PHYSIOLOGY

CHANGES IN ACTIVITY OF TACTILE RECEPTORS UNDER SYMPATHETIC INFLUENCES

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Sympathetic facilitatory influences on tactile receptors of phasic and static type and on fatigue processes, and the dependence of the effect on stretching of the skin have been demonstrated. It is suggested that a humoral agent is concerned in the production of this sympathetic effect.

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The study of the influence of the sympathetic system on cutaneous receptor activity has a long history. Several workers [3-6] observed permanent changes in cutaneous sensitivity after sympathectomy. In the 1930s, Orbeli [3] postulated the adaptive-trophic influence of the sympathetic system. However, these workers presented only indirect evidence of the existence of sympathetic influences on receptors, based on changes in reflex excitability demonstrated in experiments on animals or on verbal responses of human subjects.

A direct answer to the question of the character of sympathetic influences on receptors could be given by recording afferent impulses in cutaneous nerves. Zhirmunskaya [1] discovered that the sympathetic system has a positive adaptive-trophic action principally on cutaneous pain receptors. In 1955-56, Loewenstein [11, 12] made a detailed investigation of changes in the responses of tactile receptors of the frog's skin during electrical stimulation of the sympathetic chain. However, these results were obtained from highly stretched skin preparations when spontaneous activity was present, and they were determined primarily by phasic receptors. Stretching of the skin itself could be a factor modifying the activity of tactile receptors [7, 8].

Experiments were carried out to study the effect of the sympathetic system on responses of different types of tactile receptors, and on development of fatigue of these receptors during the application of a successive series of mechanical stimuli to unstretched and stretched pieces of frog's skin.

EXPERIMENTAL METHOD

Cutaneous nerves usually contain fast-conducting sympathetic fibers (3-6 m/sec). Experiments were carried out on a piece of skin taken from the dorsomedial surface of the frog's (Rana temporaria) thigh using pinpoint mechanical stimulation of tactile receptors. Stimulating electrodes were applied to the ramus communicans of the sympathetic chain below the 8th sympathetic ganglion. In this way preganglionic fibers of the sympathetic pathways leading to the investigated piece of skin were stimulated. The SIF-3 stimulator was used. Responses of the receptors were recorded by a pair of silver electrodes from the cutaneous branch (medial cutaneous nerve of the thigh) of the 10th spinal nerve.

EXPERIMENTAL RESULTS AND DISCUSSION

In the absence of spontaneous activity in the nerve from the unstretched skin preparation sympathetic influences on responses of phasic and static tactile receptors were studied during pinpoint mechanical stimulation. Stimulation of the sympathetic chain led to changes in the character of the spike responses of the tactile receptors. The sympathetic influences differed in degree for different types of discharges of the tactile receptors. The sympathetic influences differed in degree for different types of discharges of the tactile receptors. With unstretched skin the greatest changes were found in the slow-adapting discharge of

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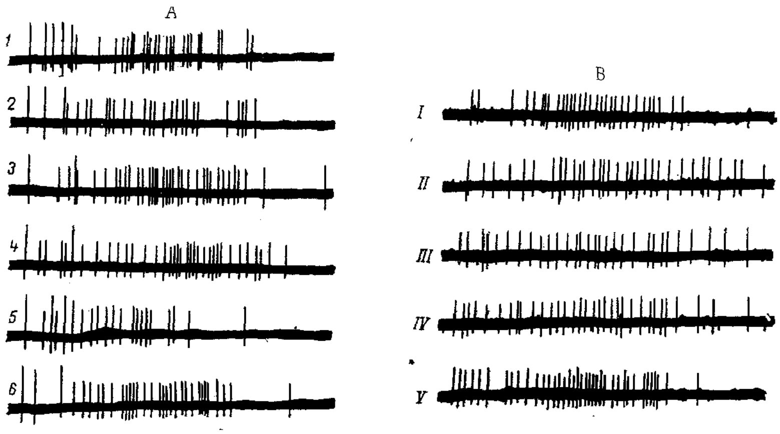

Fig. 1. Effect of electrical stimulation (10 Hz, 5 msec, 7 V, duration 5 sec) of sympathetic chain on spike response of tactile receptors. A: 1) initial response; 2, 3, 4, 5, and 6) responses 15, 30, 60, 180, and 300 sec respectively after stimulation of sympathetic chain; B: 1) initial response; II, III, IV, V) responses after stimulation of sympathetic chain. Explanation in text.

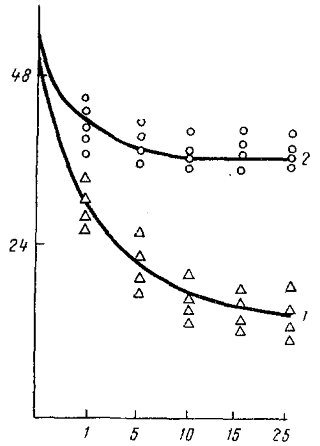

Fig. 2. Graph of fatigue of tactile receptors. Abscissa: number of repetitive stimuli; ordinate: number of spikes in discharge. 1) Before; 2) after stimulation of sympathetic nerve.

static type, which was considerably increased in duration, frequently accompanied by an increase in the number of spikes in the discharge. Under these conditions the fast-adapting phasic type of discharge showed no significant change.

The response of a tactile receptor point, consisting of impulses of two types, is illustrated in Fig. 1A: short-latency, fast-adapting high-voltage spikes of phasic type (120 μV) and lower-voltage (100 μV), slow-adapting spikes of static type. Stimulation of the sympathetic chain (7 V, 10 Hz, 5 msec, total duration 5 sec) led to an increase in the duration of the static discharge by 25% and in the number of spikes in the discharge by 35%. The sympathetic effect appeared after a relatively long latent period (30 sec) and was maintained for 3-5 min. Meanwhile the number of spikes in the phasic discharge not only did not increase, but on the contrary, decreased slightly while the duration of the discharge remained unchanged. An example of a sympathetic effect of different type, characterized merely by an increase in duration of the static discharge of the receptor, without any increase in the number of spikes, is illustrated in Fig. 1B. The development of this effect with time was identical with the first case.

