

ipsilateral connections. This hypothesis is based on the following experimental data and concepts. In a parallel investigation we found that NPC have not only classical (lemniscal), but also nonclassical (extralemniscal) connections with structures of the contralateral ventrobasal nuclear complex of the thalamus [4]; moreover, the latter extralemniscal afferent projections of NPC have an additional decussation in the region of the diencephalon. These extralemniscal connections may perhaps be complemented by connections of a certain number of relay cells of the opposite NPC. On the other hand, bilateral inhibitory control of each half of the forebrain by symmetrical NPC is evidence that the common "targets" of this control (the corresponding lemniscal and extralemniscal neuronal elements of the symmetrical NPC) have closely similar functional properties.

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#### ANTIDROMIC VASODILATATION INDUCED BY $A_\delta$ -AFFERENTS IN THE FROG

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Stimulation of the peripheral end of dorsal roots VII-X in the frog leads to vasodilatation in the hind limb [2, 5, 6]. Since this response is determined by the action of impulses traveling along afferent fibers in the peripheral direction, it is called antidromic vasodilatation [4, 5]. In mammals antidromic vasodilatation is induced by impulses traveling along unmyelinated C-afferents [9, 10] and also, hypothetically, along the most slowly conducting A-afferents [9]. In amphibians, however, antidromic action on blood vessels may be a feature characteristic of impulses of myelinated fibers and, in particular, of fast-conducting A-afferents. In frogs, in fact, in response to stimulation of the submaxillary nerve, dilatation of arterioles develops in the homonymous muscle; this response, moreover, is induced by impulses in the fibers possessing the high excitability that is a feature of fast-conducting A-afferents [1]. Fibers on activation of which vasodilatation takes place in the hind limb also are present in the frog sciatic nerve. These fibers are more excitable than the unmyelinated vasoconstrictor fibers of the same nerve [2, 7]. It maybe that the more excitable fibers are afferent.

The aim of the experiments was to discover if this is in fact true, and if it is, to determine the group of afferents to which they belong and the closeness of the excitability of fibers of the sciatic and submaxillary nerves, which are analogous from the standpoint of their action on vessels.

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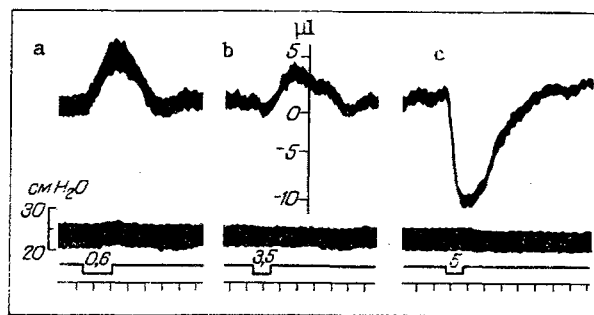


Fig. 1. Responses of frog hind limb vessels to stimulation of peripheral segment of sciatic nerve by stimuli of increasing amplitude (shown above stimulation marker, in volts). From top to bottom: plethysmogram, pressure in left sciatic artery, stimulation and time (1 min) markers. Contraction of muscles abolished by Flaxedil. Stimulus duration 1 msec.

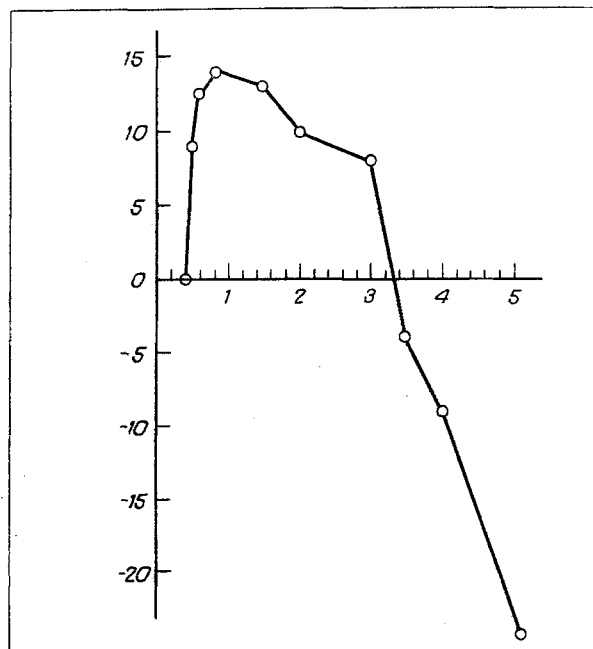


Fig. 2. Dependence of direction and magnitude of responses of hind limb vessels of one frog on amplitude of pulses used to stimulate sciatic nerve. Abscissa, amplitude of stimulating pulses (in V). Ordinate, changes in blood volume in hind limb at maximum of responses (in  $\mu$ l). Pulse duration 1 msec. Contraction of muscles abolished by Flaxedil.

