FREQUENCY OF THE RHYTHMIC CONTRACTIONS OF THE SMALL INTESTINE

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When studying the mechanisms of nervous control of the motor function of the intestine and the paths of transmission of excitation to its neuromuscular apparatus we used the method of division of the intestinal tube, and during chronic experiments we found that division of the wall of the intestine leads to a severe fall in the frequency of the rhythmic contractions distal to the point of division [1].

In view of the important role of rhythmic contractions in the process of digestion and absorption, and also of the importance attached to it by the gradient theory of intestinal polarity [2, 3], we made a detailed study of the frequency of the rhythmic contractions.

EXPERIMENTAL METHOD

The investigation was carried out in the form of chronic experiments on 26 dogs (fasting and fed) with fistulae of the stomach, duodenum and jejunum. Two of the animals also had a fistula of the ileum 30 cm proximal to the ileocecal sphincter. Experiments were performed before and after division of the intestinal tube at predetermined levels in normal dogs and in dogs after ligation of the vagus and splanchnic nerves.

Patency of the intestine was ensured by means of external anastomoses or by the formation of entero-enterostomies. Movements of the intestine were recorded by a graphic method using balloons.

EXPERIMENTAL RESULTS

In the healthy dogs the frequency of contraction of the duodenum and the proximal jejunum varied between 17-19, and in some of the experimental dogs — between 18-20 contractions per minute. The frequency of rhythmic contraction of the jejunum at a distance of 40-70 cm caudal to the duodenal ligament (ligament of Treitz) was the same as in the initial part of the jejunum, or slightly lower (by 0.5-1 contraction per minute). In an area of the intestine situated 20-30 cm proximal to the ileocecal sphincter it was 12-13.5, and in some dogs 12.5-14 contractions per minute.

After division of the intestinal wall at a distance of a few centimeters (2-5 or 8-10 cm) caudal to the duodenal ligament (passage of food was ensured outside the experiment through an external anastomosis joining the oral and caudal sections of the bowel), a sharp decrease was observed in the frequency of rhythmic contractions of the jejunum caudal to the division, whereas in the neighboring area, oral to the division, the normal frequency of rhythmic contraction was maintained.

Whereas in the normal dogs the upper part of the jejunum contracted at the rate of 18-20 per minute, after division of the intestine the frequency of these contractions in areas situated caudal to the divison was 12.8-13.2 per minute in the first few days after the operation. On the 10th day after operation it rose and after

