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ACTIVITY IN MYELINATED CUTANEOUS NERVE FIBERS IN RESPONSE TO COOLING IN CATS

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UDC 612.815.1-06:612.592

By means of the colliding impulses method and methods improving the signal to noise ratio in antidromic action potentials recorded from a cutaneous nerve, afferent impulses in its fibers were analyzed in response to cooling in cats. Fibers of group $A\delta_1$ and $A\delta_2$ were shown to conduct impulses during cooling of the skin receptors. A small group of fibers with conduction velocities of 13.0-7.5 m/sec showed inhibition of activity in response to cooling. A group of "mixed" fibers mainly responded by inhibition of activity, and only a few fibers of this group responded by excitation to cooling of the skin receptors.

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

Afferent activity in response to cooling has been adequately studied in cutaneous nerves of animals of different species [8]. Whereas in primates thin myelinated fibers have been shown to participate in the transmission of excitation to cooling of the skin [9], in rats and cats their activity has been confirmed only in the case of cooling the skin of the scrotum and the dorsum of the nose [10, 11]. The writers found only one reference in which the response of mechanoreceptors with myelinated fibers of the hairy skin to cooling is described in cats [5]. In these experiments myelinated fibers gave a very short spike discharge with low frequency (10-20 spikes/sec). Among authors who have studied temperature reception there is no general agreement as regards the degree of participation of myelinated fibers of the hairy skin in the transmission of information about cooling. Some workers consider that myelinated fibers in general are not excited during cooling, whereas others have shown that these fibers, which are mechanoreceptors, give a very small discharge during cooling [6], and on that basis they are dubious of their role in the perception of temperature sensation. However, there is indirect evidence that the temperature sensitivity of the hairy skin in cats is equal to the sensitivity of the skin in primates [7].

The object of this investigation was to determine the degree of participation of thin myelinated fibers in the transmission of information about cooling of the whole receptor field of the hairy skin in cats.

EXPERIMENTAL METHOD

Experiments were carried out on nine adult cats anesthetized with hexobarbital. The common trunk of the saphenus nerve was divided in the region of the inguinal fold and placed on stimulating platinum electrodes. Conduction velocity along the nerve was disturbed proximally to the stimulating electrodes. The lateral cutaneous branch of the saphenus nerve was

Department of Bionics and Biocybernetics, Institute of Applied Mathematics and Cybernetics, N. I. Lobachevskii Gor'kii University. (Presented by Academician of the Academy of Medical Sciences of the USSR, V. N. Chernigovskii.) Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 86, No. 10, pp. 400-403, October, 1978. Original article submitted November 18, 1977.

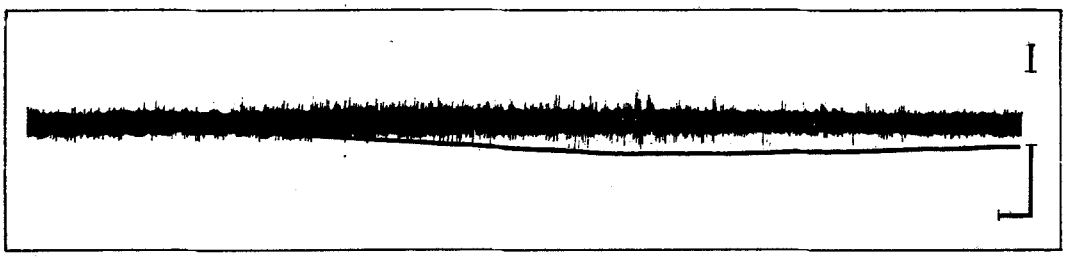

Fig. 1. Spontaneous impulsation recorded from cutaneous branch of saphenus nerve during cooling of its receptor field. Top curve — spontaneous activity in nerve; bottom curve — change in temperature of skin flap. Calibration: top 10°C; bottom 20 μV, 1 sec.

