THE EFFERENT CONTROL OF RECEPTORS (ON THE EXAMPLE OF THE CHEMORECEPTORS OF THE TONGUE)

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In recent years the problem of the efferent control of receptors has attracted the increasing attention of physiologists both in the Soviet Union and abroad. In the USSR this problem has been studied intensively in the laboratory of the physiology and pathology of the sense organs of the Institute of Normal and Pathological Physiology of the Academy of Medical Sciences of the USSR. Workers in this laboratory [1-4] have discovered important facts concerning the physiological activity of the receptors, evidence of the "tuning" of the receptor systems, i.e., the ability of these systems to react in strict accordance with the requirements of the external and internal environment. Physiological analysis of these phenomena leads to the recognition of the important role of processes of efferent regulation of the various receptor apparatuses. The work of several researchers abroad, notably of the Scandinavian school of physiologists, has given the precise electrophysiological characteristics of the processes of efferent control, mainly concerning the elements of the retina [7, 9], the cochlea [Galambos (1956)] and the olfactory bulbs [10, 13].

Very little work has been done on the receptors of the tongue. In this connection may be noted only the work of Dodt and Walther [8]. These authors, however, confined their studies to the efferent control of the temperature receptors of the tongue. They showed, in particular, that in certain conditions of stimulation of the lingual nerve by an electric current a change in the frequency of cold impulses was observed. In their opinion this was not the result of a direct efferent influence on the state of the receptors, but was due to a change in the blood flow observed under these circumstances. Finally, Appelberg, Kitchel and Landgren [6] have recently shown that the reticular formation may influence the electrical activity of the thalamic and cortical regions of the brain, caused by electrical stimulation of the tongue.

Zaiko [2], using the method of functional mobility, demonstrated a relationship between the activity of the receptors of the tongue and the condition of the interoreceptors of the stomach. She showed that the taking of food leads to a considerable decrease in the number of active taste buds, i.e., to the demobilization of the receptor apparatuses of the tongue, and she put forward the hypothesis that this phenomenon was reflux in nature.

P. G. Snyakin accordingly set us the task of defining the electrophysiological characteristics of this phenomenon and of demonstrating the possible role of the central nervous system in the mechanism of efferent control.

1. The Influence of the Interoreceptors of the Stomach on the Character of the Afferent Flow from the Receptors of the Tongue

EXPERIMENTAL METHOD

Investigations were carried out by the method of Zotterman [14] on frogs (Rana temporaria and Rana esculenta). The index of the state of the taste apparatuses of the tongue was the flow of afferent impulses in the lingual nerve, which was recorded on the OB-2 oscillograph. The potentials were tapped by means of a pair of silver electrodes, the distance between which was 2.5-3.0 mm. As taste stimuli we used standard solutions of common salt (5%), quinine (0.0025%) and tap water. Stimulation of the tongue was applied by irrigation of its surface from a pipette for 10-12 seconds. The bioelectrical activity was recorded 3-4 seconds after application of the stimulus. The order of the experiments was standardized: First the initial level of the electrical activity of the lingual nerve in response to stimulation of the receptors of the tongue by the taste substances was established, after which the influence of the various factors on the initial level of afferent activity was studied.*

EXPERIMENTAL RESULTS

The study of the influence of the interoreceptors of the stomach on the taste receptor apparatus showed that mechanical stimulation of the stomach (distension by filling with water) has a marked action on the character of the flow of afferent impulses from the receptors of the tongue.

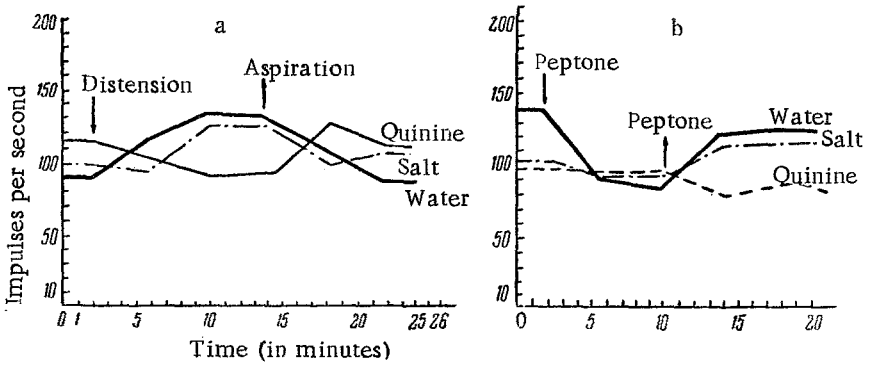

Fig. 1. Changes in the afferent electrical activity of the lingual nerve during mechanical stimulation of the stomach (a) and introduction of peptone solution into the stomach (b). Along the axis of ordinates is plotted the frequency of afferent impulses in the lingual nerve; along the axis of abscissas the time of recording. The arrows indicate the times of application and cessation of mechanical (distension with water) and chemical (introduction of peptone) stimulation of the stomach.