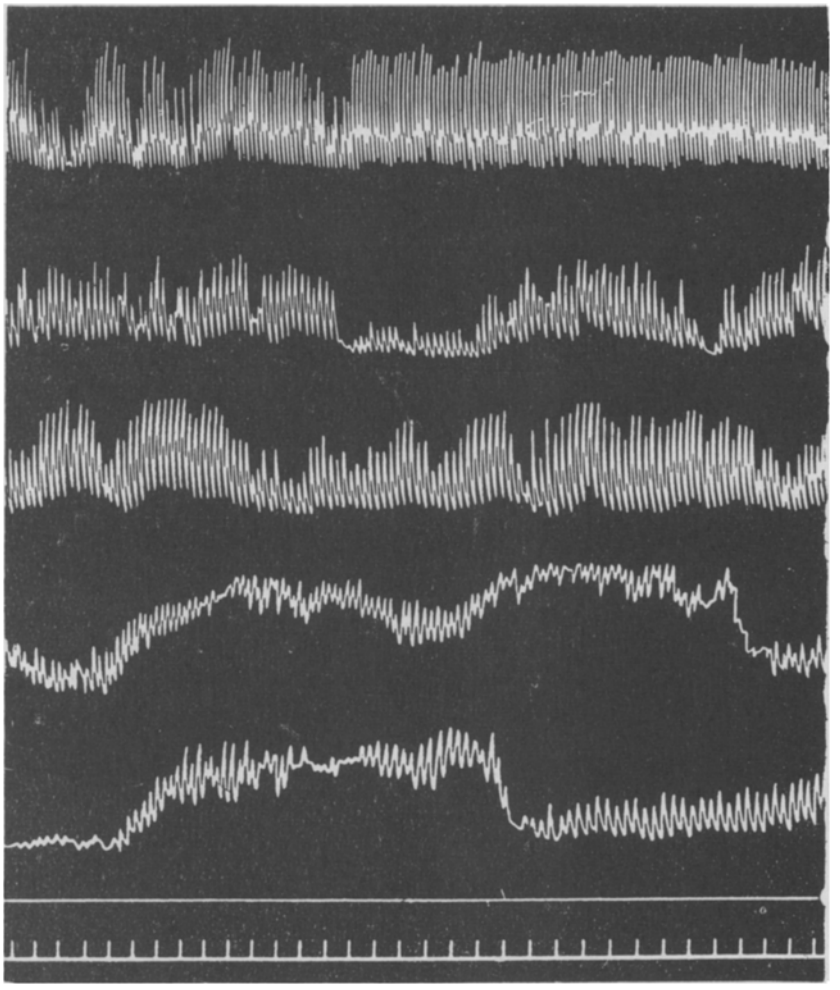

Fig. 1. Frequency of contraction of different areas of the small intestine, recorded simultaneously, in a chronic experiment on the dog Lotsman after division of the intestine at various levels.
Significance of the curves (from above down): contractions of the lower third of the duodenum; contractions of the jejunum distal to the division at the ligament of Treitz (Thiry-Vella segment); contractions of the jejunum distal to a division carried out 30-35 cm caudal to the ligament of Treitz; contractions of the terminal part of the ileum proximal to a division made 25 cm from the ileocecal sphincter; contractions of the terminal part of the ileum distal to this division; line of the stimulation marker; time marker (17 seconds).

20-40 days it reached 13.5-14.7 contractions per minute. No further tendency for the frequency of contraction caudal to the division to increase was observed.

Recording of the movements of the jejunum at distances of 25, 45 and 65 cm caudal to the division showed that a sharp fall in the frequency of rhythmic contractions was observed not only in the caudal areas adjoining the site of division, but also more distally along the bowel, at least for 60-70 cm.

For this reason the statement of Alvarez [3] that the fall in frequency of contraction of the jejunum after novocainization or compression of the bowel at the level of the duodenal ligament, as observed in Douglas's

experiments [6], was characteristic of only the segment of jejunum adjoining the site of compression or novocainization, does not correspond to the facts. The unsoundness of this view could not have been revealed by Douglas's experiments with division and re-anastomosis of the intestine above the exteriorized loop (by Biebl's method [4, 5]), for in recording the contractions of the intestine, Douglas was able to utilize only a small area of the small intestine in his experiments.

Thus in the first few days after division of the bowel at the duodenal ligament the frequency of rhythmic contraction of the upper part of the jejunum, caudal to the division, was no higher than the frequency of contraction of the terminal part of the ileum, i.e. there was no sign of a gradient of frequency of contraction caudal to the division. However, 20-40 days later, the gradient was re-established to a definite degree. Whereas, however, in the normal animal the difference between the frequency of contraction of the upper areas of the jejunum and the ileum at a distance of 20-30 cm oral to the ileocecal sphincter was 5-6 contractions per minute, from 1-1$\frac{1}{2}$ months after division of the wall of the intestine at the level of the duodenal ligament the difference was only 0.8-1.5 contractions per minute. Such a fall in the frequency of the rhythmic contractions caudal to the division of the bowel wall was observed in all the experimental dogs.

1 month 11 days after division of the bowel near the duodenal ligament, in one dog (Lotsman) a second division of the bowel wall was made at a distance of 30-35 cm caudal to the first. The area of bowel between the first and second divisions was exteriorized in the manner of a Thiry-Vella segment, and the passage of food along the intestine was assured, outside the experiment, by an external anastomosis joining the duodenum to the initial part of the segment of jejunum caudal to the second division. The area of intestine caudal to the second division (1 month after this operation) had a frequency of 13.2-14.2 contractions per minute, whereas in the normal animal before division of the bowel this area had a frequency of 17-19 contractions per minute. The frequency of contraction of the duodenum at this time in the dog was 18-20 contractions per minute; the frequency of contraction at a distance of 20-30 cm oral to the ileocecal sphincter was 12-13.5 contractions, and in the Thiry-Vella segment — 13.5-14.7 contractions per minute (Fig. 1).