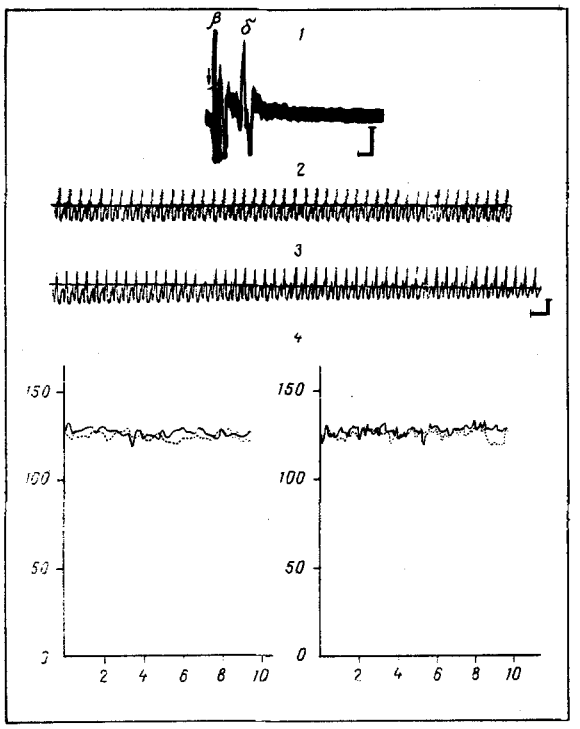

Fig. 2. Response of myelinated fibers of modal group of Aδ fibers to cooling of skin receptors. Abscissa, time (in sec); ordinate, amplitude of AP (in μV). 1) component AP of myelinated cutaneous nerve fibers. Conduction velocity in fibers of modal group Aδ 20.6 msec; 2) record of potential of Aδ fibers at temperatures of adaptation of receptors of 38°C. Frequency of antidromic stimulation 10/sec; 3) record of same potential during cooling of receptors by 10°C. Horizontal line in curves 2 and 3 shows state of tension of skin flap. Downward deflection denotes contraction; 4) graph showing amplitude of potentials of Aδ fibers recorded before (continuous line) and during (broken line) cooling of skin receptors with a frequency of antidromic stimulation on nerve of 5 (left) and 10 (right) pulses/sec. Calibration: for 1) 50 μV, 1 msec, for 2 and 3) 10 μV, 0.5 sec. Arrow denotes time of stimulation of nerve.

isolated in the region of the knee and placed on recording electrodes connected to the input of an AC amplifier. The isolated segments of the nerve were flooded with warm mineral oil. The temperature of the nerve was kept constant at 36-38°C.

An area of skin innervated by the branch to the knee joint was separated from the underlying tissues. One end of the flap was rigidly fixed, the other end connected to a steel plate and strain gauge, so that the tension of the skin could be measured. The skin flap was

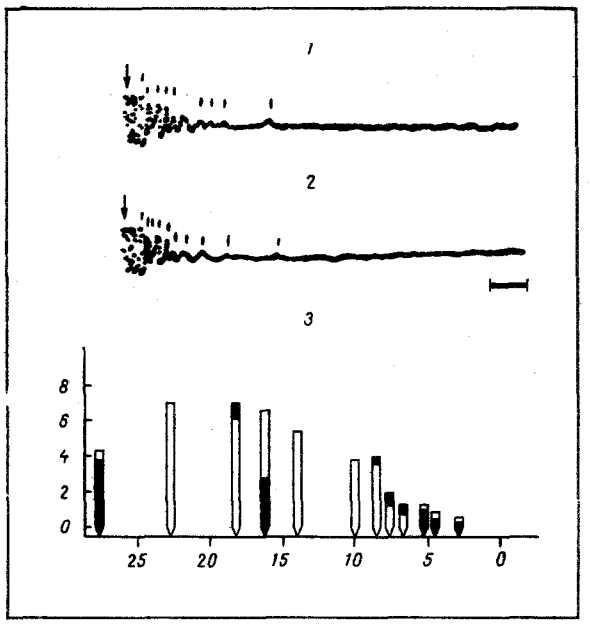

Fig. 3. Responses to cooling of cutaneous nerve fibers whose AP were distinguished from apparatus noise. Abscissa, conduction velocity (in m/sec); ordinate, amplitude of AP distinguished from noise (in μV). 1) Averaged component AP of cutaneous nerve recorded at adaptation temperature of 38°C. Short lines above curve indicate AP of modal group of Aδ fibers and AP which were distinguished from apparatus noise; 2) activity of same nerve after lowering of temperature of skin flap by 10°C; 3) amplitudes of AP recorded in 1 and 2, shown graphically. Black regions of columns indicate amplitude of potentials during cooling of skin receptors. Calibration for 1 and 2) 5 msec. Arrow indicates time of nerve stimulation.

placed inside a thermode with a temperature of 37°C. To prevent the flap from drying it was wrapped in a thin layer of gauze soaked in Ringer's solution and covered with mineral oil. The distance from the thermode to the surface of the skin was 0.5 mm.

The skin was cooled by changing the temperature of the water flowing through the thermode. The cold water temperature was chosen so that the skin temperature, measured on its hairy surface by an electrothermometer of TPM-1 type, changedat a speed of 1°C/sec. The skin was cooled from 37 to 27°C.

