SOME PROPERTIES OF THE PACINIAN CORPUSCLES

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The properties of the Pacinian corpuscles have been intensively studied in recent years [1, 2, 7, 9, 10], but some aspects of these solitary mechanoreceptors have not received the attention of researchers.

The object of this article is to examine some of the special features distinguishing the Pacinian corpuscles.

EXPERIMENTAL METHOD

Experiments were carried out on solitary Pacinian corpuscles isolated from the mesentery of the small and large intestine of the cat. The corpuscles were kept in oxygenated Krebs–Henselwhite solution at 36-38°. The receptors were stimulated by mechanical impulses of different form, generated by specially made mechanical stimulators, and the amplitude of stimulation was accurately variable. Usually unipolar leads were used to record the potentials from the nerve fiber at its point of emergence from the capsule of the corpuscle. Sometimes bipolar leads were used and the position of the electrodes relative to the corpuscle was varied. In some experiments the capsule of the receptor was removed and the electrical activity was recorded from different parts of the nerve fiber inside the corpuscle. In certain cases the capsule was pierced by a metallic microelectrode and recordings were made from deep inside the corpuscle. To facilitate puncture, the capsule of the receptor was first treated with a solution of hyaluronidase and trypsin (0.5 mg/ml of each). The potentials were amplified by means of an ac amplifier and recorded photographically from the screen of a cathode-ray oscillograph. Usually 5-15 sweeps of the beam were recorded on one frame of the film, thus averaging the results. The frequency of rhythmic stimulation in these cases was 5-15 cps. The method was described in detail earlier [1-3].

EXPERIMENTAL RESULTS

Specimens of the responses of the Pacinian corpuscles obtained with different conditions of recording and stimulation are given in Fig. 1. If the duration of the stimulus was short (0.2-2 msec) the most typical form of response was that shown in Fig. 1A, I-IV. The amplitude of stimulation increased with each successive series of tracings. At a distance from the receptor only spike potentials (SP) of identical shape and amplitude could be seen (Fig. 1A, I). As the recording electrodes were moved toward the corpuscle fluctuation of the amplitude of the SP was observed (Fig. 1A, II). This was not always present, and hence was not an essential part of the response reaction. If the currents were recorded near still to the nerve ending, a receptor potential (RP) was recorded, with the SP in its ascending phase or at its apex. If fluctuations of the amplitude of the SP were present, they reached their maximum at a point nearest to the receptor. In Fig. 1A, III the RP can be seen clearly, increasing in amplitude with an increase in the strength of stimulation, with a fluctuating 1st phase of the SP (upward deflection of the beam) and a relatively steady 2nd phase (downward deflection passed over the electrode situated in the corpuscle itself, and the 2nd phase when it passed over the electrode situated approximately 8-10 mm from the receptor. A similar experiment (but with unipolar leads) is illustrated in Fig. 1A, IV. The latent period of the reaction was always shortened when the stimulus was strengthened, and in these circumstances the fluctuation in amplitude and latent period of the responses was reduced and disappeared completely.

