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ACTIVITY IN MYELINATED FIBERS OF A CAT CUTANEOUS NERVE IN RESPONSE TO HEATING

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It was shown by the colliding impulses method combined with methods of distinguishing weak signals in a nerve from apparatus noise that heating the hairy skin causes a change in the character of activity recorded in fibers of the A_{γ}, A_{δ_1}, and A_{δ_2} groups and in the group of "mixed" fibers. A relatively large number of fibers of these groups is excited, and only a few of them inhibit their activity in response to heating the skin receptors. An increase in the spontaneous discharge and relaxation of the skin were shown to take place during heating.

KEY WORDS: myelinated nerve fibers; afferent impulsation; heating the skin.

Among investigators who have studied temperature reception in the hairy skin of the cat the view is held that heating the skin causes excitation only of those receptors which are innervated by unmyelinated fibers [9, 11]. However, myelinated fibers which participate in the conduction of afferent impulses arising during heating have been found in the skin of the nose and in the tongue of the cat [7]. Activity has been recorded in afferent myelinated fibers of the hairy skin of the cat in response to its rapid heating [13]. Similar fibers have been found in the cutaneous nerves of primates [8].

In the course of investigations of changes in combined activity of a whole nerve during heating of the skin receptors contradictory results have been obtained: Some workers consider that spontaneous activity is reduced [12], others found no change in activity in the cutaneous nerves during heating [5], and the third group observed an increase in activity of the whole nerve during heating [14].

The object of the present investigation was to determine the degree of participation of thin myelinated fibers in the transmission of information about heating the hairy skin in cats.

EXPERIMENTAL METHOD

Experiments were carried out on cats under intramuscular hexobarbital anesthesia. Nerve structures responsible for the perception of cold stimuli are considered to be located in the superficial layers of the skin and those responsible for the perception of heat stimuli in its deeper layers [10]. A dissected skin flap was therefore placed in a thermode, so that the temperature of its superficial and deep layers could be changed simultaneously. The skin temperature was changed by changing the temperature of the water flowing through the thermode. The rate of heating of the skin, measured on its hairy surface by means of a type TPM-1 thermometer, was 1 °C/sec. To ensure that because of inertia of the thermometer the skin was not heated to an injurious temperature (45°C), in control experiments a calibrated semiconductor thermistor was inserted beneath the epidermis. Temperature changes recorded by the thermistor exceeded the values of temperature obtained by means of the TPM-1 thermometer by a maximum of 1.5-2.0°C.

The skin temperature varied from +32 to +42°C. After application of the temperature stimulus and restoration of the skin temperature to the adaptation temperature, an interval of 15 min was allowed before stimulation was repeated.

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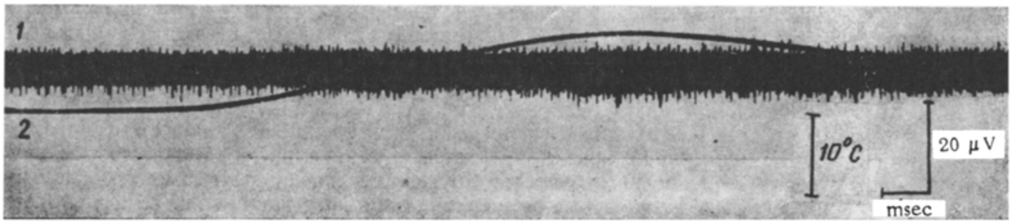

Fig. 1. Changes in spontaneous activity recorded from whole trunk of lateral cutaneous branch of saphenous nerve in response to elevation of skin temperature and return to initial adaptation temperature.

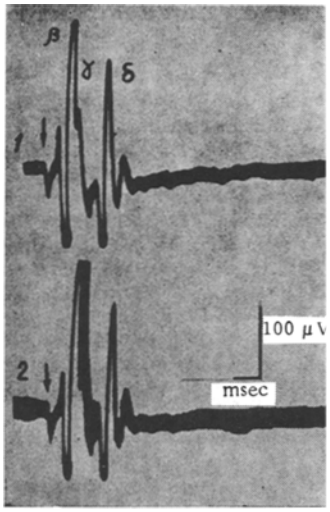

Fig. 2. Changes in complex AP of myelinated fibers of cutaneous nerve during heating of skin receptors. 1) Superposition of 50 antidromic AP of myelinated fibers during electrical stimulation of nerve at frequency of 5 Hz; 2) change in same AP during skin heating. Arrow indicates moment of electrical stimulation of nerve. Conduction velocity is modal A_δ-group 19.6 m/sec.

