ROLE OF ANTIDROMIC INFLUENCES IN THE PERIPHERAL INTERACTION BETWEEN TACTILE RECEPTORS

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There are two aspects of the function of any receptor structure: the first, the most general, is the transformation of the energy of external stimulation into an electrical process and the second, the more special, is the communication of information.

The receptor itself is not a passive link in the transmission of information, but it selectively emphasizes the most important features of an adequate stimulus. For instance, certain tactile receptors are specialized for the receptor of only certain aspects of mechanical stimulation. Some of these—the "phase" receptors—react to active deformation of the skin, while others—the "static" receptors—also discharge at the moment of the deformation "plateau" [2, 5, 9, 10]. Often tactile receptors possessing different properties are united into a single functional group [8, 13], so that information concerning different aspects of an acting stimulus may probably be transmitted simultaneously.

Information from a single receptor is determined not only by its own activity, but also by the resultant of the combined activity of a group of receptors. Examples of this can be seen in the photoreceptors of the eye [4, 7] and the taste buds of the tongue [2].

A single tactile nerve fiber is usually highly ramified, and innervates several receptor points, forming a receptor field. Considerable overlapping of the receptor fields takes place. This anatomical organization probably creates favorable conditions for the peripheral interaction of the tactile receptors of the skin, and the object of the present investigation was to study this problem.

EXPERIMENTAL METHOD

Experiments were carried out on an isolated skin flap of the hind limb of the frog (Rana temporaria), supplied by the medial cutaneous branch of the femoral nerve. Pin point stimulation was produced with a hair (diameter 0.3 mm), moving freely through a hole in the center of the ends of a metal cylinder. The cylinder was fixed to a micromanipulator. Contact was produced by means of the micrometer screw of the micromanipulator, and continued for 1.5 sec. The impulses arising in response to contact with the receptor points of the skin were picked up from the nerve by a pair of silver electrodes, with an interelectrode distance of 3-4 mm. Recordings were made on an "Alvar" myocathograph. Electrical stimulation of the cutaneous nerve was provided by means of a type SIF-3 stimulator, and the stimulating electrodes were applied proximally to the detecting electrodes.

EXPERIMENTAL RESULTS AND DISCUSSION

The activity of the tactile receptor point investigated clearly changed after light mechanical stimulation of neighboring tactile receptors of the same receptor field. This change was shown both by a distinct reduction in the number of impulses in the discharge and by a change in the character of the responses to application of the same over-threshold adequate stimulus.

The dynamics of the responses of a tactile receptor point after light mechanical stimulation of neighboring receptors for 60 sec is shown in Fig. 1. A decrease in the number of impluses in the response of the investigated receptor was found 5 sec after discontinuing mechanical stimulation of the neighboring receptors, but the maximal decrease (by 70%) was observed 1-2 min later. The flow of impulses was most clearly inhibited in the middle part of the discharge, where the impulses almost completely disappeared. In this case the response assumed the character of the discharge of a "phase" receptor, because the same

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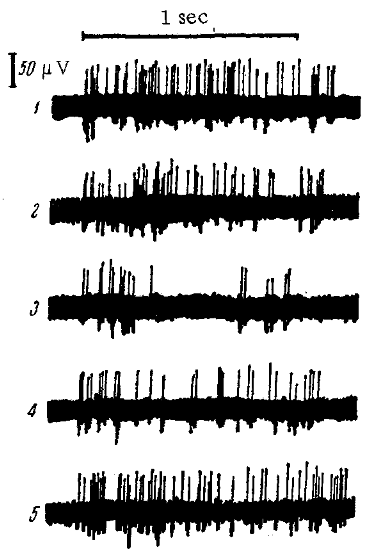

Fig. 1. Changes in responses of a single tactile receptor point under the influence of neighboring receptors of the same receptor field. 1) response of a receptor point to touching by a hair before mechanical stimulation of neighboring receptors; 2-5) the same responses 30 sec, and 1, 3, and 5 min after mechanical stimulation of neighboring points.

adequate stimulus evoked impulses only at the beginning and end of its action. The frequency of the impulses and the character of the discharge returned to their initial state after 4-5 min.

