FORMATION OF NEW PACINIAN CORPUSCLES AFTER ADDITIONAL SOMATIC INNERVATION OF THE MESENTERY

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After transplantation of a cutaneous nerve of the hind limb into the mesentery of the small intestine in cats (after preliminary removal of the Pacinian corpuscles from the mesentery), new encapsulated mechanoreceptors were observed to appear against the background of rapid regeneration of the fibers of the grafted nerve. Various stages of development of the Pacinian corpuscles were distinguished. The receptors formed under the conditions of this foreign innervation were indistinguishable in their morphological and functional properties from the ordinary type.

KEY WORDS: Pacinian corpuscles; mesentery of the small intestine; change of innervation.

The formation of receptor structures is an important aspect of the problem of formation of the specificity of nervous connections. During interaction between nerve fibers and various tissues, highly specialized nerve endings adapted for the reception of stimuli of a particular modality are formed. To study this problem a convenient model is the regeneration of peripheral nerves, when connections are restored between differentiated tissues and nerves. Despite the extensive literature on the regeneration of nerve fibers [2, 11, 13], few investigations have been made of regeneration of nerve endings, especially the encapsulated type, and the results are largely contradictory. Whereas some workers have observed regeneration of encapsulated receptors even under conditions of foreign innervation [5, 12, 14], others deny that such regeneration can take place [3, 15].

The object of this investigation was to study the possibility and times of appearance of new encapsulated mechanoreceptors (Pacinian corpuscles) after additional innervation of the mesentery of the cat's large intestine with a somatic sensory nerve (the saphenous nerve).

EXPERIMENTAL

Chronic experiments were carried out on 30 sexually mature cats and 15 kittens aged 1 month. Under sterile conditions the saphenous nerve was divided at the level of the knee and the mobilized proximal segment of the nerve, retaining its connection with the spinal cord, was passed beneath Poupart's ligament into the opened peritoneal cavity. The end of the nerve was then mechanically teased into thin bundles and passed by means of a Deschamps needle between the two layers of the peritoneum of the large intestine in a region either initially not containing Pacinian corpuscles or into areas of mesentery in which the receptors had been removed by enucleation. Splitting the nerves into bundles and removal of the receptors were carried out under the control of the MBS-2 microscope. In the postoperative period the animals received a parenteral course of vitamin B_1 to stimulate growth of the nerve fibers [9]. The animals were killed from 1 to 8 months after the operation. Material for histological investigation was fixed in 10% neutral formalin. Total preparations of the mesentery were impregnated with silver by the Bielschowsky–Gros method, dehydrated, and mounted in Canada balsam. To study connections between newly formed receptors