#### EXPERIMENTAL METHOD

After induction of anesthesia with ether, Viadril (0.13 mg/g body weight) was injected into the abdominal vein of male frogs (*Rana temporaria*, weight 40-60 g) for basal anesthesia and Flaxedil (0.08-0.1 mg/g) for relaxation. The blood pressure was recorded in the left sciatic artery, for which purpose it was connected to a DMI-01 inductive electromanometer by means of a cannula filled with heparin solution. Using a dorsal approach, the right sciatic nerve was ligated and divided in the thigh and its peripheral end was placed on a bipolar stimulating electrode. The right hind limb, including the distal half of the thigh, was placed in the glass chamber of a plethysmograph. A rubber packing ring was fixed to its open end. The inner free edge of this flexible ring was glued to the skin of the thigh with MK-2 acrylic glue, thus closing the chamber hermetically. It was then filled with tap water. Fluctuations of pressure in the chamber, proportional to changes in the volume of blood in the limb vessels, were

received by a capacitive manometer with high volume compliance (Krasnogvardeets Model 062). The signal from the latter was recorded on a KSPP-4 apparatus. With maximal dilator responses the pressure in the plethysmograph rose by not more than 2-3 mm water. Before injection of Flaxidil, by stimulating the sciatic nerve (ÉSL-2 stimulator) the amplitude of the pulses was determined at which the most excitable motor fibers of the nerve were activated. Extension of the digits served as the indicator. Flaxidil was then injected and the threshold of onset of the vasodilator response determined. By increasing the intensity of stimulation step by step, dependence of the vasomotor reactions on it was determined. The frequency of the pulses in this case was 10 Hz and their duration 0.1 or 1 msec. To establish the type of fibers possessing vasodilator action, thresholds of excitation of different groups of afferent fibers of the sciatic nerve were determined and the velocity of conduction of excitation along the fibers of these groups measured. For this purpose, at about mid-thigh level the sciatic nerve was isolated, divided, and its central end was placed on a stimulating bipolar electrode. After the spinal canal had been opened, dorsal root VIII, IX, or X was divided close to the spinal cord, placed on a bipolar recording electrode, and the compound action potential (CAP) was recorded from it during stimulation of the sciatic nerve with single electric pulses with a duration of 0.1 or 1 msec. To detect waves of CAP of low amplitude, the signals were amplified (in the 0.1-3 kHz band) and applied to an averager ("Disa," 11G14). Usually 20 realizations of CAP were averaged. In all the experiments the frog was placed on a table heated so that the animal's temperature was between 16 and 19°C. The nerve and roots were protected against drying by covering them with thick petrolatum. The frog was covered in gauze, which was regularly soaked with tap water.

### EXPERIMENTAL RESULTS

Traces of responses of an increase and decrease in blood volume of the limbs in response to stimulation of the sciatic nerve by pulses of increasing intensity are given in Fig. 1. These responses are due to dilatation and constriction of the vessels. Dilator responses (Fig. 1a) appeared after a latent period of 5-15 sec and reached a maximum 1.5-2 min after the beginning of stimulation. The blood volume of the limb 2-3 min after the end of stimulation was close to its initial value.

With an increase in amplitude of the pulses stimulating the sciatic nerve, three main waves of CAP appeared consecutively in the dorsal roots. Determination of the velocities of conduction of excitation showed that the first wave is formed by synchronized discharges of  $A_{\alpha\beta}$ -fibers (conduction velocity 38-14 m/sec), the second by  $A_\delta$ -fibers (12-3.5 m/sec), and the third by C-fibers (1.9-0.2 m/sec). These data are in good agreement with those obtained previously for A- and C-afferent fibers of the frog somatic nerves [3, 8].