The activity of the investigated receptor changed not only after stimulation of receptors of the same field, but also after adequate stimulation of neighboring receptor fields supplied by another branch of the femoral nerve. In this case the character of the changes in the responses of the tactile receptor point was similar to that described above. Consequently, the activity of each tactile receptor during perception of an adequate stimulus depends on influences of surrounding receptor points belonging to the same or to neighboring receptor fields

One possible mechanism of the observed interaction may be antidromic influences spreading from excited receptors into neighboring branches of the nerve fiber.

To test this hypothesis experiments were carried out with electrical stimulation of the peripheral segment of the medial cutaneous branch of the femoral nerve.

The experimental results showed that electrical stimulation of the cutaneous nerve led to clear changes in the activity of the tactile receptors it supplied. The character of these changes depended on the parameters of the electrical stimulation.

Electrical stimuli of short duration (0.5 msec), but of high frequency (100 cps) led to marked inhibition of the activity of the tactile receptors. This effect was expressed both by a decrease in the total number of impulses and a change in the character of the responses. As Fig. 2 shows, touching with the hair excited two nerve fibers possessing different physiological characteristics. One fiber possessed impulses of high amplitude (190 μV) and a short latent period, and was adapted more rapidly. It responded at the beginning and end of the action of the stimulus and it could be regarded as a structure sensitive only to dynamic deformation (a "phase" receptor). The other fiber possessed impulses of lower amplitude (90 μV) and a longer latent period, and it responded mainly at the moment of the deformation "plateau." It was evidently a structure sensitive to static deformation.

The oscillograms (Fig. 2, A) show that the discharge of the fiber responding to static deformation was inhibited first and most severely. Its low-amplitude impulses almost disappeared during the first seconds after electrical stimulation of the nerve. During the next 3-4 min the number of high-amplitude impulses also fell by 40%. The activity returned to its initial level after 8-10 min.

When the cutaneous nerve was stimulated by electrical stimuli of long duration (7 msec) but low frequency (10 cps) the activity of the tactile receptors was usually intensified. It is clear from Fig. 2, B that 30 sec after stimulation of the nerve the number of impulses in the response increase by 40%, and returned to its initial level only gradually in the course of 10 min. It is interesting that changes in the activity of the tactile receptors of similar character of observed not only in response to antidromic stimulation of the nerve supplying them, but also to stimulation of the nerve supplying the neighboring receptor field. The effect of electrical stimulation of the cutaneous nerve was seen most clearly on the threshold responses of the tactile receptors.

It is clear from Fig. 3 that the frequency of the threshold response of the investigated receptor fell by 50% after electrical stimulation of the cutaneous nerve, whereas the response to an adequate stimulus ten times over the threshold level fell by only 25%.

Pin point tactile stimuli acting on a single receptor structure are rarely found in nature. Usually the adequate stimulus is a tangible surface, in which case many receptors belonging to the same or to several receptor fields are stimulated simultaneously. The tactile receptors may thus interact during perception of the stimulus. In fact, in the present experiments the activity of each tactile receptor depended on the state of the surrounding receptors, belonging to the same or to a neighboring receptor field. If these other