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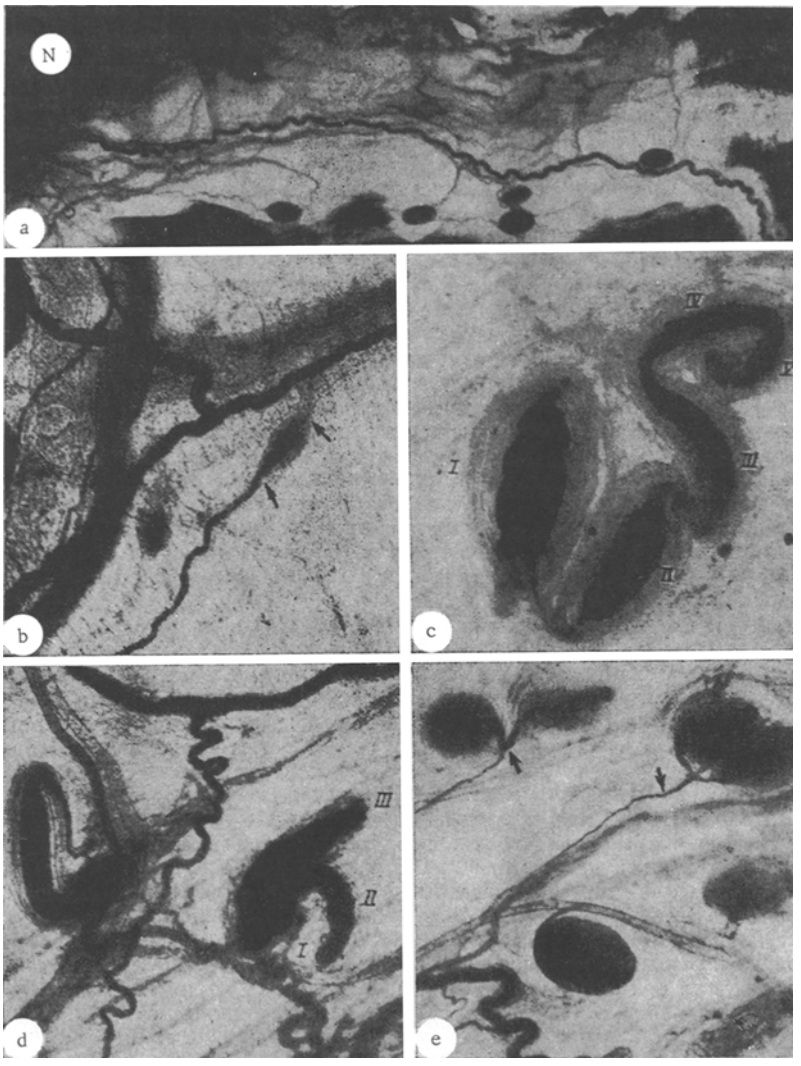

Fig. 1. Total preparations of Pacinian corpuscles in the mesentery of the cat's large intestine after transplantation of the saphenous nerve into it (Bielschowsky–Gros method): a) newly formed receptors 4 months after operation; N) saphenous nerve (10 ×); b) newly formed Pacinian corpuscle 5 months after operation with nerve fiber passing through it (70 ×); c) newly formed "bead-like" receptors consisting of five (I, II, III, IV, V) Pacinian corpuscles 4.5 months after the operation (70 ×); d) newly formed Pacinian corpuscles 4 months after operation: I, II, and III – three corpuscles in the "budding" stage (50 ×); e) newly formed Pacinian corpuscles on ends of dichotomously branched afferent fibers of a kitten 4 months after operation (50 ×).

and the grafted nerve, some preparations were impregnated more strongly. The specimens were examined under the phase-contrast microscope.

RESULTS

On investigation of those parts of the mesentery into which the saphenous nerve was grafted, the nerve was found to have taken well in the tissues of the mesentery. Sites of survival of the nerves were distinguished by their strong argentophilia and by the formation of amputation neuromas. Chaotic growth of nerve fibers in all directions, characteristic anastomoses between fibers, and branching of fibrils in a "goose-foot" pattern were observed in them. Both the neuromas and the grafted nerve trunk gave off numerous collaterals consisting of newly formed thin myelinated fibers, spreading in the tissues of the mesentery. Pools of

axoplasm were observed on the endings of the surviving nerve, some fibers terminated in bulbs of growth, and sometimes free nerve endings were found. This picture could be seen at all stages of survival of the nerves. However, starting from 3 months after transplantation of the saphenous nerve, Pacinian corpuscles numbering from two to 14 per animal were found on its terminal branches. Usually the largest of the collaterals given off by the saphenous nerve divided into several thinner branches ending in Pacinian corpuscles measuring 2000 × 700 μ (Fig. 1a). The diameter of the myelinated nerve fibers of the newly formed Pacinian corpuscles in the extracorpuscular part was indistinguishable from normal (4-15 μ); the thickness of the unmyelinated part of the afferent fiber was about 2-3 μ.

