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THE IMPORTANCE OF TONUS FOR THE MOVEMENTS OF THE ALIMENTARY CANAL *

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Four years ago, during an investigation of movements of the esophagus after total vagus section, I was struck by the difference between the primary and the secondary results of the operation. The primary result, seen during the first twenty-four hours after the esophagus is isolated from the central nervous system, is apparently a complete paralysis. Food, pushed onward by the still efficient cervical gullet, accumulates in a widely distending mass in the lower esophagus and may stagnate there for hours with no indication of any reaction of the encircling wall. In a few days, however, a remarkable recovery of function occurs in the lowest part of the tube, which is provided with smooth muscle. Contraction and peristalsis now appear in this region when food accumulates. An important factor for arousing these activities seems to be the stretching of the esophageal wall. For example, in the first days of recovery, a slender mass spread along the tube may lie for some time unmoved; the addition of a second mass, which causes further distention of the wall, results instantly in contractions and peristalsis. And similarly after some of the food has been driven into the stomach, the strand that remains, now reduced to a slender mass again, lies for long periods without arousing any movements of the gullet. As days go by, the lower thoracic esophagus becomes more responsive to the presence of contained material, for the material is forced into the stomach with increasing rapidity, and even slender masses are now sufficient cause for peristalsis.¹

What is true of the lower thoracic esophagus is also true of the stomach. If the splanchnic nerves are severed (in the cat), the normal movements of the gastro-enteric canal are not altered. If now the vagus nerves are cut, the immediate result is defective functioning. For twenty-four hours after isolating the stomach from the central nervous system,

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1. Cannon: *Am. Jour. Physiol.*, 1907, xix, 441.

the discharge of food is much retarded. Later there is a recovery of almost normal activity.²

A suggestion of the condition which makes possible the restoration of peristalsis in both the isolated esophagus and the stomach was found at autopsy of animals killed two weeks after total vagus and splanchnic section. The stomach was found in remarkable tonic contraction.³ In two instances the diameter through most of the length ranged between 1.5 and 2 cm.—a smallness of size almost incredible when compared with the diameter of the stomach filled with food. The question at once arose as to whether this tonic contraction was not in fact fundamental to the rhythmic movements.

This suggestion was first tested by injecting material into the stomach when that organ was in different degrees of contraction. If the abdomen is opened under warm normal salt solution, sometimes the empty stomach is found large and flabby, with collapsed walls, at other times it is small and contracted. Under these different circumstances the injection of a mushy mass has quite different effects. The flabby stomach simply gives way before the pressure of the injected material, without any reaction; the tonically contracted stomach, on the other hand, begins, as soon as sufficiently distended, to exhibit peristaltic waves.

The importance of the tonic state is further attested by injecting into a vein a small dose of epinephrin (P. D. & Co.) while the gastric peristaltic waves are running. This produces complete relaxation of the stomach and a cessation of peristalsis. The pressure on the stomach contents (which measures the tonus of the neuromusculature) falls to zero. A careful record of the movements of the gastric wall in the pyloric end, with simultaneous record of intragastric pressure, shows that the pressure begins to rise in the stomach, i. e., the tonic state begins to be established, before peristaltic waves begin to travel towards the pylorus.

The importance of tonus to rhythmic activity can be demonstrated also with the excised stomach. If an inactive stomach is removed from the body, is filled with warm water, is tied at the two ends, and placed in warm oxygenated Ringer's solution, it usually shows no sign of peristalsis. If, now, a small amount of barium chlorid is added to the Ringer's solution, the stomach becomes tonically contracted and peristaltic waves are generated.

