ON THE RELATION BETWEEN THE MOTOR FUNCTION OF THE INTESTINE AND THE GRADIENT OF ITS NERVOUS ELEMENTS

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In a number of studies carried out in the laboratory of Kh. S. Koshtoyants, [2,4,8] and devoted to the motor function of the small and large intestine, a certain step by step gradient of muscular activity was found to exist throughout the length of the digestive tract.

There are also reports in the literature [7,13,20,22], according to which the intramural nervous apparatus of the intestine in various animals and in man is characterized by a peculiar structure and by the uneven distribution of its nervous elements. In particular the investigations of B. I. Lavrent'ev and his co-workers [5] became widely known, in the course of which the authors were able to show that, in a number of animals, cells of Dogiel type I predominated in the cranial and caudal part of the gastrointestinal tract, whereas in the central part cells of Dogiel type II were predominant. It could further be shown that the gradient of the mechanoreceptors corresponds, as a whole, to the location of Dogiel type I cells, and that of chemoreceptors to the arrangement of Dogiel type II cells. [12].

On the basis of these facts a number of authors [3,4,7,16,18,19,21] postulated a close relation between the automatic movements of the intestine and its intramural innervation, although they did not exclude other factors or accepted the myoneurogenic theory [2,16,18].

It was the aim of the present paper to establish whether a certain relation exists between the character of the intestinal motor activity and the structure of the intramural nervous apparatus in the intestine.

TABLE 1. Features Characterizing the Motor Function in Different Sections of the Intestine in the Experimental Rabbits (Average Values)

Section of intestine	No of contractions per min	Amplitude of contractions (in mm)	No of tonic contractions per min
Duodenum	18	6.1	1.8
Jejunum	13.2	4.3	1.5'
Ileum	11.7	4.1	0.9
Cecum	3.8	3.1	0.5
Colon	4.3	3.2	0.8
Rectum	9.2	3.8	0.9

METHOD

The experiments were carried out on 38 male rabbits weighing between 1100 and 1500 g. The animals of the first group (20 rabbits) were immobilized by transection of the spinal cord at the level of the 7th cervical vertebra and were placed into a special cask in which a permanent temperature was maintained. The abdominal cavity was opened. A bottomless beaker was attached to the abdominal wound by means of a pursestring suture and filled with Ringer-Locke solution warmed up to 37° C. Single loops of the duodenum, jejunum, ileum, cecum, colon and rectum were pulled out into the beaker. The spontaneous movements of the loops were recorded on a kymograph by means of an Engelmann lever. 102 experiments were performed in the manner described above.

In the second group of animals (18 rabbits) the sections of the intestine mentioned above were stained with methylene blue by the method of Dogiel-Vorob'ev to demonstrate their intramural nerve plexuses. The finished preparations were investigated under a binocular lens and under the microscope. The number of ganglion cells in the nervous plexus of the muscular layer was established in an area of 1 cm^2 by means of a micrometric grating. The average number of ganglion cells along the mesenteric and along the free edge of the gut was calculated from a number of counts.

RESULTS

Like other authors [2,4,8,21] we took the following features into account: the species of the animal, its weight, prolonged (42-58 days) feeding of a monotonous vegetable diet, and a permanent body temperature during the experiment.

Our experiments revealed that the peristaltic movements in various parts of the rabbit intestine (Fig. 1, Table 1) are of relatively permanent character.

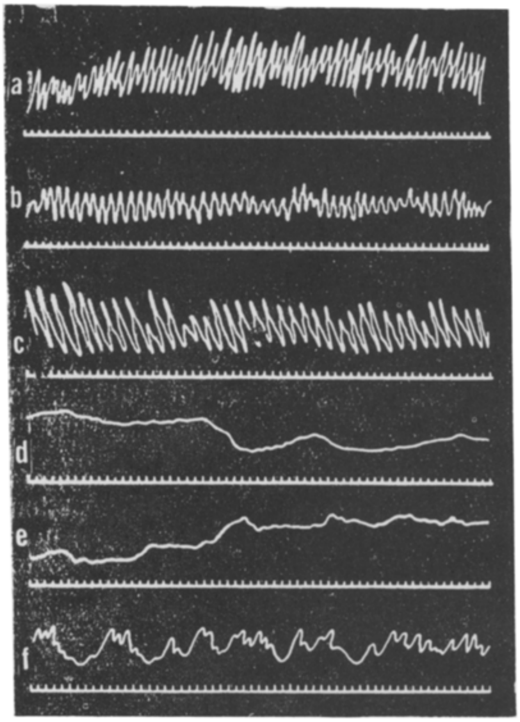

Fig. 1. Recording of movements of various portions of the intestines of a rabbit. a) Of the duodenum; b) of the empty intestine; c) of the iliac intestine; d) of the caecum; e) of the colon; f) of the rectum. A time scale is given under each curve (5 seconds).

