PERISTALSIS, SEGMENTATION, AND THE MYENTERIC REFLEX.

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THE neuromuscular structures of the alimentary canal, from the lower oesophagus onward, are singularly uniform. Smooth muscle arranged in an outer longitudinal layer and an inner circular layer, with a primitive nerve plexus between, constitutes in both the stomach and the intestines the machinery by which all the mechanical factors of digestion are managed. The structure of the nerve net in the stomach, so Auerbach reported, is similar to that in the intestines. This view is slightly modified by Dogiel, who states that the ganglia of the net and the individual cell bodies of the neurones are larger in the small intestine than in the stomach and colon. The axones of the "motor cells" in the plexus, according to Dogiel's description, pass through several ganglia, giving off collaterals to each, before ending in branches to muscle cells. Histological evidence, therefore, indicates a local nervous system fairly typical for all parts of the digestive tube, and so arranged as to correlate the activities of closely neighboring parts.

THE MYENTERIC REFLEX.

The experiments of Nothnagel and Lüderitz showed that stimulation of the small intestine causes contraction above the stimulated


2 DOGIEL: Archiv für Anatomie und Entwicklungsgeschichte, 189, Supplement-Band, p. 137.

3 NOTHNAGEL: Archiv für pathologische Anatomie, Physiologie, und klinische Medicin, 1882, lxxxviii, p. 4.
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spot. Basing his judgment on Nothnagel’s studies of intussusception, Mall clearly inferred that while a mass in the intestine is arousing contraction above (a contraction which forces the mass downward and thus arouses fresh regions above to contract), active dilatation below is at the same time ‘inviting an easy descent.’ The truth of this inference was demonstrated by Bayliss and Starling, whose well-known experiments led them to state, as the ‘law of the intestine,’ ‘Excitation at any point of the gut excites contraction above, inhibition below.’ The co-ordinated character of this response, which occurred in the absence of cerebrospinal connections, made them believe that it was a local reflex controlled by Auerbach’s plexus—a conclusion which Magnus verified by obtaining evidence of the ‘law’ in excised gut from which Meissner’s plexus had been removed.

The method used by Bayliss and Starling in studying the small intestine they applied to the large intestine as well, and found the local reflex present in the colon of both the dog and the rabbit. That the cat’s colon also is the seat of similar co-ordination was discovered by Elliott and Barclay-Smith, who observed that distention of the middle third of the large intestine in this animal causes constriction above the distended area and relaxation below.

By means of a slight modification of the method employed by Magnus I have studied the response of excised portions of all the large divisions of the alimentary canal. The portion to be examined was removed from the body immediately after the animal (cat) was quickly etherized, pithed, and bled, and was placed in oxygenated Ringer’s solution kept at body temperature. A silk thread fastened midway in the piece of digestive tract was tied to an L-shaped glass tube (through which the oxygen bubbled), and thus the structure was anchored in the solution. Another silk thread, attached directly opposite the first, connected with a writing lever. The pull of the lever was about 1 gm. The contractions of the muscular ring between the threads

* Mall: Johns Hopkins Hospital reports, 1896, i, p. 71.
* Bayliss and Starling: Journal of physiology, 1899, xxiv, p. 110.
* Magnus: Archiv für die gesammte Physiologie, 1904, cii, p. 132.
* Bayliss and Starling: Journal of physiology, 1900, xxvi, p. 107.
* Elliott and Barclay-Smith: Ibid., 1904, xxxi, p. 281.
were thus recorded, and this ring thus acted as an indicator for influences initiated by stimuli applied above and below.

Fig. 1 is a record from a piece of large intestine about 3 cm. from the ileocolic valve. The stimulus was a pinch. When applied below the recording ring, a contraction resulted; when applied the same distance above the ring, not contraction, but slight relaxation, was recorded.

In observations on the esophagus and stomach the best results were obtained from parts removed three or four days after both vagi had been severed, and the movements of these regions had thus been given time to regain their normal character. Fig. 2 is a record from the lower end of the esophagus deprived of its remaining vagus nerve supply three days before. Again stimulation by pinching below the recording ring with small forceps caused contraction of the ring, whereas pinching above caused not contraction, but slight relaxation.