The foregoing observations on the relation of tonus and peristalsis in the stomach are amplified and elucidated by an examination of these relations in the colon. All investigators who have studied antiperistalsis

2. Cannon: *Am. Jour. Physiol.*, 1906, xvii, 437.

3. "Tonus" is used in this paper to designate a state of more or less persistent shortening of the circular muscle of the alimentary canal.

of the colon have noted that the waves start from the narrow constriction, or tonic ring, nearest the cecum; but the part played by this ring has been overlooked. Two years ago I reported that by producing a tonic ring in the proximal colon (exposed under warm normal salt solution), either by pinching or by applying a weak solution of barium chlorid, moving waves could be made to appear at will. A ring at the cecum repeatedly sends off downward-running waves; a new ring made now near the terminus of these waves starts reversed waves; and a tonic ring made midway in the proximal colon not infrequently will originate waves which pass away in both directions. These phenomena occur not only in the large intestine connected with the body, but also in the excised colon. The phenomena of the tonic ring are therefore of prime importance in explaining the occurrence of antiperistalsis of the colon and possibly also the similar peristalsis of the stomach.

The antiperistalsis of the colon and the peristalsis of the stomach are alike in presenting a series of waves following one another in rhythmic succession. They must, therefore, have a source that is rhythmically active. Careful inspection of the exposed colon over which antiperistaltic waves are passing reveals the interesting fact that the tonic ring, from which they start, pulsates, and that each pulsation sends away a moving ring of constriction.

The pulsations of the tonic ring and the discharge of waves from it are dependent on a state of tension. Thus if, while the waves are running from a ring, the fluid contents are largely withdrawn, visible waves cease. Reintroducing the fluid starts the waves again. The observation which I reported in 1901, that antiperistalsis begins whenever new material is pushed into the colon from the ilium, agrees completely with the experimental evidence that distention of the intestine is the condition for the appearance of the waves.

Mechanical stretching is well recognized as a most efficient stimulus for exciting activity in smooth muscle. The evidence already cited for the esophagus, stomach and colon, is supported by similar observations on the small intestine,⁴ ureter⁵ and bladder.⁶ Since smooth muscle surrounds hollow organs, which gradually fill and must be emptied, the value of distention as a stimulus is obvious.

The extension of smooth muscle which evokes a contraction must not, however, be merely the elongation of non-elastic substance. This is a point which I wish especially to emphasize. When an organ with walls of smooth muscle is flaccid and toneless, distention calls forth no response. As already noted, such is the case in the isolated esophagus

4. Bayliss and Starling: *Jour. Physiol.*, 1901, xxvi, 134.

5. Sokoloff and Luchsinger: *Arch. f. d. ges. Physiol.*, 1881, xxvi, 467.

6. Guyon: *Compt. rend. Soc. de Biol.*, Paris, 1900, lli, 712.

and stomach immediately after severance of the vagus nerves; such is the case in the rectum⁷ and bladder⁸ immediately after the nerves have been cut which supply them with tonic impulses; such is the case also in the atonic colon. I have repeatedly attempted to call forth rhythmic contractions both in the atonic stomach and in the atonic colon, by distention, but without success. Only when the muscle is shortened and resilient, i. e., in a state of tonus, does stretching result in a contraction. The tonic state, therefore, is quite as important as the internal pressure—indeed, it is the condition for the existence of that pressure. And when stretching is said to be the efficient stimulus for rhythmic contraction of smooth muscle, the statement implies that the muscle is in a condition to be *stretched*.

Moderate loads applied to smooth muscle extend it more when it is in a short state than when it is in a long state.⁹ At the tonic ring of the colon, therefore, the neuromusculature, because shortened, is especially subject to distention by internal pressure. And being in a tonic state, it will respond by contraction.

A single contraction in a rhythmic series consists of almost symmetrical stages of shortening and relaxation. During the stage of shortening and the first part of the stage of relaxation there is evidence that the neuromusculature of the alimentary canal is relatively refractory to stimulation.¹⁰ When the tonic ring, therefore, begins to contract in response to distention, it becomes non-irritable to the stimulus, i. e., to the internal pressure. It begins again to be subject to this stimulus after having reached its most contracted state and having become partly relaxed—when again readily distensible. Now on being distended by the internal pressure, the ring is stimulated and, as before, responds by contraction. Thus the neuromusculature in a tonic state responds to a distending pressure by contraction, and the refractoriness which develops during the contractile phase and the lessened irritability during relaxation assure a rhythmic response. These factors can all be reasonably invoked to explain the pulsations of the tonic ring.