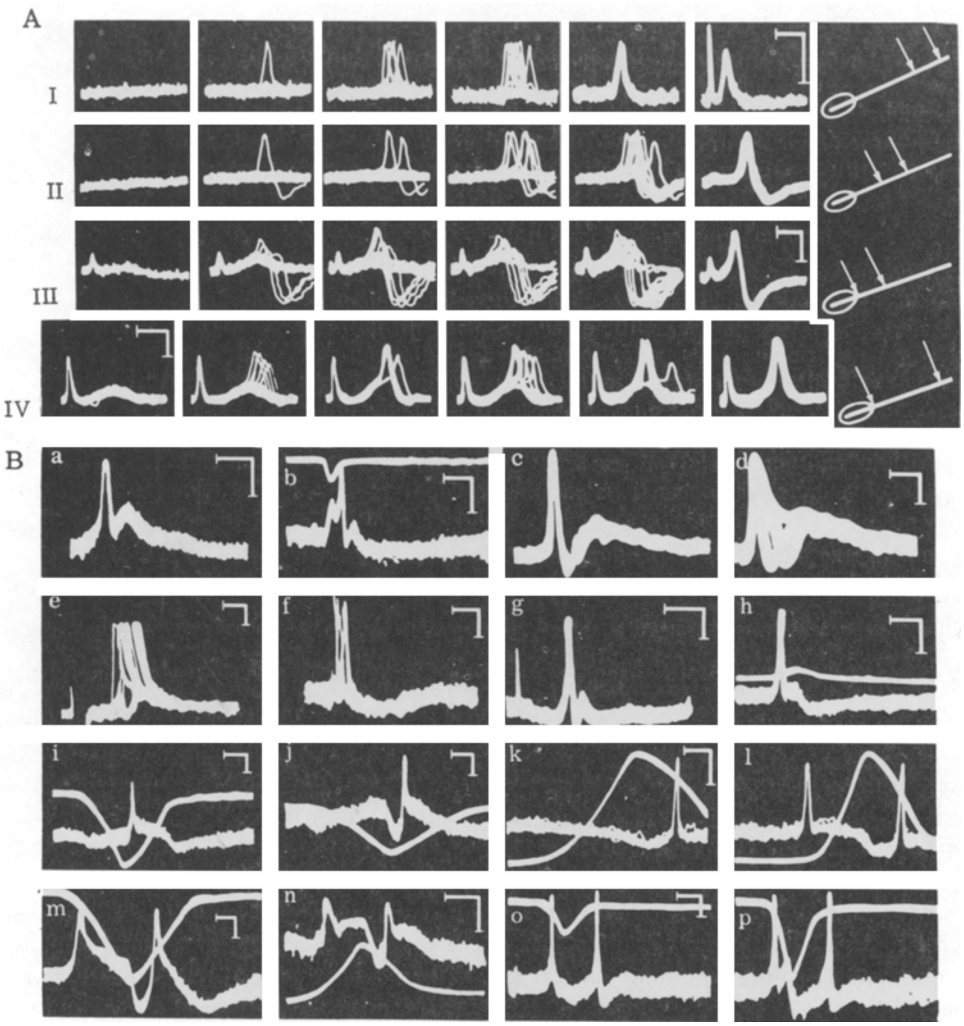

Fig. 1. Bioelectrical activity of Pacinian corpuscles with different conditions of recording (A) and examples of different response reactions of the Pacinian corpuscles (B). Scheme of recording is shown on the right. a) SP arises in the ascending part of the RP; b) in descending part of RP; c, d) changes in shape of SP with strengthening of stimulation; e) strong after-depolarization; f) after-hyperpolarization; g) appearance of RP and SP against a background of hyperpolarization; h) appearance of hyperpolarization after depolarization during a change in the direction of the stimulus; i) appearance of RP and SP against a background of developing hyperpolarization; j-p) appearance of high hyperpolarization against the background of RP during a change in the direction of movement of the stimulating rod. SP appears immediately after hyperpolarization. The magnitude of hyperpolarization is the greater, the greater the amplitude of the initial RP (see k and l, o and p).

All experiments were conducted on whole corpuscles. Potentials were recorded in the region of the 2nd and 3rd nodes of Ranvier. In experiment B the potentials were recorded with a microelectrode from the interior of the corpuscle. Tracings i, j, and m were obtained after the brief action of small doses of procaine. The second beam in oscillograms b and h-p recorded the mechanical stimulus. Regardless of the direction of recording, the stimulating rod always moved initially toward the corpuscle and then away from it. Time marker (in msec): I-III, 2; IV, 1.5; a, 4; b, 5; c-d, 2; e, 1; f, 5; g, 2; h, 2; i, 5; j, 5; k-l, 3; m, 5; n, 4; o-p, 5. Calibration (in μV): 1-2, 250; 3, 150; 4, 250; a, 25; b, 25; c-d, 250; e, 250; f, 15; g, 50; h, 50; i, 10; j, 15; k-l, 25; m, 10; n, 50; o-p, 10.