In Fig. 3 is registered the response of the body of the stomach about 2 cm. below the cardia. The right vagus had been severed nineteen days, and the left five days before. The stimulus was a pinch with forceps applied about 1.5 cm. above, and again the same distance below, the recording ring. The typical contraction occurred when the stimulus was applied below; and no contraction, instead a slight relaxation, occurred when the stimulus was applied above. The same result was obtained when a ring nearer the pylorus was used as an indicator. Since these observations on the stomach were first reported, Sick and Tedesko, using chemical in place of mechanical

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10 See CANNON: This Journal, 1906, xvii, p. 447; 1907, xix, p. 438.
11 CANNON: Ibid., 1908, xxi, p. xx.
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stimulation, have likewise obtained contraction of the gastric muscle above the stimulated spot, but they usually noted also some contraction below. 12

From the foregoing evidence it is clear that, by applying to the esophagus, the stomach, and the colon the method used to show the presence of the local reflex in the small intestine, there can be demonstrated, throughout that part of the digestive tube which is composed of smooth muscle, the presence of an intrinsic arrangement whereby a stimulus causes a contraction above and a relaxation below the point of application. And not only where the tube is open, but also at the sphincters—certainly at the cardiac and pyloric sphincters 13—is there reason to believe that the mechanism for the local reflex is present.

Magnus proved that in the small intestine the local reflex was due to the functioning of the nerve net lying between the muscular coats. In the new anatomical nomenclature this net is called the "myenteric plexus," and is described as such for the entire alimentary canal. I have suggested, therefore, that the local reflex of the alimentary canal be called the "myenteric reflex." 14

THE VARIETIES OF PERISTALYSIS.

I. In the stomach and colon. — Although there is the foregoing evidence of a mechanism throughout the digestive tube, assuring an

12 SICK and TEDESKO: Deutsches Archiv für klinische Medizin, 1908, xcm, p. 431.
13 See CANNON: this Journal, 1907, xx, p. 283; and 1908, xxiii, p. 105.
14 CANNON: Ibid., 1908, xxiii, p. xxvi.
orderly progress of the contents, there is evidence also that this
mechanism is not always operative. For example, in the proximal
colon and at times in other parts of the large intestine, antiperistaltic
waves occur quite normally. And in the pyloric part of the stomach,
likewise, reversed waves may be seen. These waves, starting from a
pulsating ring more tonically contracted than other parts of the tube,
move in a direction opposed to that in which the myenteric reflex
would be effective. Furthermore normal gastric peristalsis does not
require the presence of the reflex mechanism, for the waves sweep from
the pulsatile source in an orderly manner to the pylorus after the
myenteric plexus has been completely interrupted by a half-dozen
incisions encircling the stomach.\textsuperscript{15} In the proximal colon, also, downward-running peristaltic waves may be started by a pulsating ring
near the ileocolic junction, but the close succession of the waves indi-
cates that any forerunning inhibition must be ineffective or of slight
extent, and therefore quite unlike the projected relaxation preceding
the moving constriction, so characteristic of the small intestine.\textsuperscript{16}

2. In the small intestine.—The common presence of the myen-
teric reflex in the small intestine, and its usual absence or submergence
in the stomach and proximal colon, suggest that these regions are
fundamentally different. This surmise is supported by the action of
nicotine, which abolishes the reflex in the small intestine, but does
not in any way disturb either peristalsis of the stomach or antiperi-
stalsis of the colon.\textsuperscript{17} Before this evidence is accepted, however, as
proving an important difference between the middle and the terminal
portions of the digestive tube, the varieties of movement manifested
by the small intestine should be examined.

That the small intestine is capable of conducting waves in either
direction any one can easily demonstrate by repeating Engelmann’s
old observation on an animal recently killed.\textsuperscript{18} A pinch starts con-
tractions towards the pylorus and towards the ileocolic valve, which
sometimes sweep over extensive reaches of the gut. Bayliss and Star-
ling, after coating the surface of an exposed coil with a cocaine solu-

\textsuperscript{15} \textit{Cannon}: this \textit{Journal}, 1911, xxix, p. 258.

\textsuperscript{16} See \textit{Bayliss} and \textit{Starling}: \textit{Journal of physiology}, 1899, xxiv, p. 113; 1901,
xxvi, p. 138.

\textsuperscript{17} See \textit{Elliott} and \textit{Barclay-Smith}: \textit{Ibid.}, 1904, xxxi, p. 304; \textit{Cannon}:
this \textit{Journal}, 1909, xxiii, p. xxvii.

