EFFECT OF SENSORY STIMULATION ON "SPONTANEOUS" EFFERENT ACTIVITY RECORDED IN COMMON NERVE TRUNK OF THE FROG

(UDC 612.828-019 + 591.181.782.8)

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(Presented by Academician of the Academy of Medical Sciences of the USSR A. V. Lebedinskii)
Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 60, No. 9,
pp. 10-15, September, 1965
Original article submitted April 28, 1964

Most of the efferent impulses which can be recorded in the common nerve trunks of the frog when the animal is at rest take the form of volleys, following one another continuously [4]. The authors have confirmed an observation made by Elizarov (1958) while a student in this department, that, when there is muscular rest, these efferent impulses are sympathetic, and are connected with activity in structures of the diencephalon and midbrain [5, 6]. There are grounds for stating that this efferent sympathetic activity develops in reticular adrenergic structures of the regions mentioned [6].

The idea has developed [2, 9, 12] that, in amphibians, despite the low degree of differential development, the reticular formation has an important integrating function, and is a structure the functional state of which is determined by the flow of sensory impulses from various afferent systems. It has been shown that stimulation of skin or viscera in warm-blooded animals has an effect on the electrical activity of the midbrain reticular formation, thalamus and skeletal muscles [1, 3, 8, 10, 11].

Afferent stimulations might naturally be expected to have an effect on efferent sympathetic activity. An attempt was made to confirm this experimentally. It had invariably been observed in investigations in this laboratory [5] that there was increase of efferent sympathetic activity before and during the development of "spontaneous" movements. It was sought to determine what changes in efferent sympathetic activity were associated with different forms of afferent stimulation and how these changes were connected with the developing movements.

EXPERIMENTAL

As in the earlier investigations [4, 6], the experiments were carried out on both whole and "somatectomized" frogs (7th, 8th, and 9th spinal nerves on the side from which efferent sympathetic activity was recorded were divided above the origin of their rami communicantes.

Knee and ankle joints were rigidly immobilized. Potentials were taken from cutaneous and muscular branches of the tibial nerve (sheaths were removed) by means of silver electrodes with an interelectrode distance of 2-3 mm. Measures were taken to prevent drying of the nerve on the electrodes. There was no interference with the blood supply to the muscle. The animal was in a screened room. A two-channel amplifier with symmetrical input and a transmission band of 100-1000 cps was used. Recording was on a loop oscillograph. Total electrical activity was recorded by an integrator, the readings of which were processed in a computer and used for the construction of graphs.

Skin was stimulated with a brush attached to the arm of a Marey capsule, and with filter paper soaked in 0·1, 0·25, 0·5, and 1·0 percent H_2SO_4, filter papers of different sizes being used for the leg and thigh on the side opposite to that from which recordings were made and for stimulation of skin on the back and head. Another form used was stimulation of the central end of a sciatic nerve with electrical pulses of various strengths and frequencies. Interoceptors in the stomach were stimulated by the introduction of 0.1 ml of 5 percent NaCl.

In all, there were about 60 experiments.