Hence after the second division also the dominant area in respect to frequency of contraction was the oral part of the bowel, situated caudal to the site of division, but here, too, there was not such a severe fall in the gradient of frequency in the direction of the terminal part of the ileum as was observed in the normal animal.

A third division of the bowel wall in the dog Lotsman was carried out at a distance of 25 cm oral to the ileocecal sphincter. The oral segment of the ileum was connected, outside the experiment, to its caudal segment by means of a second external anastomosis. 10 days after the third division of the bowel, and on subsequent days, the frequency of rhythmic contraction of the proximal segment of the ileum was 12.5-14 contractions per minute, whereas in the distal segment 9.5-11.6 contractions per minute were observed (Fig. 2). The frequency of contraction of the intestine distal to the division of the bowel was equally low in all the fed or fasting animals, both at the beginning and the height of the process of digestion.

In dogs after bilateral transdiaphragmatic division of the vagus nerves, and in dogs after division of the splanchnic nerves and extirpation of the sympathetic chains in the lumbar region, the frequency of rhythmic contractions of the small intestine was no different from that observed under normal conditions (before division of the nerves).

In order to exclude completely any nerve supply to the intestine from the vagus nerves, after the normal frequency of contractions had been established in three dogs with fistulae of the stomach and jejunum, a bilateral vagotomy was performed in the neck. The frequency of rhythmic contractions in the small intestine after the operation was the same in all three dogs as before. Occasionally, in the first 7-10 days after the operation a pyloric rhythm was observed for 10-20 minutes, after which the normal frequency of contraction of the jejunum was restored.

If in the dogs in which the splanchnic or vagus nerves or both were divided, the intestine also was divided at the level of the duodenal ligament or slightly caudal to it (5-8 cm), the frequency of rhythmic contraction of the jejunum caudal to the division fell sharply (12-13 contractions per minute), and 1-2 months after this operation it reached a value of not more than 14-14.5 contractions per minute.

The results obtained showed that the frequency of rhythmic contraction of different segments of the small intestine in the normal animal is determined not by the extrinsic innervation and not by the food passing through

the lumen of the bowel, but by the activity of the area or of the structures present in the walls of the digestive tube, oral to the ligament of Treitz.

It was necessary to find out which particular area of the digestive tube oral to the ligament of Treitz was responsible for the rhythm of the contractions of the small intestine. In order to solve this problem we employed the method of division of the bowel and subsequent formation of an end-to-end anastomosis, since after such an operation in our experiments we always observed the same fall in the frequency of the contractions distal to the anastomosis as after division of the intestine and subsequent restoration of the patency of the bowel by means of an external anastomosis [1].

