μV.

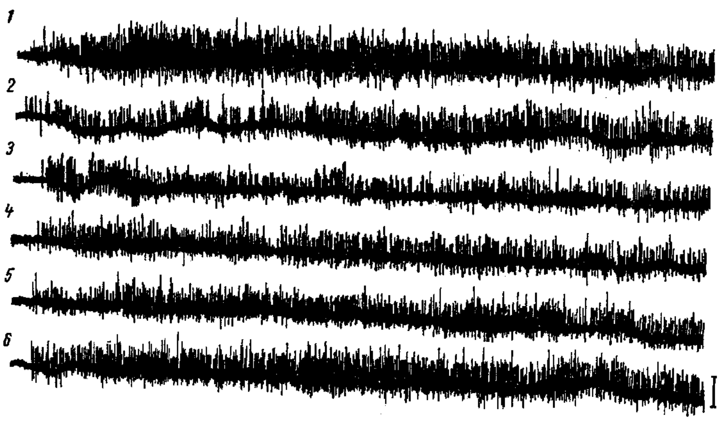

Fig. 2. Dynamics of changes in responses to salt (3% NaCl solution) during thalamic stimulation: 1) original response; 2-5) responses 1, 3, 5, and 9 min after beginning of thalamic stimulation; 6) 10 min after stopping stimulation. Amplitude calibration 100 μV.

to a threshold stimulus is clearly seen in Fig. 1A; both the frequency of the impulses and the duration of the response (from 4.8 to 2.5 sec) were reduced despite continued stimulation of the chemoreceptors. A decrease in sensitivity of the receptors was also observed 5-8 min after stopping stimulation of the brain. During the action of stimuli of above-threshold strength, the inhibitory effect was seen most clearly on stimuli of low intensity (1.5% NaCl solution; Fig. 1B). This effect could last for 5-7 min after stimulation of the brain section had been discontinued.

During stimulation of higher intensity (3% NaCl solution), inhibition of afferent impulse activity from the chemoreceptors was observed throughout the period while the salt crystal was applied to the brain section (9 min), and it stopped only 10-12 min after removal of the crystal and washing of the brain section with Ringer's solution (Fig. 2). Responses of the chemoreceptors to glucose and water showed similar changes under these conditions.

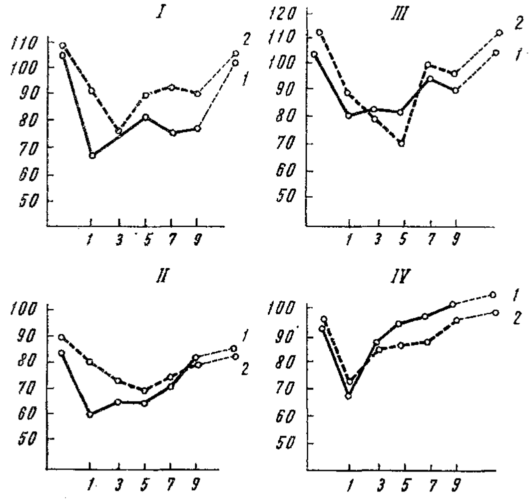

Fig. 3. Graphs showing changes in impulse activity in initial phase (1) and phase of steady discharge (2) during thalamic stimulation. I) Dynamics of response to salt; II) dynamics of response to glucose; III) dynamics of response to water; IV) dynamics of response to salt during thalamic stimulation. Abscissa, time of investigation (in min); ordinate, magnitude of responses (spikes/sec).

In the curves shown in Fig. 3 each point represents the mean results of 10 experiments. The dynamics of development of inhibition of the afferent flow of impulses in the initial phase (number of spikes during the 1st and 2nd second of the discharge) and during the phase of a stable receptor response (number of spikes during the 3rd and 4th second of the discharge) is illustrated. The greatest degree of inhibition affected the "salt" (Fig. 3, I) and "water" (Fig. 3, III) responses. During the 5-6 min from the beginning of thalamic stimulation they were considerably reduced; later, recovery of afferent activity was observed.

As a rule, the greatest decrease in spike activity was observed in the initial phase of discharge of the receptors. Inhibition reached a maximum more rapidly for the initial phase than for the phase of a stable response. For example, whereas the maximum of inhibition of the initial phase of the "salt," "glucose," and "water" responses occurred during the first minute, in the phase of the stable discharge of the "salt" response it was shifted to the 3rd minute, and the maxima of "glucose" and "water" responses were shifted even to the 5th minute. This means that the phase of stable discharge of chemoreceptors undergoes inhibition during thalamic stimulation much later than the initial phase of the response. Repeated stimulation of the thalamic section could again reproduce a similar pattern of inibition of spike activity from the chemoreceptors.

Stimulation of more caudal brain sections had a less marked inhibitory action and, in some cases, it actually had a facilitatory action.

The changes in chemoreceptor activity described above also appeared after application of filter paper soaked in adrenalin solution to the brain section.

The effects observed are evidently mediated through efferent fibers in the lingual nerves because after their division the inhibitory effect was considerably weakened. In addition, in some fibers of thin branches of the lingual nerve, following sympathetic denervation of the tongue, it was possible to record efferent impulses either occurring spontaneously at a frequency of 1-2/2 sec or absent under normal conditions and appearing during stimulation of the brain sections, thereafter continuing throughout the period of stimulation at a frequency of 4-6/sec. This efferent activity consisted of single spikes (20-30 μV); it was reduced after stimulation of the brain section had been discontinued, and it disappeared after division of the central end of the lingual nerve.

Changes in the afferent flow from chemoreceptors of the tongue in response to thalamic stimulation were the results of descending influence from the reticular formation, the highest integrative center in amphibians [1, 8, 12]. The thalamic reticular formation under these experimental conditions did not exert a selective effect on sensitivity of the receptors to stimuli of different taste qualities but produced a general lowering of sensitivity. However, its influence was seen differently in the initial phase and during the subsequent stable discharge. The relative resistance of the phase of stable discharge to inhibitory influences assists in the retention of information concerning prolonged external stimuli, a factor of special significance for such relatively slowly adapting receptors as chemoreceptors. Despite the inhibitory state developing in some motor centers of the spinal cord in Sechenov inhibition and the marked decrease in flow of afferent information, the information regarding prolonged stimuli remains relatively unchanged for a long time. For receptors of this type, a long-acting stimulus is evidently of greater biological and informative value, a factor of significance in seasonal and diurnal cycles of awakening.

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