\textsuperscript{18} \textit{Engelmann}: Archiv für die gesammte Physiologie, 1871, iv, p. 35.
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Peristalsis, or injecting nicotine or muscarine, still saw waves of constriction run along the gut, but as often in one direction as in the other.\(^{19}\) I have removed loops of small intestine from the cat, tied them at each end, filled them with 1 per cent strychnine sulphate, and placed them in oxygenated Ringer’s solution kept at body temperature. In one instance I observed repeatedly during a half-hour rings of constriction running along a loop in the normal direction. Then, by pinching the loop midway of its length, I produced a strong contraction which first brought the moving waves to a stop. In about ten minutes, however, the contracted region, having relaxed, was pulsating and sending away waves, in both directions. On another occasion a loop thus filled with 1 per cent strychnine sulphate was hung in a moist chamber. The lower end of the loop was dipping in Ringer’s solution, to which barium chloride \((2:1000)\) had been added. Oxygen bubbled through the solution and filled the chamber. The part in the solution soon entered a state of high tonic contraction; but after a brief period reversed waves were seen, starting from the region of increased tone and passing upward to the other end of the loop. In both these instances not only were reversed waves observed, as in Engelmann’s and in Bayliss and Starling’s experiments, but these waves started from a pulsating source. The small intestine, therefore, is capable, under these evidently unnatural conditions, of exhibiting the same sort of activities that are seen in the colon and stomach.

The question now arises, May the peculiar peristaltic mechanism of the small intestine be absent in conditions more natural than those just described? Although the reversed waves described in the above paragraph were probably not preceded by an area of inhibition, it is of interest that several observers have noted, in experiments on the small intestine, an area of inhibition above the stimulated spot. Thus Bayliss and Starling found instances of stimulation below a balloon in the gut, causing inhibition of the muscle about the balloon.\(^{20}\) Magnus obtained the same result at times in experimenting on the isolated intestine.\(^{21}\) And Langley and Magnus have recorded similar observations.\(^{22}\) In the dog, cat, and rabbit, on which these effects were

\(^{19}\) Bayliss and Starling: Journal of physiology, 1899, xxiv, p. 115.

\(^{20}\) Bayliss and Starling: Ibid., 1899, xxiv, p. 113.

\(^{21}\) Magnus: Archiv für die gesammte Physiologie, 1904, cii, p. 134.

\(^{22}\) Langley and Magnus: Journal of physiology, 1905, xxxiii, p. 47.
seen, stimulation of the small intestine, unaffected by drugs, may therefore at times evoke relaxation above the stimulated spot. In this connection the testimony of Bayliss and Starling is pertinent, that repeated stimulation of the same piece of gut results in the peristaltic mechanism becoming fatigued. Under these circumstances, they declare, the most striking difference from the normal condition "is the absence of inhibition below the bolus."

The discussion thus far suggests that the myenteric reflex does not hold the small intestine in a fixed and rigid mode of action, but may at times be so far in abeyance as to permit waves of constriction to pass in a direction opposite to the normal. This reversal of peristalsis has been seen in the living animal by means of the X-rays. An obstruction was present about 10 cm. beyond the pylorus. The course taken by food passing along the duodenum was carefully traced on transparent paper laid over a fluorescent screen. After the mass which accumulated above the obstruction had been worked over for some time by alternating periods of segmentation and peristalsis, it was suddenly divided, and the proximal portion was moved rapidly back along the course which had been traced, even up to the pylorus. This reversed conveyance of the food was seen repeatedly with perfect clearness. Other evidence that antiperistalsis may occur in the small intestine has been secured by watching directly, some time after operation, the action of a reversed part of the gut. More than three months after operation Kelling thus saw intestinal contents moved towards the colon through a reversed portion by distinct peristaltic waves. Similar observations have been reported by Enderlen and Hess, Beer and Eggers, and McClure and Derge. And the clinical evidence that in cases of intestinal obstruction continued vomiting of offensive decomposed material occurs after the stomach has been repeatedly washed, can also be interpreted as due to upward-running waves in the intestine. Although, as Mall and others have shown, reversal of a piece of gut is likely to result in the early accumulation of indig-
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tible stuff at the region of the upper suture,26 the results above cited show that in time conditions may arise which alter the functioning of the small intestine in situ to such a degree that it can exhibit antiperistalsis.

In recently published papers I have presented evidence that colonic antiperistalsis and gastric peristalsis are responses of the tonically contracted organs to being stretched by the contents.27 The rhythmically repeated waves start at a pulsating tonic ring. They resemble, therefore, the waves seen in excised small intestine filled with strychnine sulphate (see p. 119). And since they are not interfered with by nicotine, they are probably of the same order as the waves which can traverse the small intestine after nicotine has been injected, and also after the establishment of obstruction or reversal. Whether in the stomach, the small intestine, or the colon, these constrictions can move in either direction along the canal.