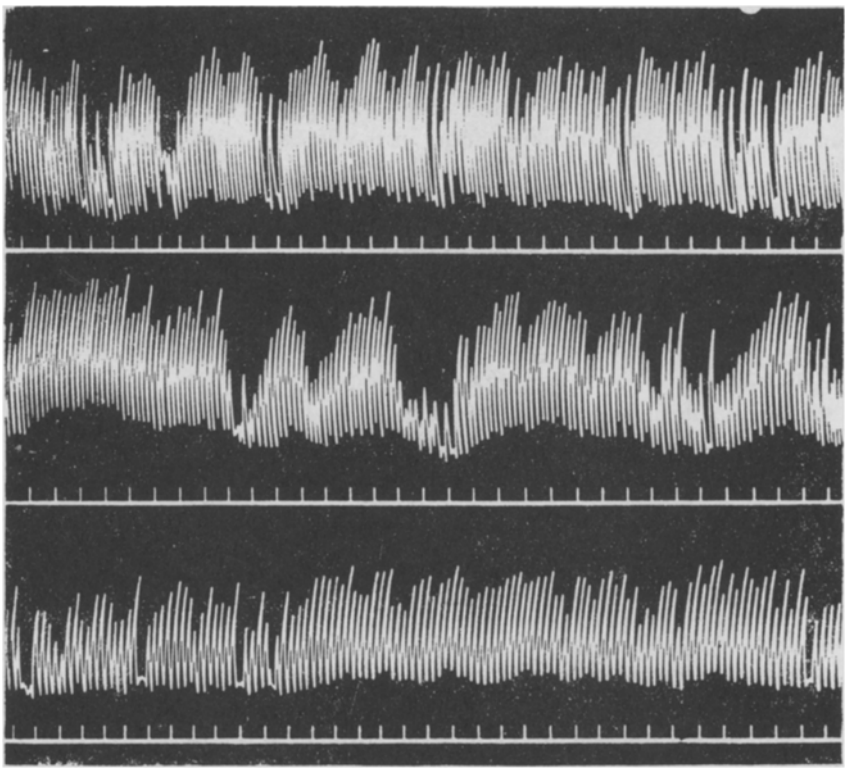

Fig. 2. Contractions of the jejunum in an area situated 15-18 cm caudal to the ligament of Treitz.
Significance of the curves (from above down): contractions in a normal dog; contractions one month after division of the bowel oral to the attachment of the body of the pancreas to the intestine and the formation of an end-to-end enteroenterostomy; contractions 4 months after division of the duodenum distal to the attachment of the pancreas and the formation of an end-to-end entero-enterostomy; time marker (15 seconds).

After division of the digestive tube at the junction of the pylorus and duodenum, or division of the duodenum above the place of attachment of the pancreas, followed by the formation on an end-to-end enteroenterostomy (experiments on 6 dogs) the frequency of contraction of the upper part of the jejunum was 17-19 contractions per minute, i.e. it was normal. Division of the bowel at the lower border of the attachment of the pancreas, followed by the formation of an enteroenterostomy at this point (experiments on 3 dogs) led to a fall in the frequency of rhythmic contractions of the jejunum. Whereas before division and anastomosis the frequency was 18-20 contractions per minute, from 1-1½ months after this operation it was 13.5-15 contractions per minute (see Fig. 2), and for the next 6 months no increase in the frequency of the contractions was observed.

It can be seen from the results of our experiments that the frequency of the rhythmic contractions of the intestine distal to the division fell sharply only when the division was made below the attachment of the body of the pancreas to the duodenum, and it remained normal in all the experiments after division of the bowel proximal to the attachment of the pancreas to the duodenum.

Thus the area of the duodenum to which the pancreas is directly applied, or some structure present in that area, evidently plays a leading part in determining the normal frequency of rhythmic contraction of the duodenum and jejunum, setting the rhythm (the "pacemaker" of the rhythm) of the intestinal contractions.

The frequency of the rhythmic contractions of each particular segment of the intestine is not a property of the neuromuscular or muscular apparatus of that segment, as asserted by Alvarez [3]. It may be determined by structures which lie outside that segment; since the intrinsic rhythm of the segments of the jejunum is considerably below that observed in the normal animal. The "pacemaker" of the rhythm, which we discovered, is of practical as well as theoretical interest, in connection with the often performed operation of resection of small areas of the small intestine, since enteroanastomosis does not restore the pathways by which the segments of the intestine are normally joined to each other.

This can be seen from the fact that end-to-end or side-to-side enteroenterostomy does not restore the normal frequency of contraction of the intestine caudal to the division. The rhythmic contractions of the jejunum caudal to a resection are maintained at a low frequency (13.5-14.6 contractions per minute) 5 years after operation.

It must be pointed out that in all the experimental dogs the Thiry-Vella segments of the jejunum had a frequency of rhythmic contraction of 13.5-14.7 per minute, whereas in normal dogs these areas of the small intestine had in some cases a frequency of 17-19 and in others a frequency of 18-20 contractions per minute. This fact has remained unnoted.