The sympathetic system thus strengthens activity of the static tactile receptors, while acting principally on adaptive processes. These results suggested that the sympathetic system may counteract receptor fatigue. Repetitive stimulation is known to reduce the amplitude of responses of tactile receptors to each successive stimulus, the rate of decrease of the responses and the time of their subsequent recovery increasing with an increase in the number of preceding stimuli [10, 13].

In the present experiments a response of receptors was established to 25 repeated touches applied during the period of 30 sec before and after short (5 sec) stimulation of the sympathetic chain. Stimulation of this type considerably slowed the decrease in amplitude of the responses to a successive series of stimuli and quickened the recovery process. Whereas under normal conditions the response to the last touch stimulus had an amplitude of only 40-50% of the initial discharge, after sympathetic stimulation this response was reduced by only 20-25%. Under normal conditions recovery of the original amplitude of the response took place 10 min after cessation of adequate stimulation of the receptor, and stimulation of the sympathetic chain shortened this time to 4-5 min. This effect is clearly seen in Fig. 2, showing the static pattern of the results obtained. After stimulation of the sympathetic fibers the curve of fatigue of the tactile

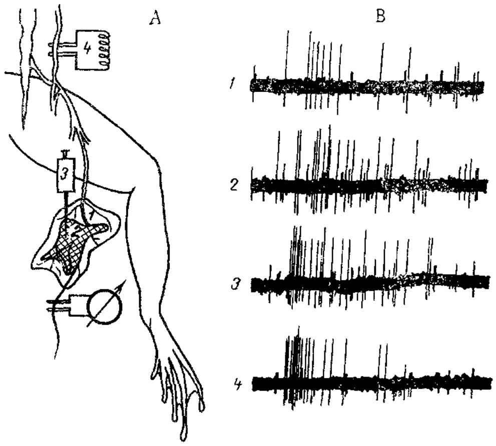

Fig. 3. Dynamics of responses of tactile receptors of "recipient" skin graft during electrical stimulation (10 Hz, 5 msec, 7 V, duration 10 sec) of sympathetic pathways of "donor" graft. A) Scheme of experiment; 1) "donor" skin graft; 2) "recipient" skin graft; 3) apparatus for mechanical stimulation; 4) electrodes for stimulation of sympathetic chain; B: 1) initial response of tactile receptors of "recipient" graft; 2, 3, 4) 40, 120, 180, and 300 sec respectively after stimulation of sympathetic chain.

receptors was marked by a smaller decline and a higher position of the end points than that of the intact animal.

The slow development and considerable duration of the sympathetic effect in these experiments, coupled with data published in the literature [9, 12], suggest that this effect takes place through the intervention of a special sympathetic mediator. This hypothesis was tested in experiments in which skin grafts cut from symmetrical dorsal and ventral surfaces of the frog's thighs were placed in contact by their inner surfaces. One such graft preserved its sympathetic nervous connection with the animal intact and acted as "donor," while the other, the "recipient," was completely isolated and the cutaneous nerve supplying it was placed on recording electrodes. The "recipient" graft was placed with its receptor side externally (Fig. 3A).

The experiments showed that activity of the tactile receptors of the recipient graft was modified after stimulation of the sympathetic nerves to the donor graft. The effect was seen most clearly in slightly stretched skin preparations, when spontaneous activity was present in the cutaneous nerve. Just as in the case of the unstretched preparation, the sympathetic effect varied in degree for different types of tactile receptors. One such experiment is illustrated in Fig. 3B. The initial response, as the tracings show, consisted of a discharge of two types of receptors: phasic and static. The first was characterized by high-amplitude spikes (120 μV), continuing throughout the period of action of the stimulus. Under the influence of stretching of the skin graft, a low-amplitude (20-30 μV) spontaneous spike activity appeared, independent of action of the adequate stimulus. The greatest sympathetic effects were shown by spontaneous spike discharges, increasing in number by 50%. The discharge of static type also underwent considerable changes: the number of spikes increased by 35% and the duration of the discharge by 20%. The phasic discharge showed definite, though transient effects. The duration of the phasic discharge was doubled, while the number of spikes was trebled. Sympathetic influences on the recipient graft appeared after a longer period (40-60 sec) and they were longer (up to 5 min) for static and spontaneous discharges than for phasic (up to 2 min).

Facilitation of responses of the tactile receptors of the recipient graft was the result of humoral transmission of the sympathetic effect. The neurohumoral nature of the effect was also confirmed by the fact that the cardiac contractions of the isolated frog's heart were strengthened by the action of perfusion fluid taken from the donor graft after stimulation of its sympathetic nerve supply. Application of adrenalin ($1 \cdot 10^{-8}$) to the skin led to an increase in the responses of the skin receptors similar to the sympathetic effect. This suggests that the humoral agent of the sympathetic influences may be adrenal in nature. Special investigations are necessary to identify it precisely.

The sympathetic system thus exercises efferent control over the activity of both types of cutaneous tactile receptors; in the manifestation of this control over phasic receptors, preliminary stretching of the skin is important. Sympathetic influences constitute one of the mechanisms determining the immunity of the receptors to fatigue during perception of repetitive stimuli.

The sympathetic action is expressed as an increase in the extent and duration of the afferent flow from one of the largest of the receptor surfaces, the animal's skin.

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