THE MYENTERIC REFLEX AND THE NATURE OF SEGMENTATION.

Although citing instances of reversal of the usual direction of peristaltic waves in the small intestine, I do not wish to give the impression that normally the waves traverse the gut quite as readily in one direction as in the other. Undoubtedly the ordinary direction for the contents to take is from the stomach onward, because of the action of the myenteric reflex. This reflex requires an extent of several centimetres along the gut for its full operation (see p. 123). As Bayliss and Starling inferred, the correlation of the portions involved in the reflex is probably mediated through paths ascending and descending from the point stimulated.28 On this assumption interruption of these paths by circular incisions through both muscular coats (thus dividing the myenteric plexus) should interfere with peristalsis. In a paper published in 1902 I pointed out that the region just beyond the first attached loop of the duodenum (in the cat) is likely to exhibit rapid

26 MALL: Johns Hopkins Hospital reports, 1896, i, p. 93; SABBATANI and FASOLA: Archives italiennes de biologie, 1900, xxxiv, p. 195; PRUTZ and ELLINGER: Archiv für klinische Chirurgie, 1902, lxvii, p. 964; 1904, lxvii, p. 415.
27 CANNON: this Journal, 1911, xxix, pp. 238, 250.
28 BAYLISS and STARLING: Journal of physiology, 1899, xxiv, p. 115.
In order to test the effect of dividing the myenteric plexus, incisions reaching to the submucous connective tissue were made encircling the gut at intervals varying between 1.5 and 2 cm. throughout the first 45 cm. of the small intestine. (Of course the operation was performed under complete anesthesia.) After the animal had fully recovered from the operation it was fed 25 c.c. mashed potato with which was mixed 5 gm. subnitrate of bismuth. After the food began to appear in the duodenum, it continued to be present there for two hours of observation. During a half-hour of continuous watching no peristalsis was seen in the region where rapid peristalsis usually occurs. The content of this region, however, was undergoing almost constant segmentation — interrupted now and then momentarily by the excitement of the animal. Later examination confirmed this first experience. The encircling incisions stopped peristalsis but not segmentation. The ordinary peristalsis of the small intestine therefore, unlike the peristalsis of the stomach (see p. 118), is seriously interfered with by division of the myenteric plexus.

The foregoing experiment shows, however, that segmentation can continue undisturbed in the presence of numerous interruptions of the myenteric plexus. The inference is justified, therefore, that segmentation is a local response to stimulation — a conclusion which is supported by the rhythmic contraction of any narrow strip of circular intestinal muscle when stretched by the pull of a recording lever. Segmentation can best be explained, indeed, as a local response to distention. Thus Bayliss and Starling observed that rhythmic contractions occurred where the distending balloon in the gut exerted the greatest tension. The observations that as a mass of food is being pushed along the intestine the back end is likely to be cut off by a constriction ring, and that in cases of intestinal obstruction the accumulated mass is violently segmented, both point to distention being the condition for rhythmic contractions. Normal segmentation also is best explained as a response to stretching, for the contraction occurs each time in the bulging region about midway between two previous contractions. Experimental evidence to the same effect I have

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30 Bayliss and Starling: Journal of physiology, 1901, xxvi, p. 134.
secured by seizing the active exposed intestine between the fingers at two points a few centimetres apart, and placing the enclosed contents under pressure sufficient to distend the gut. The distention was followed by the contraction of a narrow ring of the circular coat; and when the finger pressure was repeated rhythmically — as rapidly as a contracted ring relaxed — a new contraction occurred, not where one had just appeared, but in a fresh region. Now here, now there, the gut responded to the distending contents, a shifting perhaps associated with lessened irritability in the region just recovering from activity.