In the duodenum (Fig. 1,a) the peristalsis is characterized by the greatest frequency and the highest amplitude of contractions and by the large number of tonic waves per min.

In the jejunum (Fig. 1,b) and ileum (Fig. 1,c) the values, mentioned above, gradually decrease as one proceeds towards the cecum, (Fig. 1,d) where they are lowest of all. The contractions of the cecum, which can be observed altogether for 5-7 min, alternate with prolonged (60-90 min) periods of relative rest. The peristalsis of the colon (Fig. 1,e) closely resembles that of the cecum, with the only difference that here the periods of "work" are somewhat longer, and last 10-15 min. Contractions of similar character in the proximal part of the colon were observed by means of the radiological method, [17], and in chronic experiments on dogs with an isolated colon section [11]. During the contractions of the rectum the lumen of the gut is gradually narrowed by consecutive waves of tonic contractions, the amplitude of which increases, whereas the tonus of the intestine shows a slight decrease. This is followed by a slow relaxation of the gut and the lumen gradually regains its original diameter. (Fig. 1,f). Contractions of this type enhance the progress of individual feces portions towards the anus.

Investigations carried out in the laboratory of Kh.S. Koshtoyants have shown [2,4,8], that the resorption of nutrient substances, - a process requiring a certain time - takes place mainly in those sections in which the motor activity is less intensive. In those sections of the intestine, in which contractions occur with greater frequency, a more active mechanical processing of the nutrient material takes place, and the progress of the intestinal contents towards the lower sections is accelerated.

Our findings concerning the character of the motor function in different sections of the rabbit intestine are consistent with the results of Kh.S Koshtoyants and co-workers [2,4,8], and are in contradiction to the conception of Alvarez [15] according to which the physiological activity of intestinal sections decreases in reverse proportion to their relative distance from the pylorus.

In the next series of experiments we studied the structure of the nerve plexuses in the intestinal wall. Here we found - in agreement with the results of other authors [5,6,7,13,20,22] - three main nerve plexuses: a subserous, a muscular and a submucous plexus. The structure of the muscular nerve plexus was studied in greater detail, as this plexus bears a direct relation to the motor function of the intestinal tract. (Fig. 2).

In the duodenum (Fig. 2,a) this plexus consists of nerve strands which cross each other, forming a rather wide trapezoid or rectangular network, the meshes of which are stretched along the intestinal axis. Between these meshes smaller meshes of angular oval shape, arranged in various directions can be seen. 37-55 meshes can be found per cm^2 of surface; their number increases, and their size correspondingly decreases towards the mesenteric edge. At the points where the nerve strands cross each other, ganglia, mainly of elongated shape, and containing 20-30 nerve cells each, can be found. In some places the ganglia and strands of the nerve plexus in the muscular layer emit short processes, covered by small groups of ganglion cells. The total number of nerve cells per cm^2 of duodenal surface varies from 2280 along the free edge to 3500 along the mesenteric edge.

The nerve plexus in the muscular layer of the jejunum (Fig. 2,b) is distinguished by the smaller size of the meshes. The ganglia are mainly elongated and spindle-shaped; the strands connecting them have a thickness between 15 and 23μ. The total number of nerve cells increases from the free edge (2088) to the mesenteric edge (2900).