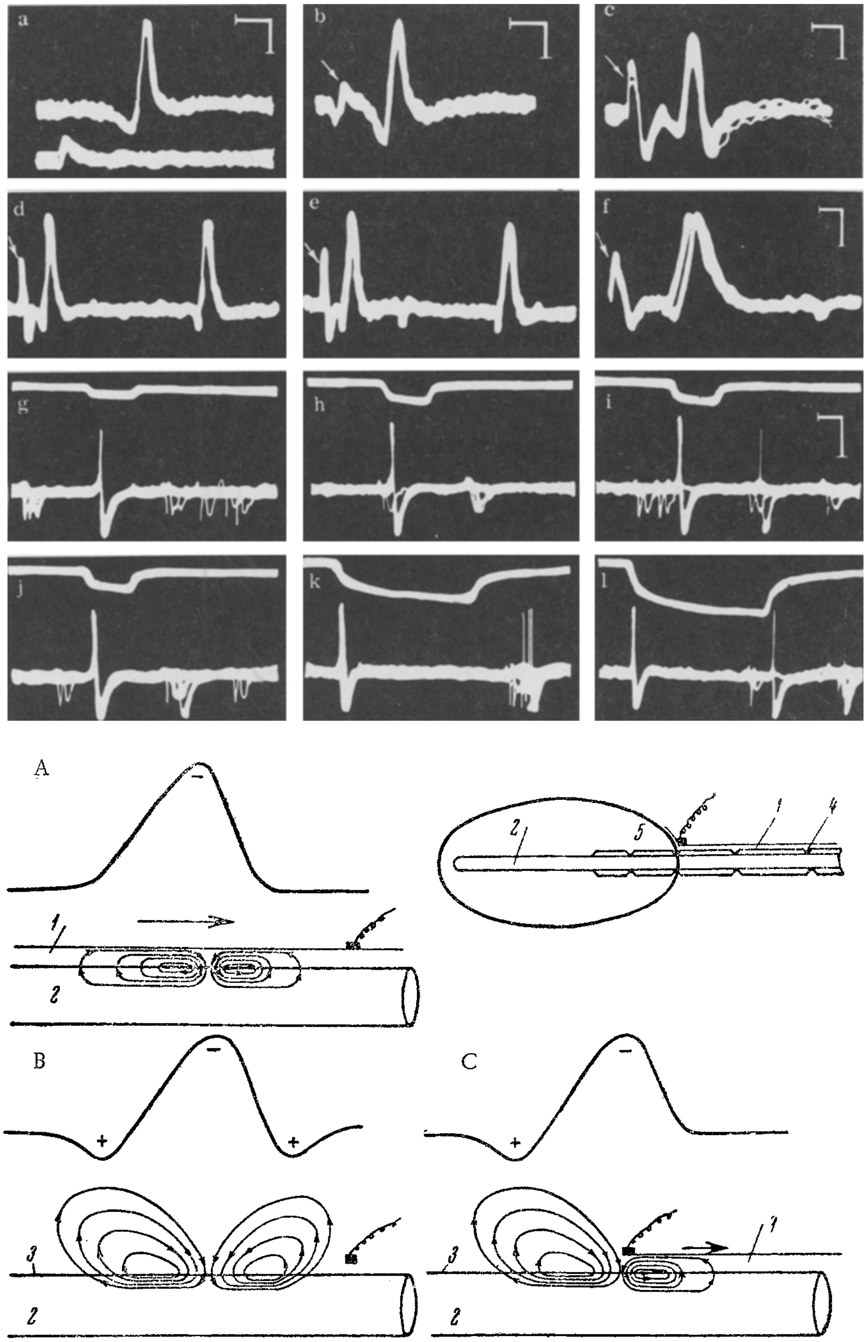

Fig. 2. Monophasic SP of Pacinian corpuscles. All oscillograms (except c) were obtained in experiments on intact corpuscles. Recordings obtained from the region of the 2nd and 3rd nodes of Ranvier. Tracings g-l were made with bipolar leads. c) Decapsulated corpuscle; electrode in the region of the 1st nodes of Ranvier. Recording of mechanical impulse: in a) bottom, in g-l) top. The arrows denote artefacts of stimulation. Time marker (in msec): a) 2.5; b) 2; c) 1; d-f) 1; g-l) 4. Calibration in all frames 50 μV. Below: scheme showing distribution of currents during recording of potentials in insulator (A), in electrolyte (B), and at junction of the two media (C). The last case corresponds to recording potentials from a Pacinian corpuscle. 1) Moist surface; 2) nerve conductor; 3) electrolyte; 4) node of Ranvier; 5) capsule of Pacinian corpuscle.

Specimens of other, less typical responses are shown in Fig. 1B. The origin of many of them is little understood. However, they have been included to demonstrate the complexity of the phenomena taking place during excitation in so simple and so well studied a receptor apparatus as the Pacinian corpuscle.

From our point of view the most interesting tracings in Fig. 1B are those demonstrating the variety in the relationships between the RP and SP. In contrast to the usual relationships between them (see Fig. 1B, a), in some oscillograms their relationships indicate that the development of the RP and SP proceeds independently (see Fig. 1B, j-p). This antagonism appeared only when an initial RP was present and it was revealed by the development of considerable hyperpolarization before the beginning of the second SP. The beginning of hyperpolarization coincided exactly with the moment of change in the direction of the triangular stimulus, and its amplitude was the greater the higher the initial RP (compare o and p in Fig. 1B).