Because these rhythmic movements were seen after the gut was poisoned with nicotine, cocaine, or muscarine, Bayliss and Starling regarded them as of myogenic origin. In opposition to this conclusion Magnus brought the discovery that so long as intestinal smooth muscle is connected with the myenteric plexus it manifests a refractory period and contracts rhythmically, but when deprived of the plexus it no longer pulsates.32

The presence in the small intestine of rhythmic segmentation, a local response involving action in the nerve net, is further evidence that the myenteric reflex is not always in control. That these two activities involve a markedly different usage of the neuromusculature of the gut is indicated in Figs. 4 and 5, which reproduce photographs of segmentation and peristalsis, respectively, in loops of small intestine exposed under warm normal salt solution. The contraction that occurs in rhythmic segmentation is narrow, involving in each instance hardly a centimetre of the circular coat; whereas the contraction

32 MAGNUS: Archiv für die gesammte Physiologie, 1904, ciii, pp. 531, 536. For further discussion see MAGNUS: Ergebnisse der Physiologie, 1905, vii. p 45.
that occurs in peristalsis extends along the canal for 4 or 5 cm. A much larger number of circular fibres are evidently called into service by the myenteric reflex to push food through the canal than are active in any single segmenting contraction. And, furthermore, the area of inhibition demonstrable in peristalsis does not exist in segmentation.

On the basis of evidence now in hand the assumption is reasonable that the rhythmic contractions of segmentation are governed by local motor centres, and that in the operation of the myenteric reflex the augmentor and inhibitory paths consist of neurones which are superintendent in function and which normally affect the subordinate local centres through considerable extents in a positive or negative manner. Dogiel's description of neurones whose axones extend some distance from the site of the cell body and give off collaterals to other neurones in ganglia through which they pass (see p. 114), offers a morphological basis for this conception. And the observation that atropin paralyzes conducting paths but not local centres in sipunculus, whereas cocaine paralyzes the motor centres before stopping conduction, suggests, as Magnus has intimated, that the drugs used by Bayliss and Starling (see p. 118), though destructive of the reflex, do not seriously affect the local nerve supply.

THE MYENTERIC REFLEX AND THE VARIETIES OF PERISTALSIS.

The evidence that the myenteric reflex is present throughout the gastrointestinal tract has been given above. Although it can take

33 Bayliss and Starling obtained records showing that the longitudinal and circular coats of the intestine contract simultaneously in any region (see Journal of physiology, 1899, xxiv, p. 105). Magnus observed that as the small intestine became tonically contracted, it elongated, and he concluded therefore that as the circular coat contracts, the longitudinal relaxes (see Archiv für die gesammte Physiologic, 1904, cii, p. 137). Quite possibly the change Magnus saw was due to the circular coat being thicker and stronger than the longitudinal, for the contraction of the circular coat through a long extent of gut must increase the area of cross-section of the cells laid side by side, and by thus elongating the tube, must stretch the longitudinal coat. I find that if a piece of intestine is cut both across and lengthwise, and permitted to go into tonic contraction, it takes such shape as permits each of the muscular layers to be in the shortest possible state. In other words, they then contract simultaneously.

34 Magnus: Archiv für experimentelle Pathologie und Pharmakologie, 1903, i, pp. 97, 103; Ergebnisse der Physiologie, 1908, vii, p. 44.
control of the neuromusculature of the canal, it certainly does not always exercise that control. The reflex is most evident in the small intestine, but, as has been shown, it does not govern the rhythmic segmentation which normally occurs in that region, and it may be so completely suppressed as to permit the gut, while still in the intact animal, to exhibit antiperistalsis. We may reasonably assume, therefore, that antiperistalsis of the colon also can occur in the presence of a mechanism which, under certain circumstances, would enforce there the local reflex. And the same assumption may be made regarding the stomach.

What causes the myenteric reflex to appear or not, when material is present, is as yet undetermined. Certainly chyme is not pushed onward continuously from stomach to colon. And yet after a mass of material has lain for some time undisturbed, or has been undergoing segmentation, a peristaltic wave will appear, force the mass onward for some distance, and then stop. If we consider the functions of digestion and absorption which peristalsis subserves, the forwarding of the nutriment might be serviceable, not because the mass as such must be advanced, but because fresh regions for digestion and absorption are needed. The degree of digestion or the status of the mucosa, or some relation between these two, might then explain the peculiarities of peristalsis in the small intestine. Some such regulatory arrangement for the progress of material through the gut is suggested by the results reported by London and his associates. They found that food-stuffs are absorbed at different rates at different parts of the tube — meat most in the upper part, starch and fat most in the lower part — and that each portion of the tract, in the case of any particular food, absorbed a constant percentage, quite independent of the amount fed. Nutriment when given in small bulk (50 c.c.) was distributed in the small intestine quite as it was when given in large bulk (500 c.c.), so that in either circumstance the entire tract was forced into service. Possibly these results are best explained as due to an invoking of the myenteric reflex by the nature of the intestinal contents or the relation between the contents and the mucosa.