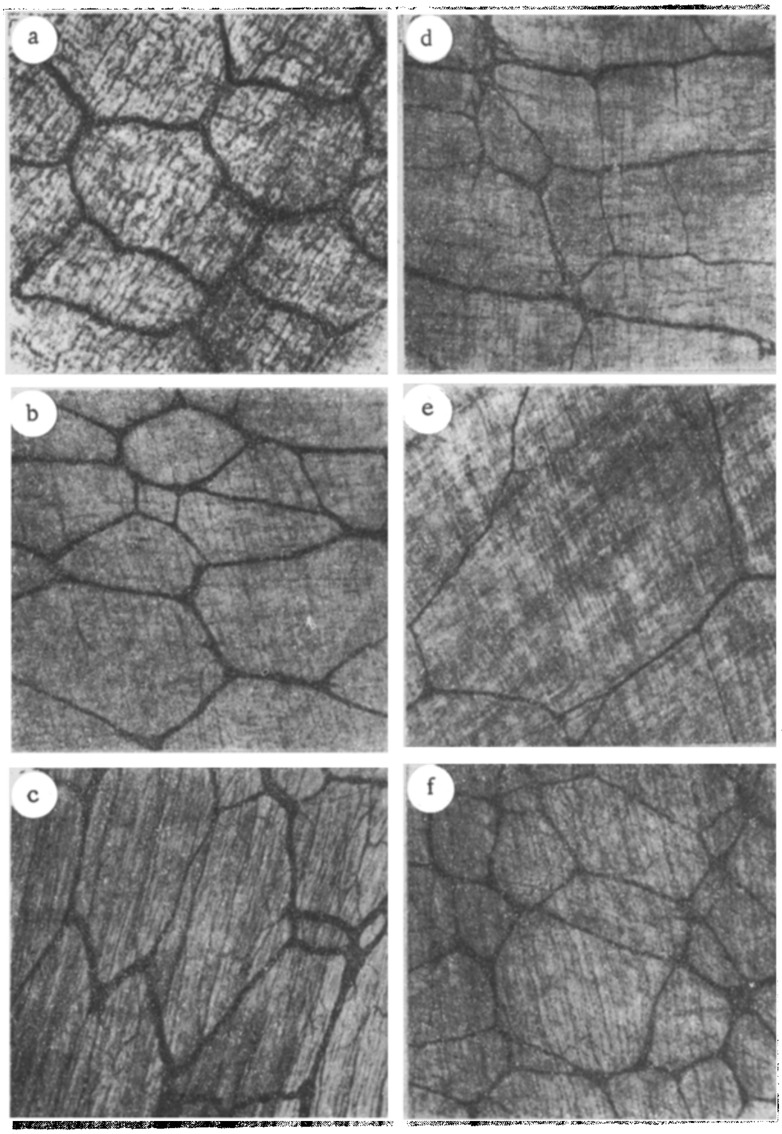

Fig. 2. The structure of the nerve plexus in the muscular layer of different sections of the rabbit intestine. Staining with methylene blue according to Dogiel-Vorob'ev. Microphotograph. Eye piece ×7; objective ×24; Microsummar; The photographs are arranged corresponding to the longitudinal axis of the intestine. a) Duodenum; b) jejunum; c) ileum; d) cecum; e) colon (haustrum); f) rectum.

In the plexus in the muscular layer of the ileum small meshes of elongated oval shape predominate (Fig. 2,c). Additional ganglia can frequently be found outside the meshes. In the region of the free edge of the ileum 2000 nerve cells, and along the mesenteric edge 2500 nerve cells can be found per cm^2.

The Auerbach plexus in the central part of the cecum is of somewhat different structure. In the region of the haustra it consists of a widemeshed network (Fig. 2,d). The meshes (between 11 and 21 per cm^2) have the shape of elongated triangles or irregular rectangles. Their size ($340 \times 140\ \mu$) is much smaller in the region of the taeniae

(150 × 70 μ). The strands of the plexus are thicker than in the higher sections of the intestine. The ganglia have numerous processes. On the average, 1760 nerve cells can be found per cm^2.

TABLE 2. Comparative Data, Characterizing the Nervous Elements in Different Sections of the Intestine.

Section of the intestine	Number		Size of meshes	Thickness of nerve strands
	of nerve cells per cm^2 along the mesenteric edge	of meshes per cm^2	in μ	
Duodenum	3500	37-55	From 80 × 60 to 280 × 110	24-40
Jejunum	2900	30-46	From 130 × 80 to 220 × 100	15-23
Ileum	2500	56-65	From 100 × 40 to 200 × 40	15-20
Cecum	1760	11-21	From 150 × 70 to 340 × 140	18-30
Colon	3375	25-28	From 120 × 150 to 120 × 300	10-60
Rectum	2940	72-81	From 50 × 60 to 130 × 40	10-25