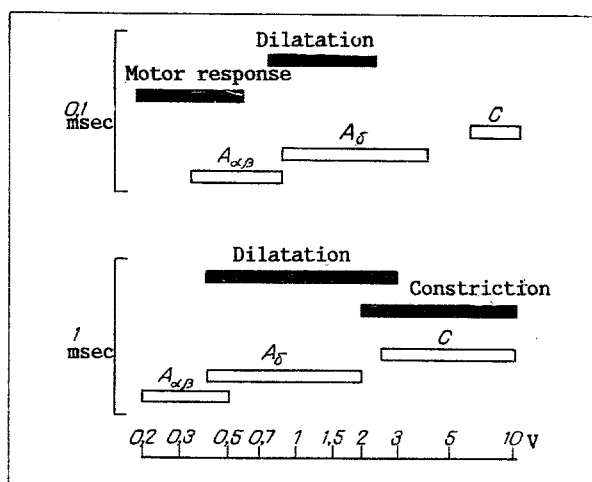


Fig. 3. Ranges of amplitudes of stimuli within which sciatic nerve stimulation evokes a motor response, vasodilatation of the limb, or vasoconstriction (black rectangles), and also the appearance of waves of the compound action potential in dorsal roots VIII-X (unshaded rectangles). Depending on the velocity of conduction of excitation these waves were identified as synchronized discharges in  $A_{\alpha\beta}$ ,  $A_\delta$ , and C afferent fibers.

The characteristic curve reflecting dependence of the direction and magnitude of the vascular responses on the intensity of sciatic nerve stimulation is illustrated in Fig. 2. The threshold of the vasodilator response in 10 frogs averaged  $0.6 \pm 0.2$  V (range 0.4-0.7 V, stimulus duration 1 msec). At 0.7-2 V this response reached a maximum, and at 1.5-2 V it was already reduced. In two frogs at 2 V and in the other eight frogs at 3-4 V threshold vasoconstriction developed, i.e., activation of vasoconstrictor fibers took place of sufficient degree to overcome the dilator action of the more excitable fibers. The responses at 2-3 V could be mixed: they began with slight vasoconstriction, which was followed by vasodilatation (Fig. 1b), or they varied in the course of the experiment, i.e., they were dilator at its beginning and became constrictor after a few hours, toward the end of the experiment. The mean threshold of the vasoconstrictor response was  $3.0 \pm 0.8$  V, and the basic range of its increase was 5-10 V (Fig. 1c, Fig. 2). In one of the 11 frogs responses of the vessels differed from the ordinary kind: dilatation did not arise, and the threshold of the constrictor response was unusually low, namely 1 V.

Values of excitation thresholds for each of the three groups of fibers are shown in Fig. 3. Thresholds of detection of each wave in all 13 frogs and for all three roots were taken into account. The same diagram shows the ranges of intensity of the stimuli within which, first, a vasodilator and, subsequently, a vasoconstrictor effect of sciatic nerve stimulation appeared and increased in intensity. It can be seen that vasoconstriction in fact took place within the range in which C-afferents were activated (2.5-10 V for a pulse duration of 1 msec). This coincidence is due simply to agreement between the excitability of the two types of unmyelinated fibers: C-afferents and sympathetic postganglionic vasoconstrictor axons. It is impossible to say whether an antidromic dilator action is characteristic of impulses in C-afferents of the frog (as in mammals), for the action of the vasoconstrictor fibers is stronger.

Coincidence of the range of intensity of the stimuli within which  $A_\delta$ -afferents are activated and vasodilator responses appear (Fig. 3) leads to the conclusion that these responses arise as a result of activation of  $A_\delta$ -afferents, including the most excitable of them. Dilatation of arterioles of the submaxillary muscle, arising in response to stimulation of the homonymous nerve [1], also evidently is determined by impulses in  $A_\delta$ -afferents. In fact, all that is necessary for this response to arise is that the amplitude of the stimulating pulses (with a duration of 0.1 msec) is only three times higher than the activation threshold of the most excitable motor axons [1]. During sciatic nerve stimulation by pulses of the same duration the threshold of excitation of these axons (determined in seven frogs) was  $0.35 \pm 0.1$  V, and the threshold of the vasodilator response was  $1.2 \pm 0.5$  V, i.e., about 3.5 times higher. Thus the excitability of those fibers which are characterized by an antidromic vasodilator action is in fact the same for both nerves: sciatic and submaxillary. It will be evident that these fibers belong to the same group, namely  $A_\delta$ -afferents. Turning to the phylogenetic aspect, a difference will be noted between amphibians and mammals: in the latter an antidromic action on blood vessels is characteristic chiefly of C-afferents [9, 10] and indeed as has been suggested [11], only of those of them which contain substance P.

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