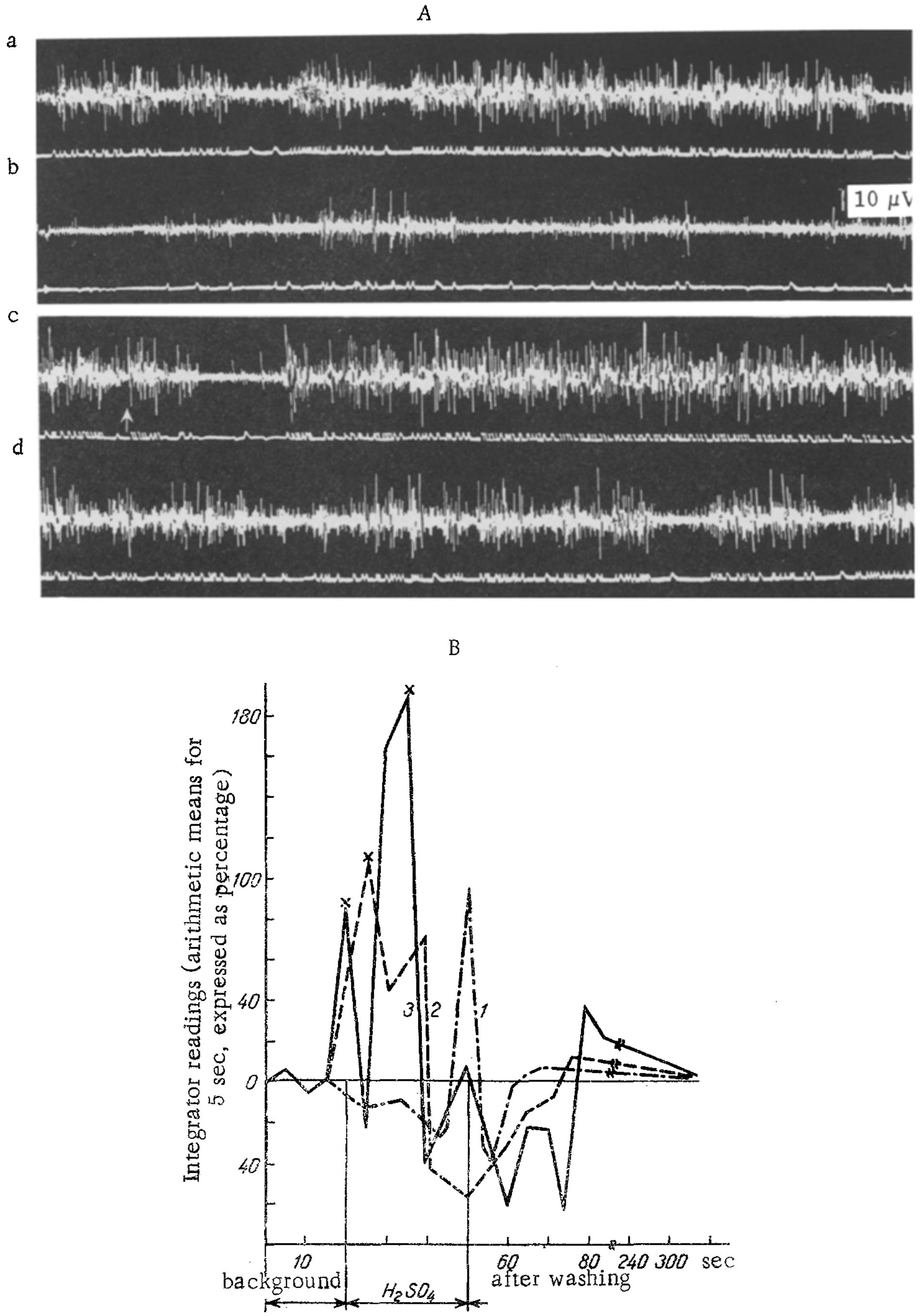
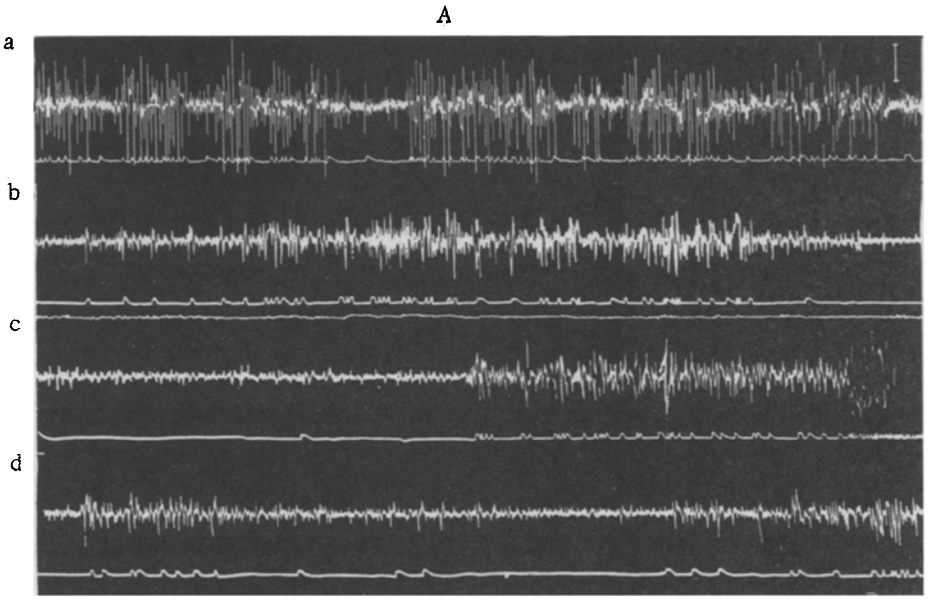


Fig. 1. Oscillogram (A) and graphs (B) showing changes in volley activity resulting from acid stimulation of skin of frog. A) Intact frog: a) initial level of volley activity 1 h after "somatectomization"; b) stimulation of skin of leg with 0·1 percent H_2SO_4; c) stimulation of skin of leg with 1 percent H_2SO_4; d) restoration of activity 3 min after last stimulation. Tracings: from top to bottom) volley activity, integrator readings, time (1 sec). Arrow indicates moment of stimulation. B) "somatectomized" frog: 1) stimulation of skin of leg with 0·25 percent H_2SO_4. 2) stimulation of skin of leg with 0·5 percent H_2SO_4; 3) stimulation of skin of back (large area) with 0·5 percent H_2SO_4; x) movement of animal. Abscissa: 0) level of background activity; below) depression of, and above) increase of volley activity (percentage of initial level).