36 LONDON and SIVRÉ: Zeitschrift für physiologische Chemie, 1909, IX, p. 201.
37 LONDON and SANDBERG: Ibid., 1908, lvi, p. 402.
In the colon as well, the nature of the contents may determine whether the myenteric reflex shall take charge of the musculature. In the distal colon, where the contents are more or less hard, onward-moving peristaltic waves prevail. And even in the proximal colon Elliott and Barclay-Smith observed (in the rat) that antiperistaltic waves appeared if the material it received was soft and moist, but that the peristaltic reflex was exhibited when the material was stiff and dry.38

To what extent and under what circumstances the myenteric reflex may assume control of the gastric musculature is not at all known. That it is quite unnecessary for normal gastric peristalsis, I have proved in the experiments already cited in which several complete interruptions of the myenteric plexus had almost no effect on the passage of the waves.

A More Exact Terminology.

The foregoing discussion has shown that besides segmentation the alimentary canal manifests several different sorts of moving waves — downward-moving waves with projected inhibition, and downward-moving and upward-moving waves without projected inhibition. All these various forms of undulation have hitherto been termed simply peristalsis. The distinctness of their character, however, justifies distinctive names. The term “peristalsis” means literally, in relation to hollow organs, “encircling contraction.” The fact that the contraction occurs around a circular tube renders the retention of peri unnecessary. The important facts to be brought out are whether the contraction moves, whether it moves down the tube or up, and whether it is preceded by an area of inhibition. The downward-moving contraction is properly designated as katastalsis. The upward- or backward-moving contraction is properly designated as anastalsis. Both anastalsis and katastalsis may occur, as stated above, in any portion of the gastrointestinal tract. The katastaltic and anastaltic waves are likely to recur rhythmically and run in a close series, i.e., with no projected inhibition. The contraction which is preceded by a demonstrable region of inhibition is of different order; it is man-

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aged by the myenteric reflex, and always moves downward. Since
the characteristic feature of this activity is the relaxing or opening of
the canal in front of the constriction, I suggest as a term to designate
it *diastalsis*, in the sense of expansion or dilation. Although each of
these words has been used either in Greek or English in a sense differ-
ent from that here intended, their significance in relation to the ali-
mentary canal is immediately clear. All three terms with *stalsis* in
their composition preserve an association with wave-motion along the
alimentary canal. The prefix in each case is significant of the pecul-
liarity of the wave motion which is designated.

Of the four mechanical activities of the alimentary canal, then,
rhythmic segmentation occurs in the small intestine, katastalsis
occurs typically in the stomach, and anastalsis occurs typically in the
proximal colon. Both katastalsis and anastalsis can occur with seg-
mentation in the small intestine. These three activities are indepen-
dent of the myenteric reflex. The fourth activity, diastalsis, is the
resultant of the local reflex in the wall of the canal, and is characterized
by an area of inhibition preceding the moving constriction.

Summary.

The myenteric plexus is fairly uniform in structure throughout
that part of the alimentary canal which is provided with smooth
muscle. Excised parts of oesophagus, stomach, and colon, like the
gastric sphincters and the small intestine, exhibit contraction above,
and relaxation below, a stimulated point. This may properly be called
the *myenteric reflex*.

The myenteric reflex is not always operative. In the stomach and
colon it is not operative when antiperistaltic waves are passing, nor
is it needed for normal gastric peristalsis. In the small intestine,
likewise, the reflex is not in control whenever that part of the canal
is manifesting antiperistalsis, as it may do after death, after being
treated with certain drugs, and after continued obstruction or reversal.
Furthermore, the reflex does not govern rhythmic segmentation in the
small intestine.

Evidence is given that segmentation is a local response to internal
pressure. Probably in the usual (reflex) peristalsis of the small intes-
the same neuromusculature is involved as in segmentation, but subject to superintending and co-ordinating neurons.

What causes the myenteric reflex to occupy at times the local neuromusculature is not known; there is some reason for thinking that the nature of the contents or the relation of the contents to the mucosa determines the appearance of the reflex.

Three terms are suggested to designate the distinctive waves of the alimentary tract: *katastalsis*, for downward-moving waves, *anastalsis*, for upward-moving waves, both usually appearing rhythmically, and not preceded by an area of inhibition; and *diastalsis*, for the downward-moving wave, controlled by the myenteric reflex, and preceded by inhibition.