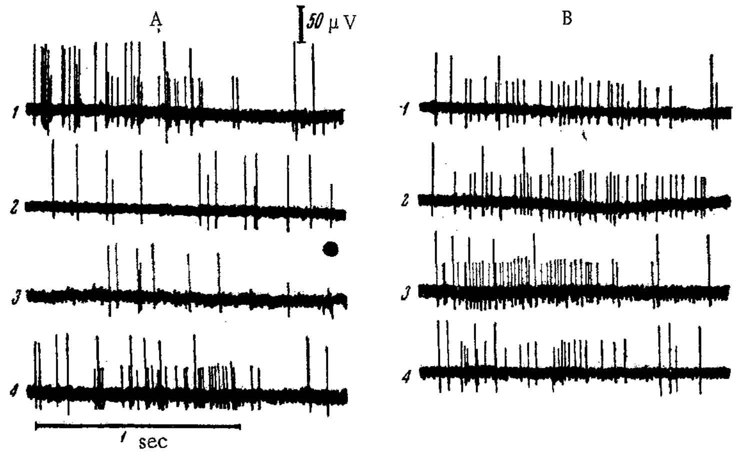

Fig. 2. Action of electrical stimulation of the peripheral end of a sensory nerve on responses of the tactile receptors supplied by it. A—electrical stimulation with parameters of 100 cps, 0.5 msec, 5 V, for 30 sec; B—electrical stimulation with parameters of 10 cps, 7 msec, 5 V for 30 sec; 1) responses of the receptor point to touching by a hair before electrical stimulation of the nerve, 2–4) the same responses 1, 5, and 10 min respectively after electrical stimulation of the nerve.

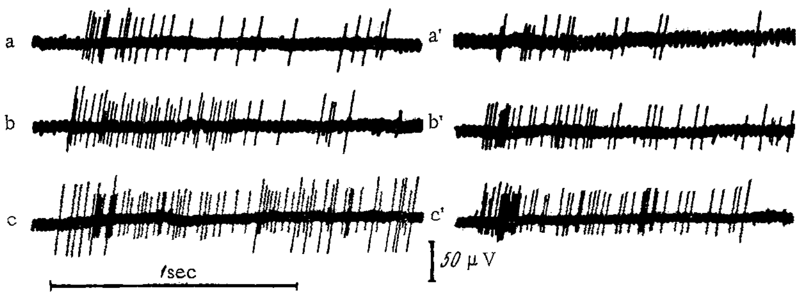

Fig. 3. Relationship between the effect of electrical stimulation of a sensory nerve and the amplitude of the adequate stimulus. a–c) responses of a tactile receptor point to touching by a hair with a weight of 0.003, 0.04, and 0.1 g respectively before electrical stimulation of the nerve; a'–c') the same responses 1 min after electrical stimulation of the nerve with parameters of 100 cps, 0.5 msec, 4 V, for 30 sec.

receptors were excited the activity of the investigated point was considerably inhibited. This inhibitory interaction between receptors was not a simple quantitative regulation of the afferent input, but was of more specific importance. As a result of this interaction, as we have seen, the "static" discharge of the receptor may assume a "phase" character.

A possible mechanism of the interaction between tactile receptors may be by antidromic influences spreading from excited receptors. The results of the experiments with electrical stimulation of the peripheral end of the cutaneous nerve confirmed this. Electrical stimulation of the nerve evoked clear changes in the activity of the tactile receptors. Depending on its parameters, both inhibition and intensification of their activity were observed. In all probability this effect was the result of antidromic influences spreading along the afferent fibers. Intensification of the activity of the tactile receptors during stimulation of the cutaneous nerve by electrical stimuli of long duration (7 msec) could be the result of excitation of the sympathetic fibers contained in it [11]. The fact that the changes in response to electrical stimulation of the cutaneous nerve took place in various directions indicates the regulatory importance of the antidromic influences. Such influences are not merely a laboratory fact, but they are one of the natural mechanisms of interaction between receptors. Cattell and Hoagland observed in cutaneous receptors [1] and Papuzzi and Cassella in the tactile receptors of the tongue [14] that an impulse from an excited receptor can only spread orthodromically, but can also be recorded in neighboring branches of the nerve fiber, which it reaches antidromically. The point of application of these antidromic influences is probably the region of the nerve endings "responsible" for the production of the speading impulses, where the conditions are suitable for post-tetanic facilitation or inhibition. This was confirmed by the experiments of Diamond and co-workers [3] and Loewenstein and Rathkamp [12], showing that antidromic influences change the conditions of formation of a moving impulse in the first node of Ranvier of a Paccinian corpuscle.

The possibility also is not ruled out that a mediator may be secreted in the region of the receptor endings as a result of antidromic influences [6]. This is probably the mechanism of the interaction occurring between receptors belonging to neighboring, overlapping receptor fields.

Hence, under the action of an adequate stimulus, complex processes of interaction take place in the tactile receptors. These determine the primary integration of information reaching the central nervous system. Both a quantitative, and a more specific regulation of the afferent input take place, emphasizing the spatial contract of the acting stimulus.

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