

ACTIVITY IN UNMYELINATED CAT CUTANEOUS NERVE FIBERS IN RESPONSE TO COOLING

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It was shown by a combination of the colliding impulses method and the method of isolation of weak nerve signals from apparatus noise, that during cooling of the hairy skin in cats impulses arise in the majority of unmyelinated fibers belonging to groups C_1 and C_2 . In a smaller proportion of unmyelinated group C_2 fibers inhibition of spontaneous discharges takes place in response to cooling.

KEY WORDS: cutaneous nerve; unmyelinated fibers; cooling.

The role of unmyelinated fibers in transmission of information on skin cooling in cats can be taken as definitely proven [9, 12]. However, the relative numbers of fibers participating in the conduction of impulses during cooling and the range of their conduction velocities are not yet clear. According to Douglas and Ritchie [10], impulses arise during cooling in 70% of unmyelinated fibers of the modal group. Conversely, workers who have studied single unmyelinated fibers consider that only a very small proportion (1.5-5.3% of the number of fibers studied) transmits excitation only in response to cooling of receptors [8, 9, 11, 13]. At the same time, unmyelinated fibers responding both to mechanical and to temperature stimulation of receptors are known to exist. According to Bessou and Perl [8], for example, they accounted for 71% of 131 fibers studied by them. If the total number of unmyelinated fibers in a cat cutaneous nerve is taken to be 2000 [14], according to the specificity hypothesis, information on cooling of the skin of the limb will be transmitted by between 30 and 100 fibers. If fibers transmitting mechanical and cold stimuli are included, the number of fibers is increased to 1500.

All the investigations cited above were carried out on unmyelinated fibers with a conduction velocity largely between 1.5 and 0.7 m/sec. Fibers whose conduction velocity may be as low as 0.15 m/sec are known to exist in a cat's cutaneous nerve [6]. It was shown previously that nearly all afferent unmyelinated fibers in the cat cutaneous nerve conduct excitation in response to harmless mechanical stimulation of receptors [7].

The object of the present investigation was to determine the degree of participation of unmyelinated fibers of modal and nonmodal groups in the transmission of information about harmless cooling of the hairy skin in cats.

EXPERIMENTAL METHOD

Experiments were carried out on 11 adult cats anesthetized with hexobarbital. An area of skin innervated by the geniculate branch of the saphenous nerve was dissected from the underlying tissues and placed in a thermode which could change its temperature from 37 to 27°C at the rate of 1 °C/sec.

Afferent activity in the cutaneous nerve fibers was analyzed by a combination of the colliding impulses method and methods of isolating weak nerve signals from apparatus noise. The method of cooling the receptive field and methods of analysis of afferent discharges were described fully previously [3-7].

EXPERIMENTAL RESULTS

The type of nerve fibers which participate in the formation of the spontaneous discharge can be determined from the amplitude of the antidromic action potential (AP) evoked by electrical stimulation of the nerve. The amplitude of the antidromic component of the AP depends on the number of excited fibers in which, at that

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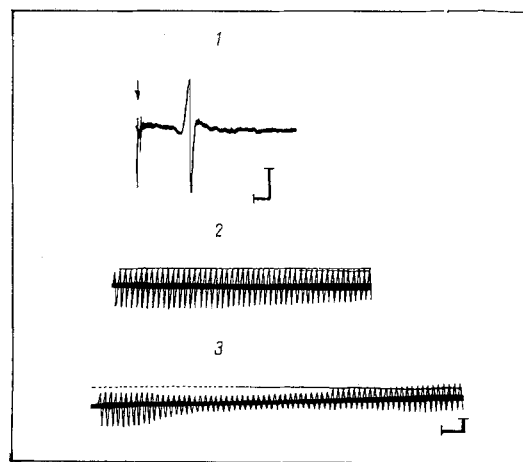


Fig. 1. Response of modal group of unmyelinated fibers to cooling of skin receptors. 1) Spike-wave (S-W) complex in cat cutaneous nerve. Velocity of conduction in fibers of modal group 1.4 m/sec; 2) recording of series of S-W complexes during electrical stimulation with a frequency of 5 Hz and temperature of adaptation of receptors 37°C; 3) series of antidromic S-W complexes during cooling of skin receptors. Frequency of electrical stimulation 5 Hz. Arrow indicates time of stimulation. Straight line above potentials shows state of tension of skin flap, and downward deflection denotes contraction. Calibration: for 1) 50 μ V, 10 msec; for 2 and 3) 50 μ V, 1 sec.