In some experiments, despite the unipolar method of recording the potentials, the SP had two or three phases: positive—negative or positive—negative—positive (Fig. 2, a-f). Moreover, sometimes an initial positive phase could be recorded separately, with no subsequent wave of ordinary depolarization (see Fig. 2, e-f). Its appearance, like that of the SP itself, obeyed the "all or nothing" law (see Fig. 2, f).

As the recording electrode was moved away from the corpuscle, the multiphasic nature of the SP disappeared. It was concluded from this that its appearance was associated with the method of recording the potentials, and that the explanation of the multiphasic potentials could be given by the theory of recording of potentials in a three-dimensional conductor [12]. The schemes in Fig. 2A and B illustrate this statement; they are taken from Brazier's book [5] and they demonstrate a simplified distribution of the currents in a nerve conductor surrounded by a dielectric (see Fig. 2A), and by a solution of electrolyte (see Fig. 2B). The scheme of the receptor shows that in our experiments excitation spread along the nerve fiber both in the conducting medium (the capsule of the corpuscle) and in the insulator (oil), so that when the potentials were recorded near the corpuscle the SP was bound to be biphasic (see Fig. 2C). It is important to note that this distribution of the currents, and consequently, the positive—negative oscillation of potential was possible only if the node of Ranvier was situated at the boundary between the two media. If the node of Ranvier was distant from the corpuscle, the net result was the recording of the potentials in the insulator (see Fig. 2A). The primary positive wave of potential was therefore observed in by no means every experiment. The second positive wave appeared only if the tissues were torn around the nerve fiber, as a result of careless disection and also as a result of decapsulation of the nerve ending (see Fig. 2, b and c); ultimately the situation shown in Fig. 2B developed.

The arguments presented above were also confirmed by the very rare case illustrated in Fig. 2, g-l, when spontaneous rhythmic activity was observed in the receptor. The developing SP for some reason or other "froze" in the corpuscle and did not spread to the nerve fiber. Accordingly, the recorded responses greatly resembled the positive waves shown in Fig. 2, e-f. The fact that these positive responses were SP blocked in the corpuscle may be deduced from the trigger character of their formation, and also from the presence of a typical absolute refractory period after their appearance (Fig. 3, i and l). As the strength of stimulation increased, the blocked impulses, which hitherto had appeared at random (see Fig. 2, g), began to be grouped at the places where the ordinary SP subsequently appeared, and were apparently the precursors of the SP (see Fig. 2, h-l).

The initial positive phase of the SP, arising in obedience to the "all or nothing" law, was observed not only in the experiments on the whole corpuscles, but also in the case of a partially decapsulated receptor, when the potentials were recorded in the region of the 1st node of Ranvier (see Fig. 2, c). Consequently, its appearance was associated with the electrical activity in the nonmedullated part of the nerve ending, which meant that the traveling wave of excitation appeared in the nonmedullated part of the receptor and not in the region of the 1st nodes of Ranvier, as several authors previously suggested [7, 9, 10]. This conclusion is in agreement with recent data published in the literature [8, 13, 14]. We discuss this question of the existence of electrical excitation in the receptor membrane of the Pacinian corpuscles more fully elsewhere.

The positive phases of the SP, which are purely physical in nature, must be differentiated from the phenomena of true hyperpolarization of the nerve ending illustrated in Fig. 1B. In the latter cases the positive phase was completely dependent on the character of stimulation. By changing its character, but not changing the conditions of recording, it was possible in the same preparation to gradually increase or decrease, or to completely remove the hyperpolarization of the receptor. The origin of this physiological hyperpolarization remains largely unexplained.

During the investigation of the Pacinian corpuscles a further special feature was observed. During stimulation of a series of receptors bimodal SP were observed (see Fig. 3, a-c and e-i). In some experiments the second