Activity in myelinated fibers of the cutaneous nerve was determined by a combination of the colliding impulses method [1] with the method of distinguishing weak signals in a nerve from apparatus noise [3, 4]. If activity appeared in fibers corresponding to a particular group of evoked action potentials (AP), distinguished from apparatus noise, after collision of orthodromic and antidromic impulses in the segments between the electrodes the amplitude of the AP recorded was reduced. With a low frequency of antidromic stimulation the probability of collision between orthodromic and antidromic impulses in the segment of nerve between the electrodes would be greater and the amplitude of the recorded AP would be smaller.

If the frequency of the volley of antidromic impulses was increased, collisions between impulses would move closer to the receptors and the antidromic AP would approach the recording electrode along a larger number of fibers. Its amplitude would therefore be increased. When the frequency of antidromic impulses exceeded the maximal frequency of the orthodromic volleys, all collisions would take place outside the segment of the nerve between the electrodes and maximal amplitude of the AP would be recorded.

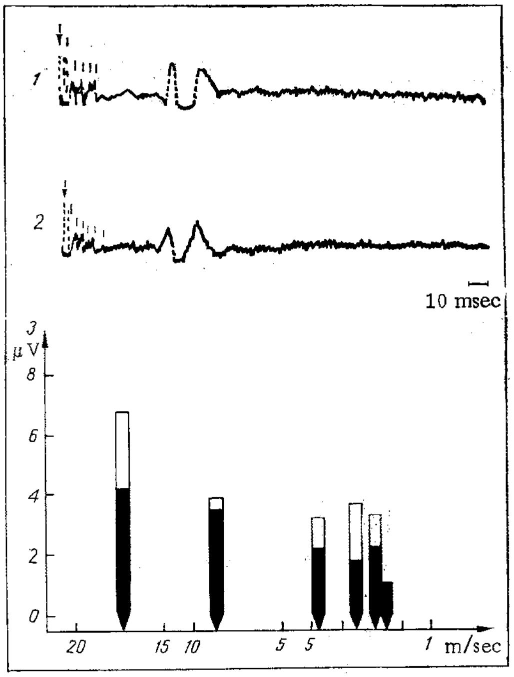

Fig. 3. Response of myelinated fibers of cutaneous nerve whose AP were distinguished from apparatus noise to heating. 1) Activity of averaged composite AP of cutaneous nerve at adaptation temperature of 32°C. Short lines above trace represent APs distinguished from apparatus noise. Arrow marks time of electrical stimulation. 2) Activity of same nerve during elevation of skin temperature by 10°C. 3) Graphic illustration of amplitudes of APs recorded in traces 1 and 2. Black portions of columns represent amplitudes of potentials during skin heating. Ordinate, amplitude of APs distinguished from noise (in μV); abscissa, conduction velocity (in m/sec).

EXPERIMENTAL RESULTS

Combined spontaneous activity was recorded from the whole trunk of the lateral cutaneous branch of the saphenous nerve. During heating the whole receptive field of this nerve by 10°C, no visible changes in activity were recorded in 13 experiments, but in 11 experiments activity was increased in frequency and amplitude (Fig. 1). This increase was often just as marked as during cooling [3]. During heating the skin relaxed, confirming data published previously [2].

The amplitude of the Aδ complex in response to heating the skin was virtually unchanged at frequencies of nerve stimulation of 5, 10, 15, and 25 Hz. At a frequency of antidromic stimulation of 3 Hz, AP usually was reduced by a very small amount (1.5-6.6% of the mean values of AP) (Fig. 2). Individual components of the A_γ AP changed considerably during heating (Fig. 2). This indicates that a small number of large myelinated fibers also takes part in the transmission of information on skin heating.

It was shown by a combination of computer and optical methods of distinguishing weak signals in the nerve from apparatus noise and the colliding impulses method that impulsation arises in fibers of the A_{δ_1} group (conduction velocity 30-14 m/sec) in response to skin heating (Fig. 3). Under these circumstances the response of diminution of AP increased with an increase in the frequency of antidromic nerve stimulation to reach a maximum at frequencies of 15-25 Hz. Among AP of the fibers belonging to this group only those which belonged to fibers of the modal groups were unchanged. The reason was that when the method of distinguishing signals from noise was used, high-voltage APs of the A_δ complex were limited in amplitude almost to the level of apparatus noise [4].

APs of fibers of the A_{δ_1} group (14-4 m/sec) were mainly reduced during skin heating, indicating an increase of activity in this group of fibers. This maximal decrease in the antidromic APs was recorded at frequencies of nerve stimulation of 3 and 5 Hz. Activity was inhibited in response to heating in individual groups of fibers within this range of conduction velocities (the antidromic AP increased in amplitude; Fig. 3). No correlation could be found between conduction velocity and inhibition of activity in response to heating.

Fibers of the "mixed" group (4-2 m/sec) were mainly excited during heating. The maximal decrease in AP took place during antidromic stimulation with a frequency of 5-10 Hz. In this group also there were individual groups of fibers whose activity was inhibited during skin heating (Fig. 3).