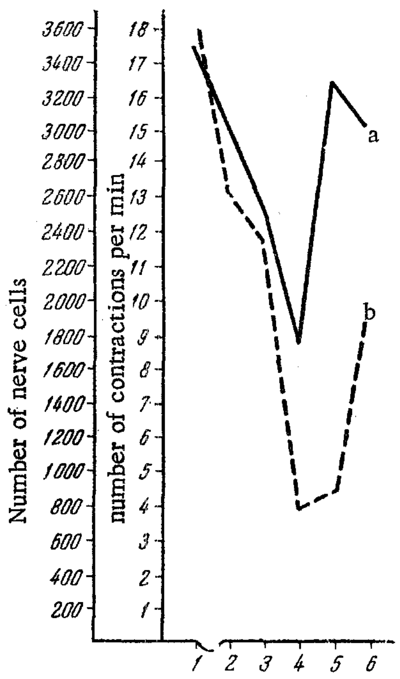

Fig. 3. Curves illustrating the relation between the gradient of the nervous elements in the rabbit intestine a) and its motor function b) (mean values). Sections of the intestine: 1) duodenum; 2) jejunum; 3) ileum; 4) cecum; 5) colon; 6) rectum.

In the colon the meshes of the muscular plexus show an uneven distribution. In the region of the haustra (Fig. 2,e) they are mainly of rhomboid shape, the longitudinal axis of the rhomboids stands almost perpendicular to the main axis of the intestine. In the region of the taeniae all plexuses consist of narrow and dense meshes. Here the meshes are frequently of oval shape and the ganglia of stellate shape with 4-6 processes. The total number of nerve cells per cm^2 reaches 3375. The meshes in the muscular nerve plexus of the rectum are distinguished by a great variety in shape and size. Here, the number of meshes is greatest compared to other sections of the intestine (from 72 to 81 per cm^2), but the strands are thinner (10-25μ). The ganglia are large, have numerous processes and a varying shape. The total number of nerve cells decreases slightly from the mesenteric edge of the intestine (2940) to the free edge (2804) and also towards the anus (2640).

More detailed data concerning the comparative structure and distribution of the nervous elements in different parts of the intestine are set forth in Table 2.

The finer structure and the character of the distribution of the ganglial elements in the muscular nerve plexuses in different sections of the rabbit intestine thus show a regular and characteristic sequence.

The greatest number of nerve cells: 3500 - can be found in the duodenum. In the regions of the jejunum (2900) and ileum (2500) investigated by us, the number of nerve cells decreases progressively towards the cecum, (1760) where it is lowest. Then the number of nerve cells gradually increases in the colon sections, (3375) to decrease again in the rectum (2940). A similar regular arrangement of the nerve cells of the intestinal tract was observed by Ohkubo [22] in monkeys.

Experiments involving the transplantation of the small into the large intestine [8] and of the appendix into the small intestine [12] showed that far reaching morphological changes, including the transformation of their intramural nervous plexuses, take place in these organs. These observations can to a certain degree, serve as argument in support of the view that our findings concerning the step-wise sequence in the number of ganglial elements found in various sections of the rabbit intestine may be caused by the prolonged feeding of a specific diet to the animals in question.

The studies of I. P. Pavlov [10] and numerous other authors [1,2,3,5-8] confirmed the dominant influence of the environment, and in particular of the character of nutrition upon the general structure of the gastrointestinal tract, its form, the structure of its wall, and its vascular and nervous apparatus.

Comparing the results of the physiological and morphological investigations carried out by us (Fig. 3), it can be established that regions with maximal motor functions (including all types of intestinal movement) coincide to a certain degree with those regions in which the concentration of nerve cells is higher and the structure of the intramural nerve plexuses more complex. This fact warrants the assumption that the motor function in various sections of the rabbit intestine depends, in addition to other factors, on the structure of their intramural nerve plexuses, and in particular on the number of nerve cells per surface unit on the intestinal wall.

SUMMARY

The motor function of various intestinal sections was studied on 38 rabbits in 102 experiments, together with the character of their macro and microscopic structure of the muscular nervous plexus. Comparison of physiological and morphological data thus obtained shows that there is a higher concentration of the ganglionic elements in the intestinal sections with the maximal motor activity and that the structure of the nerve plexuses here is more complicated. Apart from other factors the motor function of the rabbit intestine is in direct relationship to the structure of the intramural nerve plexuses themselves, as well as to the number of nerve cells per unit of its surface.

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