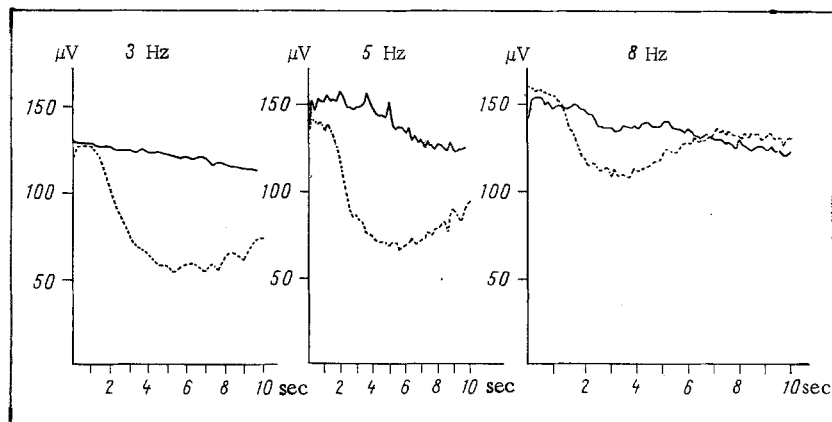


Fig. 2. Graph showing amplitudes of AP of modal group of unmyelinated fibers recorded before (continuous line) and during (broken line) cooling of receptors. Abscissa, time (in sec); ordinate, amplitude of AP (in μ V). Frequency of antidromic stimulation shown above each graph.

moment, there are no impulses coming from receptors. If impulses are coming from receptors, the amplitude of the antidromic AP will be smaller, in proportion to the number of fibers transmitting these impulses. If the frequency of stimulation is increased, the point of collision between the antidromic impulses and spontaneous impulses will be shifted from the interelectrode region and the amplitude of the antidromic AP will rise [13]. In the present experiments the amplitude of the antidromic AP of unmyelinated fibers evoked by electrical stimulation of the nerve was increased to 20% in response to the first electrical stimuli. The higher the frequency of antidromic stimulation, the faster the orthodromic impulses were displaced from the interelectrode region of the nerve, and the faster the amplitude of AP increased. With a frequency of stimulation of 8-10 Hz this acceleration of the increase in amplitude of AP ceased. This showed that the spontaneous discharge along unmyelinated fibers travels at frequencies of not more than 8-10 Hz.

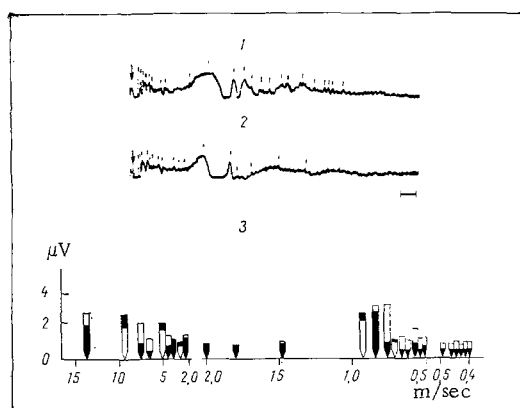


Fig. 3. Response of cutaneous nerve fibers whose AP were isolated from apparatus noise. Abscissa, conduction velocity (in m/sec); ordinate, amplitude of AP (in μV). 1) Trace showing averaged compound AP of cutaneous nerve at temperature of adaptation of 37°C . Short lines above curve indicate S-W complexes of modal group and potentials isolated from apparatus noise; 2) activity of same nerve during lowering of skin temperature by 10°C ; 3) graph of amplitudes and conduction velocities of AP recorded in traces 1 and 2. Black columns show amplitude of potentials during cooling. Arrow marks time of stimulation. Time marker 10 msec.