This effect took the form of a considerable increase in the strength of the afferent impulses from the receptors of the tongue in response to water and to salt solution. The afferent flow of impulses in response to quinine was unchanged in these conditions: Initially the impulses even became less frequent, then more frequent, although this took place after cessation of distension of the stomach. The picture of the change in the bioelectrical activity of the lingual nerve in response to distension of the stomach is shown graphically in Fig. 1a.

Besides mechanical stimulation of the stomach, chemical stimulation by the introduction of a solution of peptone was applied. The results of these experiments were opposite to those described above. The introduction of 0.5 ml of peptone solution into the stomach through a syringe led to a considerable decrease in the afferent flow of impulses and to inhibition of the afferent electrical activity. The greatest inhibiting influence was felt by the afferent impulses in response to stimulation with water, and the bioelectrical activity caused by the action of salt solution was inhibited to a lesser degree, while the response to quinine was almost unchanged (Fig. 1b).

Stimulation of the mechanoreceptors of the stomach (distension) thus led to an increase in the electrical activity of the receptors of the tongue (to water and salt); stimulation of the chemoreceptors (peptone) led to a

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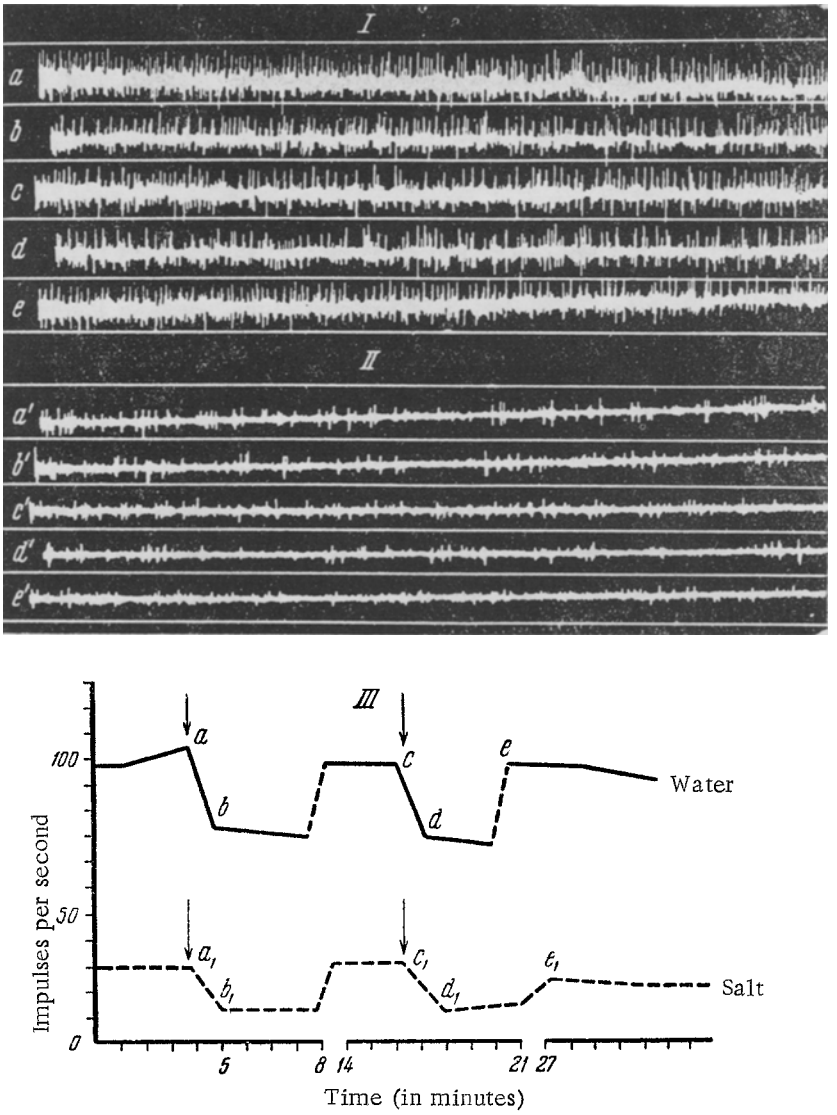