The experiments described above show that in nerves innervating the hairy skin of cats there is a relatively large number of myelinated fibers which conduct impulses from receptors during heating of the skin to 42°C with an increasing frequency (see Figs. 1 and 3). This conclusion is in agreement with observations of workers who used a sudden exposure to heat [13]. However, most investigators found either no change or a decrease in activity in response to heating [12, 9]. In the present experiments inhibition of spontaneous activity was found only in a very few fibers within the range of conduction velocities from 14 to 2 m/sec (Fig. 3). On the whole activity was unchanged or increased. This disagreement between the present results and those obtained by the authors cited above can be explained by the different experimental conditions. In the present experiments, despite the relatively slow rate of change of temperature (1°C/sec), the skin was heated from both sides. Under these circumstances the temperature gradient through the thickness of skin was minimal and the heat-insulating properties of the hair cover in this case were of no great significance. Under natural conditions such a rate of change of temperature in all layers of the skin following contact with a temperature stimulus is evidently never found. In the present experiments temperatures below the injury threshold were used. It may be that for the transmission of information about a nociceptive stimulus along myelinated fibers it is not the absolute value of the temperature of exposure which matters but the rate of its rise in the deep layers of the skin.

The A_δ AP complex was virtually unchanged in the present experiments (Fig. 2), whereas low-amplitude APs of fibers of the various groups distinguished from apparatus noise were considerably reduced in response to heating (Fig. 3). This difference can be explained by the fact that the A_δ-complex consists of APs of a large number of nerve fibers.

During heating, evidently, activity appears in only relatively few fibers (not more than 10%), forming the modal group. The possibility cannot be ruled out that the amplitude of the evoked A_δ AP of the modal group of fibers was unchanged because impulsation increased in some fibers forming this complex in response to heating, whereas in others it decreased. If the numbers of these fibers were approximately equal, the change in amplitude of the composite A_δ AP would not exceed the limits of error of measurement. The number of fibers whose APs were distinguished from apparatus noise was very small [4]. The percentage of active fibers during the action of the temperature stimulus was high in this case, so that the task of finding fibers along which impulses were transmitted during heating of the skin was facilitated (Fig. 3). Unlike the response to cooling, during heating of the skin no fibers with determined conduction velocities were found in which activity was inhibited. In a group of fibers (13.7-7.5 m/sec) in which activity was always inhibited in response to cooling, it was excited during heating [3].

In the group of "mixed" fibers, by contrast with the response to cooling [3], increased impulsation predominated during heating.

If the response of all groups of fibers studied to cooling [3] and heating is compared, it will be noted that many more fibers responded to heating and with a much higher mean spike frequency. This fact can be explained by increased sensitivity of the receptors to the stimulus [6], for the method of distinguishing signals from apparatus noise requires frequent repetition of receptor stimulation for the accumulation of results and subsequent averaging.

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PARTICIPATION OF CONTRACTILE ACTIVITY OF SKELETAL MUSCLE IN RESPONSE OF THE CIRCULATORY SYSTEM TO ORTHOSTASIS

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In experiments on anesthesized cats abolition of the contractile activity of the skeletal muscles by means of a muscle relaxant sharply increased the initial fall and substantially reduced the compensatory recovery of the arterial pressure (BP) during the orthostatic test (OT). The response of the cardiac output during OT was not significantly altered. An increase in BP was found, synchronized with the motor responses, and could be abolished by the muscle relaxant. It was shown by means of an aritifical circulation (by-passing the left ventricle) that compensatory constrictor responses of resistive vessels during OT are abolished by the muscle relaxant. In some experiments, administration of the muscle relaxant significantly increased the retention of blood in capacitive vessels.

KEY WORDS: orthostasis; contractile activity of skeletal muscle; resistive and capacitive vessels; retention of blood.

The role of skeletal muscle in the development of compensatory hemodynamic responses to orthostasis in man and animals has received little study. Although investigations have shown an increase in tone of skeletal muscles during the orthostatic test in man [12], the importance of this phenomenon for compensatory reactions of the circulatory system has virtually not been studied.

Interest in this problem is increased, first, by evidence that the "muscle pump" participates in the formation of certain systemic circulatory responses [5, 7] and, second, by the fact that orthostatic resistance is reduced by hypokinesia in man [4, 10] and after blocking of skeletal muscle activity in animals [3].

The objects of the present investigation were: 1) to compare the dynamics of changes in the arterial pressure (BP) and cardiac output (CO) during orthostasis when the contractile activity of the skeletal muscles was intact and excluded and 2) to determine the degree of participation of the resistive and capacitive vessels in the mechanism of the effect of contractile activity of skeletal muscle on the circulatory system during orthostasis.

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