A study of the newly formed Pacinian corpuscles revealed marked evidence of polymorphism stuff as well as fully formed Pacinian corpuscles; many early forms were observed: these were distinguished by their small size (from 110 to 800 μ in length, from 85 to 670 μ in width), fewer layers of the outer capsule, and a concentration of cells with large nuclei at the site of the as yet undifferentiated inner bulb. These forms of receptors correspond to the Pacinian corpuscles described [1] in cat fetuses at the age of 7-8 weeks, in the prenatal period of development. During regeneration the Pacinian corpuscles thus repeat the stages [1] of histogenesis. The newly formed Pacinian corpuscles (Fig. 1b) often exhibited an interesting feature: fibers "en passant" through the receptor. The diameter of the fiber at the proximal end of this corpuscle was much larger (15 μ) than the diameter of the poorly myelinated fiber leaving the distal end of the receptor (5 μ). The possibility cannot be ruled out that these forms of receptors subsequently go on to form so-called bead-like Pacinian corpuscles, described as isolated findings in areas of skin with an increased functional load [7, 10]. Under ordinary conditions they are extremely rare in the cat mesentery. In the present experiments, however, in nearly every case of innervation of the mesentery by the cutaneous nerve chains of two or three encapsulated receptors were observed in which a nerve fiber, entering one of the extreme corpuscles of the chain and running through the inner bulb, then emerged and entered the subsequent corpuscles. Often these forms of receptors were found in more complicated variants, in which the distal Pacinian corpuscles, each with its own more or less well-defined capsule, were joined together by the surface layers of a common outer capsule (the phenomenon of polycapsularity) [7]. This phenomenon is illustrated by Fig. 1c, in which three distal Pacinian corpuscles (III, IV, V), differing in size and shape, lie on the same nerve fiber and the surface of their outer capsules are common, whereas in the two large proximal corpuscles (I, II) the outer capsules are separate and the nerve fiber can be clearly seen to cross from one receptor into the other. These findings are confirmation of the view that the "bead-like" forms are one stage in the process of budding of Pacinian corpuscles [7, 10], described as their method of multiplication [6-8]. Budding Pacinian corpuscles, with a common afferent fiber, were frequently observed in the specimens in the present experiments (Fig. 1d).

As might be expected, regeneration proceeded more intensively still in the young animals – kittens undergoing the operation at the age of 1 month. The appearance of new Pacinian corpuscles was observed as soon as 1.5 months after transplantation of the nerve into the mesentery, and in one animal the total number of corpuscles reached 22. Some of the many newly formed receptors with well formed inner bulbs appeared on dichotomously branched nerve fibers (Fig. 1e).

The forms of Pacinian corpuscles that demonstrate the processes of their formation are thus as follows: nerve fibers running "en passant" through Pacinian corpuscles, the numerous "bead-like" forms, and the budding receptors are evidence that during innervation of the tissues of the mesentery by a foreign sensory nerve a process of intensive formation of new Pacinian corpuscles takes place on the terminal branches of the grafted nerve. The normality of the new and completely formed Pacinian corpuscles was confirmed not only by morphological examination but also by the study of their functional characteristics by adequate electrophysiological methods [4]. During mechanical stimulation of these receptors, receptor potentials and spikes with latent periods of 0.2 to 0.5 msec, corresponding to the normal parameters of Pacinian corpuscles, were recorded.

The results indicate that after transplantation of a cutaneous nerve into the mesentery the fibers of the surviving nerve regenerate rapidly and this is accompanied by the organization of their endings as highly specialized encapsulated mechanoreceptors, characteristic of that tissue. It must be emphasized that newly formed receptors were found only on the terminal branches of the transplanted nerve. In a control series of experiments (observations lasting 3 to 8 months) no regeneration of Pacinian corpuscles was observed on nerve fibers remaining after enucleation of these receptors [16]. In the case of transplantation of a large trunk of a sensory nerve, which under normal conditions in the hairy part of the skin of the leg gives rise to a minimal number of Pacinian corpuscles, into the mesentery as a result of considerable regeneration of the nerve fibers, their number per unit area of tissue increases. Because of this, according to the

concept of Zika and Singer [17], the innervation threshold, i.e., the minimal number of nerve fibers required for regeneration and the formation of new receptors on the terminal branches of the transplanted nerve, is reached.

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