Fig. 2. Inhibition of the afferent bioelectrical activity of the lingual nerve during stimulation of the central end of the contralateral lingual nerve. I) oscillographic recording of the action currents of the lingual nerve in response to irrigation of the dorsal surface of the tongue with tap water; II) the same during the action of salt solution; a,b,c,d,e and a_1, b_1, c_1, d_1, e_1 – individual moments of recording the electrical activity of the lingual nerve in time (see Fig. 3); III) graph showing the changes in the afferent electrical activity of the lingual nerve. The arrows indicate the moments of stimulation of the contralateral lingual nerve.

decrease in the activity of the receptors of the tongue. The influences from the interoreceptors of the stomach were evidently selective in their action, decreasing or increasing the electrical activity of the receptors in response to water and salt solution, and either leaving unchanged or changing in the opposite direction the electrical activity in response to the action of quinine solution on the tongue.

This effect was undoubtedly reflex in nature, for it was abolished by the action of cocaine on the interoreceptors of the stomach and by extirpation of the medulla.

The results of the experiments with peptone were analogous to those obtained by Zaiko [2], who observed a decrease in the number of active taste buds after the taking of food. In Zaiko's experiments, however, which

were conducted on human subjects, the problem of the level of exclusion of the sensation of taste was unsolved. In the experiments which we have described, in which we recorded the bioelectrical activity of the lingual nerve, the importance of the peripheral taste apparatuses of the tongue was clearly emphasized.

2. The Role of the Central Nervous System in Regulation of the Functions of the Receptors of the Tongue

In view of the important role of the intact medulla in the mechanism of the reflex from the stomach on the taste receptor apparatus of the tongue, we postulated that the state of the nerve centers of the medulla may have a controlling influence on the functions of the receptors. In order to elucidate this point experiments were carried out in which the central end of the lingual nerve, the nucleus of which is situated in the medulla, where it is a component of the ninth pair of cranial nerves, was stimulated by an induction current. In these experiments the index of the functional state of the receptors of the tongue was the afferent flow of electrical impulses in the contralateral lingual nerve.