Afferent impulsation in the myelinated fibers of the cutaneous nerve was analyzed by the colliding impulses method together with computer and optical methods of isolation of weak signals in the nerve from apparatus noise [1, 3, 4]. Antidromic action potentials (AP) were evoked by square pulses 0.1 msec in duration. Their amplitude was chosen to be supramaximal for Aδ fibers. The frequency of nerve stimulation varied from 1.5 to 25 pulses/sec. Accumulation and subsequent averaging of the antidromic AP during cooling of the skin were carried out in short series lasting not more than 10 sec. After application of the next temperature stimulus and recording of antidromic AP an interval of 15 min was allowed from the time of restoration of the initial temperature, after which the recording was repeated. Antidromic AP recorded before and during cooling of the skin were compared. Orthodromic impulsation was judged from the changes in amplitude of the antidromic AP [1].

EXPERIMENTAL RESULTS

Combined activity of the cutaneous nerve fibers during cooling of the skin by 10°C increased in both frequency and amplitude (Fig. 1). It was impossible from the pattern of change of the combined activity to determine the type of nerve fibers concerned in the conduction of excitation, for the amplitude of AP in this case depended not only on the type of nerve fibers, but also on the mutual arrangement of the recording electrodes and the nerve fibers.

By means of the colliding impulses method it was possible to determine the types of nerve fibers along which the afferent activity spread, and its frequency. The component AP of myelinated fibers of the nerve (Fig. 2:1) and a series of records of one single Aδ complex before (Fig. 2: 2) and during (Fig. 2: 3) cooling of the skin flap are illustrated in Fig. 2. The visible component of the Aδ potential was virtually unchanged in response to cooling. A graph of changes in amplitude of the same potential is shown in Fig. 2: 4. The basic complex of the Aδ AP at a frequency of antidromic stimulation of 3-5 and 15-25 pulses/sec was virtually unchanged in amplitude (fluctuations of the mean value of AP before and during cooling were ±2-5%).

The Aδ fibers constituting the modal group have conduction velocities in different animals which vary from 28 to 14 m/sec [2]. The degree of participation of myelinated fibers with slower conduction velocities in the transmission of impulsation from the cooled skin flap was determined by the colliding impulses method together with the method of isolation of weak nerve signals from apparatus noise (Fig.3) [3]. Nerve fibers of group $A\delta_1$ (conduction velocities 30-14 m/sec) either did not respond to cooling of the skin receptors or increased their activity (Fig. 3); the maximal decrease in AP of the $A\delta_1$ fibers took place at a frequency of antidromic stimulation of 5 pulses/sec. AP which did not change their amplitude during cooling belonged most frequently to fibers composing the modal group of the visible Aδ complex. On the record this AP was almost limited to the level of apparatus noise, and for that reason changes in it could not be observed.

For fibers of the $A\delta_2$ group (14-4 m/sec) there was a fairly well demarcated subgroup with conduction velocities of 13.0-7.5 m/sec, whose AP as a rule increased in amplitude considerably (up to 40%) in response to cooling (Fig. 3). The increase in amplitude of AP could be explained by the existence of fibers which inhibit their activity in response to cooling of the skin. AP of fibers with conduction velocities higher and lower than those in this subgroup were always reduced during cooling. The slowest conducting fibers of the $A\delta_2$ group (5.0-4.0 m/sec) usually gave a maximal response of a reduction in AP (100%) to cooling of the skin. In this subgroup a maximal increase in amplitude of AP occurred at a frequency of antidromic stimulation of 10 pulses/sec. In the group of fibers with conduction velocity of 4-2 m/sec, which could include both myelinated and also unmyelinated (the group of "mixed" nerve fibers [4]) fibers, the response of an increase in amplitude of AP during cooling predominated at nearly all frequencies of nerve stimulation. In this group of fibers also, inhibition of spike activity in response to cooling thus predominates. Only a very few of these fibers responded by a brief increase in impulsation to cooling of the skin receptors.

In response to supramaximal electrical stimulation for Aδ fibers no deformation of the skin flap was observed, whereas during cooling it began to contract (Fig. 2: 1 and 2). These results confirm those obtained previously [2].

The experiments thus showed that myelinated fibers of group $A\delta_1$ and $A\delta_2$ conduct excitation during cooling of the receptors of the hairy skin in cats; only very few fibers with conduction velocities of 13.0-7.5 and 4.0-2.0 m/sec, moreover, inhibit their activity during cooling. The remaining fibers with conduction velocities within these ranges increase their impulsation in response to cooling.

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