In response to electrical stimulation of a nerve changes are observed in the visible spike-wave (S-W) complex arising from contraction of pilomotor [2]. For the preparation of this paper experiments were specially selected in which no contractions of the skin flap were recorded during electrical stimulation of the nerve (Fig. 1). The absence of contraction of the skin during electrical stimulation of unmyelinated fibers was evidently associated with the small number or total absence of pilomotor in this particular region of the skin in certain animals. During cooling, however, the skin contracted (Fig. 1) and the visible S-W complex was reduced to 70% of its original amplitude (compare Figs. 1 and 2). These observations confirm previous results which showed that during cooling, deformation of bundles of collagen fibers takes place [1, 2]. Changes in tension of the collagen lead to excitation of mechanoreceptors connected with about 70% of unmyelinated fibers of the cutaneous nerve.

It was shown by means of a combination of the colliding impulses method [3] and methods of isolation of weak nerve signals from apparatus noise [4, 6] that all fibers of group C_1 (with conduction velocities of between 2 and 1 m/sec) change their activity during cooling. Mainly an increase in activity is observed in this group of fibers in response to cooling, although inhibition of spontaneous activity in certain groups of fibers is frequently found also (Fig. 3). No regular pattern could be discovered in the distribution of fibers of this group by conduction velocities depending on whether they increased or decreased their activity during cooling. A "mosaic" pattern of distribution of excitation appeared in the various fibers during cooling: Some fibers increased their activity during cooling, others decreased it (Fig. 3). Since the amplitude of the principal visible S-W complex during recording was limited almost to the level of apparatus noise [4], it was practically unchanged by cooling ($\pm 10\%$). However, the area occupied by this potential on the trace of nerve activity was considerably reduced. The decrease in area occupied by the visible S-W complex indicates that fibers of this complex also conduct excitation during cooling.

The response of fibers of group C_2 (1-0.3 m/sec) to cooling differed from responses of fibers of the previous group. During cooling the amplitude of AP of fibers of this group, isolated from noise, often increased. In some, however, the AP were reduced (Fig. 3). At low frequencies of antidromic stimulation (1.5-3 Hz) during cooling of the skin AP were generated that were not present during electrical stimulation of the nerve alone.

The appearance of antidromic AP can be explained by the existence of constant tonic activity in the fibers of this group, which was reduced during cooling of the skin receptors. Inhibition of spike activity was observed most frequently in fibers with the slowest conduction velocities (0.4-0.3 m/sec).

It was thus shown by the colliding impulses method that spontaneous tonic activity exists in unmyelinated cutaneous nerve fibers. In the fibers of the modal group the mean spontaneous discharge frequency did not exceed 8-10 spikes/sec, whereas in fibers of the C_2 group it could be higher. During cooling of the skin the

spontaneous discharge frequency in most fibers increases, and only in some of the thinnest unmyelinated fibers does it decrease. Between cooling the skin is known to contract because of shortening of collagen fibrils [1, 2]. The collagen fibers in the skin are not all strictly oriented and equal in length. As a result of their shortening in different parts of the skin, besides areas of increased tone there may also be areas of relaxation. Changes in activity during cooling evidently reflect the state of tone of the tissues surrounding the receptors.

During mechanical stimulation of the skin receptors up to 70% of fibers constituting the visible S-W complex [8-10] and all fibers of groups C₁ and C₂ whose AP were isolated from apparatus noise [7] become excited. During cooling of the skin up to 70% of fibers forming the visible S-W complex also become excited [5]. As the present investigation shows, all unmyelinated fibers whose AP were isolated from apparatus noise also alter the amplitude of their AP during cooling. In them, just as in fibers of the A_{δ1}, A_{δ2}, and "mixed" groups [4], in response to cooling a mosaic pattern of distribution of excitation arises. This "mosaic" pattern is individual for each animal. This change in the character of response of the mechanoreceptors is perhaps one of the features which distinguishes signals indicating a change in skin temperature.

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