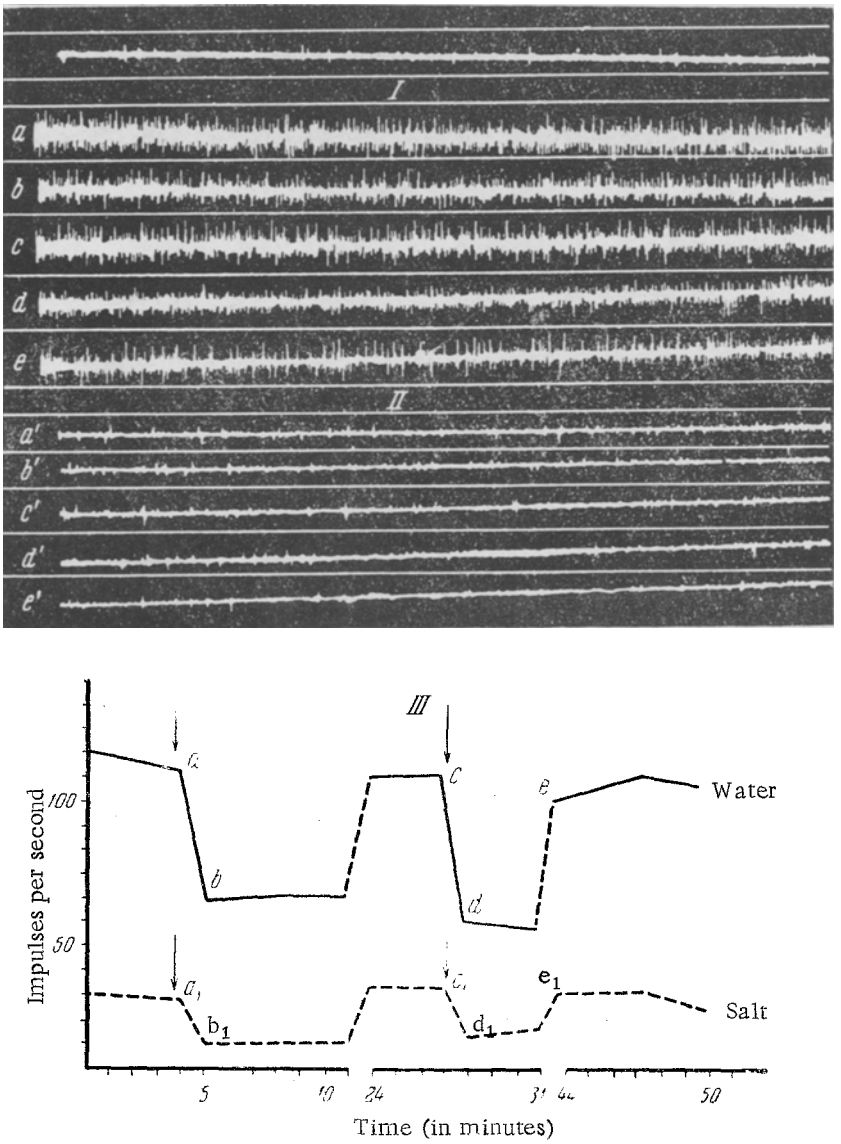

Fig. 3. Inhibition of the efferent bioelectrical activity of the lingual nerve during antidromic stimulation. Legend as in Fig. 2. Time of stimulation 30 seconds.

The results of these experiments showed that stimulation of the central end of the lingual nerve with a weak induction current for 30-45 seconds led to a considerable weakening of the electrical activity of the contralateral lingual nerve when the taste stimuli were acting on the tongue. Under these circumstances there was a decrease in the frequency of the impulses by 40% and more (Fig. 2). The original level was regained 12-13 minutes after stimulation. Our results were similar to those obtained in experiments on the retina [12] and olfactory bulbs [10, 13].

This series of experiments was of interest from the point of view that stimulation of the central end of the lingual nerve while the electrical activity of the contralateral nerve was recorded apparently imitated signals from the excited receptors of the tongue, proceeding to the central nervous system.

Strong or prolonged excitation of the receptors of the tongue (during the action of stimuli) thus led to reflex inhibition of their activity, inhibition due to the participation of the medulla and also, probably, to other divisions of the central nervous system.

Analysis of the results of this group of experiments suggests that the nerve centers of the medulla are responsible for the regulation of the functional activity of the taste receptors, depending on the character of their flow of afferent impulses. This regulation of the physiological activity of the receptors is in all probability effected by the sending of efferent signals of a definite purpose.

Having postulated that the active influence of the nerve centers on the receptor apparatuses of the tongue was of such a character, we were concerned to carry out experiments in which it might be possible to show that the excitation proceeding along the lingual nerve to the receptors of the tongue under these particular experimental conditions could, in fact, inhibit their total afferent electrical activity. The results of these experiments showed that stimulation of the peripheral end of the lingual nerve leads to marked inhibition (by 50% and more) of the afferent flow of impulses in the same or the contralateral lingual nerve (Fig. 3). This effect was transient, and 20-25 minutes later the afferent electrical activity regained its initial level. Our findings in these experiments were similar to those obtained for the optic nerve [11] (Motokawa and Ebe) and the lingual nerve [8].

The physiological activity of the chemoreceptors of the tongue, when expressed as the combined afferent bioelectrical flow of impulses, is thus subjected to the controlling influence of the interoreceptors of the stomach. The processes of efferent control of the chemoreceptors, effected by particular divisions of the central nervous system, in all probability bear the character of "reversible" connections, and are of importance in tuning the receptors to a certain level of activity, to correspond to the requirements of the external and internal environment.

SUMMARY

The relationship of the afferent bioelectrical activity of the lingual nerve upon the condition of gastric interoreceptors was studied.

It was shown that the gastric interoreceptors exert a significant effect on the afferent bioelectrical flow from the lingual receptors. The processes of the efferent control of the lingual chemoreceptors are affected by definite parts of the central nervous system (the role of the medulla is shown); in all probability they have a feedback character and are meant for tuning of the receptors to a definite level of activity in accordance with the requirements of external and internal environment of the organism.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.