The fall in the frequency of rhythmic contraction of the terminal part of the ileum caudal to the division, compared with the frequency in this area in the normal animal, showed that the rhythm of the contractions of the ileum evidently depended on structures which were situated proximal to the point of division of the ileum which we selected, for division of the bowel at the level of the ligament of Treitz had no effect on the frequency of the contractions of the ileum.

The results obtained are of great importance for an understanding of the mechanisms of peristalsis. The gradient theory of peristalsis (polarity) of the intestine is unacceptable even in the form in which it is described in the latest edition of Alvarez' monograph [3], for it does not explain the physiological connection between the gradients and the caudal advancement of the peristaltic wave [1, 8]. In addition, according to this theory, the wave of excitation arising at any point in the intestine must spread to the side of its greatest excitation, but in fact the peristaltic wave spreads along the intestine in a caudal direction i.e. toward the side of its least excitation.

Thus the wave of excitation spreads not with but against the gradient of excitation.

Our experimental results show that the area of the duodenum to which is attached the pancreas, or structures present in this area, fulfil the function of "pacemaker" for the rhythm of contraction of the duodenum and jejunum.

According to preliminary findings, the "pacemaker" for the rhythm is located in the area of the outlet of the bile duct and the accessory pancreatic duct into the intestine. From this "pacemaker" for the rhythm, impulses constantly pass out to the neighboring areas of the intestine and spread further distally along the intestine.

In consequence of the presence of a "pacemaker" or of "pacemakers" for the rhythm, it is possible to show the cause of the spread of the peristaltic waves in a caudal direction. Impulses constantly passing out from the "pacemaker" do not allow the spread of the wave of excitation in the oral direction, because in case of spread of such a wave (an antiperistaltic wave) it is very rapidly or even immediately extinguished by the phase of diminished excitation after each descending impulse. A similar mechanism has also been suggested by Thomas [8].

The rate of extinction of the antiperistaltic wave depends on the strength of the wave of excitation and the

depth of refractoriness which follows behind the excitation produced by the descending impulse from the "pacemaker" of the rhythm. The descending impulses from the "pacemaker" of the rhythm enable the wave of excitation to spread in a caudal direction and bring about the strengthening and acceleration of the rapid peristaltic waves. Extinction of a peristaltic wave, which may take place at any level of the intestine, can be explained by the diminished excitation of the distal segments of the bowel or by active inhibition through the extrinsic nerves of the intestine in response to the action of stimuli on particular segments of the bowel or on divisions of the gastrointestinal tract.

The position of the "pacemaker" of the rhythm in the area of the bowel to which the pancreas is attached creates conditions in the initial part of the duodenum for the spread of the wave in a caudal direction (peristaltic waves) and in an oral direction (antiperistalsis). When the intestine is divided caudally to the "pacemaker" of the rhythm, the function of the latter is evidently taken over by the oral area of the intestine distal to the division, since the frequency of the rhythmic contractions of this area is greater than the frequency of contraction of the terminal part of the ileum [1].

SUMMARY

Chronic experiments were performed on dogs with divided intestine at the level of Treitz ligament. A sharp decrease in the frequency of jejunal rhythmical contractions (by 25%) caudal to the site of division was noted. Following intestinal division between the pylorus and duodenum, and 3-4 weeks after the division of the duodenum (oral to the attachment of the pancreas) and placing end-to-end enteroenterostomies – normal frequency of rhythmical contractions was noted, distal to the site of division. Division of the duodenum 0.5 to 1 cm caudal to the attachment of the pancreas resulted in a sharp and stable decrease in the frequency of intestinal rhythmical contractions distal to the cut. The presence of an intestinal contraction automatic "pacemaker" is inferred, found in the intestinal portion directly adherent to the pancreas. The functioning of such a pacemaker explains the mechanism governing the extension of peristaltic contractions in the caudal direction.

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