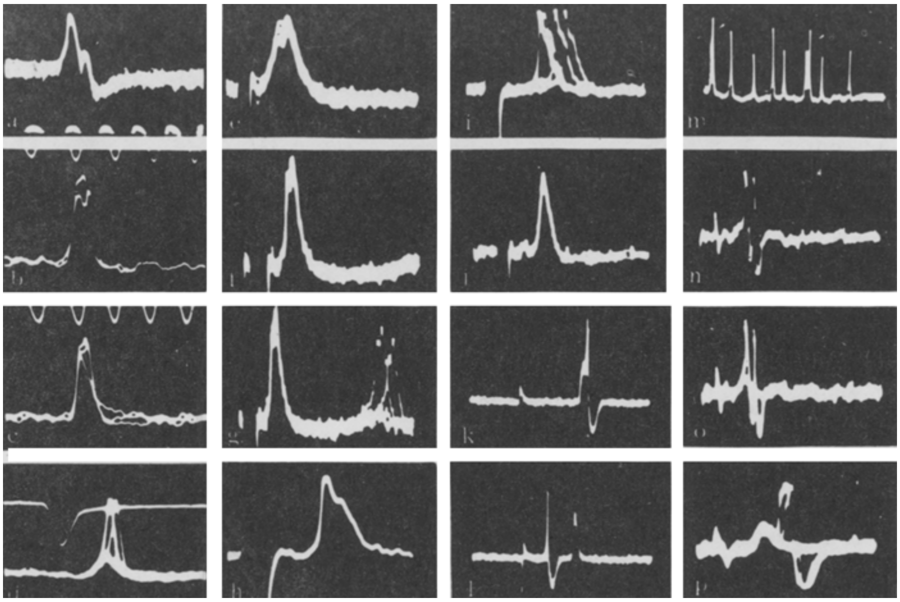

Fig. 3. Complex SP of Pacinian corpuscles. a) High-amplitude RP (marked by an arrow); b-d) modified forms of SP in the course of the experiment; i-j) ditto; e-h) bimodal SP, the form of the response not changing during the experiment. Trigger character of the appearance of these responses (g); k-m) responses of two receptors closely interconnected. In l the point of stimulation is changed from that in k; m) spontaneous activity of two corpuscles. The arrows point to double SP; n-o) double SP arising in one Pacinian corpuscle. The form of the response changes in the course of the experiment. Top beam in d) tracing of form of mechanical impulse. Time marker (in msec): a, 2; b-d, 2; e, 0.6; f-g, 1; h, 0.5; i-j, 1; k-l, 3; m, 5; n-o, 3; p, 2.5. Calibration (in μV): a, 50; b-d, 25; e, 125; f-g, 150; h, 250; i-j, 250; k-l, 50; m, 100; n-p, 100.

peak, although always appearing later, gradually changed as the strength of stimulation was varied, and its origin was connected with the presence of a high-amplitude RP (see Fib. 3, a) [1]. In other cases, in the course of the experiment a complex SP "split" (probably because of a change in the functional state of the preparation), demonstrating the presence of two SP (see Fig. 3, b-d). A similar picture was observed in the presence of two closely connected nerve endings (see Fig. 3, k-m). Only in these experiments could the aggregated SP be broken down into its individual elements easily by changing the direction, site, and strength of the blow. Finally, in a third group of experiments the bimodal SP, arising as usual in accordance with the "all or nothing" principle, could not be separated (see Fig, 3, e-h). The form of the responses in these cases remained unchanged with changes in the parameters of the mechanical stimulus, but sometimes it gradually assumed the ordinary appearance of the SP a short time after the beginning of the experiment (see Fig. 3, i-j). All attempts to find a morphological substratum for the reactions described above, using the ordinary histological methods, were unsuccessful. Externally these corpuscles were completely indistinguishable from the other receptors with the usual type of reaction.

Responses of a rather different type are shown in Fig. 3, n-p. In this case one receptor generated two separate SP. The time interval between them was so small that it absolutely ruled out the possibility that the two SP developed in the same fiber. In some Pacinian corpuscles, besides the medullated nerve fiber, another nonmedullated (of Timofeev) fiber is known to exist [4, 6, 11]. It may be that the experiment demonstrating this phenomenon (and, perhaps, some of the other experiments cited earlier) are cases of excitation of this second nerve fiber by the spike of the first, or even by the RP of its nerve ending (see Fig. 3, p). A more definite conclusion regarding this type of Pacinian corpuscle must evidently await an electron microscopic study of these structures.*

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SUMMARY

Experiments on isolated Pacinian corpuscles showed a wide variety of receptor reactions. These variations were due to the properties of the nerve-endings themselves, specific methods used for registering their activity, and the characteristics of the stimulus. Certain characteristics of mechanoreceptor reactions are discussed in greater detail (multiphasic SP, double SP).

The problems related to the site of origination of SP in Pacinian corpuscles and the correlations between RP and PP are also discussed.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.