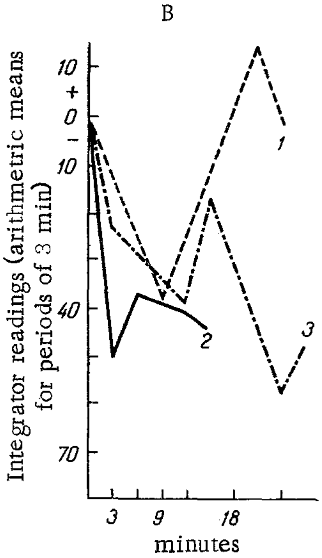


Fig. 2. Oscillograms (A) and graphs (B) showing changes in volley activity on interoceptive stimulation. A) Intact frog: a) initial activity; b) immediately after laparotomy and extraction of stomach; c) 1 min; and d) 9 min after introduction of 5 percent NaCl (motor impulses seen in end part of c). Significance of tracings as in Fig. 1. Time) 0.2 sec. B) "Desomatized" frog: 1) extraction of stomach; 2) 5 percent NaCl introduced into stomach; 3) further introduction of 5 percent NaCl into stomach (20 min later).

RESULTS

Effects of Interoceptive Stimulations

It was found with chemical stimulation of the skin that more efferent sympathetic activity was caused by the same strength of acid when the area of skin stimulated was increased.

The relationship between change in efferent sympathetic activity and acid concentration was as follows. Stimulation with weak acid (0.1 percent) was followed, first, by a short pause in efferent sympathetic activity (1-5 sec), after which there was development of slow and generally small activity (Fig. 1A, b). Removal of the acid and subsequent washing led to some increase of afferent sympathetic activity and, after about a minute, return to the original level (Fig. 1B).

A point of great importance was that in the case of weak acid stimulation, all the changes in efferent sympathetic activity described occurred without the development of any general response movements. It followed, therefore, that the changes in efferent sympathetic activity, for which structures in the diencephalon and midbrain are responsible, could cause excitation in the somatic motor formations of the central nervous system.

Stimulation of the skin on the leg or thigh with stronger acid (0·5 and 1·0 percent), in contrast to stimulation with lower concentrations, led at once to increase of efferent sympathetic activity (Fig. 1A, c), which preceded the reflex motor response.

The skin on the back and head appeared to be particularly sensitive, as the application of 1·0 percent H_2SO_4 produced one or two successive attacks of general movements in the course of half a minute, whereas prior to this the animal's spontaneous movements were not more frequent than one in several minutes (see Fig. 1B). Furthermore, stimulation of these surfaces was often followed by excessive secretion of mucus over the entire body surface.

With more powerful chemical stimulation, efferent sympathetic activity was increased throughout the period of stimulation, and for 2-4 or sometimes 10 min thereafter activity tended to fluctuate upwards and downwards, reflecting, as it were, the fluctuating character of fading in central structures. Also, stimulation of the skin, particularly the skin of the head, often caused the animal to emit a cry, probably because the stimulation was painful. The increase of efferent sympathetic activity illustrates the part played by the sympathetic system in responses to nociceptive stimulation [7].

Tactile stimulation of the skin (brush) produced extraordinary volleys of large impulses. Several such stimulations in rapid succession produced a prolonged response volley and sometimes led to increase of efferent sympathetic activity and movement. This obviously indicates summation of excitation and spread to an ever increasing number of brain structures.

The response to electrical stimulation of the central end of the sciatic nerve was dependent on the strength and duration of stimulation of the same frequency. More prolonged stimulation at subthreshold strength (i.e., a strength not producing a reflex movement) or a short period of stimulation at threshold strength caused first a decline, then an increase and, after 1-2 min, return to normal of efferent sympathetic activity. These were similar to the changes seen when the skin was stimulated with weak acid. Efferent sympathetic activity was suppressed by prolonged electrical stimulation of the nerve at threshold strength.

Other similar forms of stimulation (chemical stimulation of stomach, mechanical stimulation of stomach, mesentery, intestine or pulmonary tissue) led to depression of efferent sympathetic activity in the absence of reflex movements. When, for example, the abdominal cavity was opened and the stomach handled (obviously a powerful form of stimulation), the frequency of the sympathetic volleys fell sharply, the volleys became greatly extended in time (1-1½ sec), the amplitude of the potentials fell from 15-12 to 6-8 μV, and the animal's movements ceased or became much less frequent. Efferent sympathetic activity tended to become stabilized again after 5-10 min and movements were restored, although in a rather slower tempo than previously (Fig. 2). The introduction of a certain volume of 5 percent NaCl into the stomach also led to reduction of the number of volleys of efferent sympathetic activity and reduction of the amplitude of the potentials (Fig. 2A, c). The animal's movements were separated by considerable intervals. The amplitude of the impulses continued to fall (Fig. 2A, d). It may be noted that interoceptor stimulation produced a more prolonged and more powerful effect than stimulation of exteroceptors (Fig. 2B).

It was thus established that stimulation of the skin which did not produce a motor reaction depressed efferent sympathetic activity, which was then gradually restored, whereas more powerful stimulation always led to intensification of efferent sympathetic activity before and during the motor reaction.

There is thus obligatory involvement of flows of efferent sympathetic impulses in the preparation for and development of both general movements of the animal developing "spontaneously" and movements produced reflexly. This means that activity of reticular structures in diencephalon and midbrain precedes activity in the more strictly motor structures and is an essential component in the production of movements.

These facts relating to interoceptor effects suggest that, in amphibians at any rate, signals from viscera tend to weaken the forms of activity in central structures responsible for the development of general movements.

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