The spread of the contraction from the pulsating ring along the intestine, as a wave, is probably another instance of a widely observed phenomenon in simple neuromuscular structures, the passage of the state of excitation from a contracted region to a stretched region.¹¹ Evidently a contraction of the tonic ring must increase internal pressure on neighboring parts of the intestinal wall. If these neighboring parts

7. Elliott and Barclay-Smith: Jour. Physiol., 1904, xxxi, 289.

8. Elliott: Jour. Physiol., 1907, xxxv, 424, 425.

9. Schultz: Arch. f. Physiol., 1903, Suppl., p. 25.

10. Ducceschi: Arch. per l. Sci. Med., 1897, xxi, 170; Magnus: Arch. f. d. ges. Physiol., 1904, ciii, 540; 1906, cxi, 152.

11. See von Uexküll: Ergebn. d. Physiol., 1904, iii., 4.

are in tonic contraction, they are thereby set in increased tension. Then distended area, the muscle rings of this area begin to contract and thus either independently, as a result of extra stretching, or because the excitation, which is manifested in pulsation of the ring, spreads into the freshly to distend the regions beyond. The wave thus passes from the pulsating ring to inactive regions of the intestine; and since the constriction trails behind it an area of lessened irritability it cannot return on its course but must always move away from its place of origin.

The precise relation between the degree of tonus and the internal pressure that results in rhythmic contraction, is difficult to define. When a tonic ring is first made in the colon, it is a deep and strong contraction and it manifests no evidence of pulsations. Only when it has to some extent relaxed does it begin to beat rhythmically. On the other hand, if the internal pressure is sufficiently increased, the waves moving along the intestine will disappear and can be seen again only when the distention is reduced. Both the tonus and the distending force, therefore, can be too great for rhythmic action.

From the foregoing evidence and discussion, it is clear that, given the state of tonus in the neuromusculature of the colon, and a locally increased tonic contraction opposing an internal pressure, the characteristic antiperistalsis can be explained. As already stated, gastric peristalsis has many features in common with colonic antiperistalsis. Can the same principles be applied to explain the rhythmic gastric movements?

The stomach when first filled has roughly a conical shape—the circumference is large at the cardiac end and progressively smaller as the pylorus is approached. If the contents are fluid or semifluid, and are subjected to the tension of the gastric musculature, the pressure throughout the contents (gravity aside) will be uniform. Every unit area of the wall will be supporting the same pressure. Obviously, then, a circumference of given width in the larger cardiac end will be subjected to greater total stress than a circumference of equal width in the smaller pyloric end.

Since the forces in the inactive stomach are in equilibrium, however, the encircling muscle of the cardiac end necessarily has to exert stronger tension than that in the pyloric end. And furthermore, since the muscular wall of the cardiac sac is thinner than that of the vestibule, there are fewer muscle fibers in equal cross-sections. The greater circumference and the weaker musculature both tend to place the cardiac region at a disadvantage. The tension of the muscle in this region, therefore, must determine the pressure in the stomach.

The necessity of tone as a condition for gastric peristalsis, and the existence of a tonic state during digestion (as shown by intragastric pres-

sure) have already been mentioned. The application to the stomach of the factors used to account for the rhythmic contractions of the colon involves first of all a consideration of the degrees of relation between tonus and internal pressure. As noted in the discussion of the activities of the colon, the internal pressure may be too slight to stimulate the tonically contracted muscle, or it may be too great. Because of the conical shape of the stomach it is quite possible for a pressure to be produced too great for the neuromusculature of the distended cardiac end and too little for that of the pyloric end. Between the large cardiac and the small pyloric ends, however, the relations between internal pressure and tonus will be intermediate, and at some point the relations will be suitable for a contractile response. The material displaced by a contraction must be accommodated in the cardiac region where the weakest muscles are working against greatest obstacles. As the contracted band relaxes, however, the tonic pressure from the cardiac end again puts it on a stretch. Thus the contraction would be repeated rhythmically at this point, for the same reasons that were given for rhythmic pulsations of the tonus ring in the colon.

Each pulsation of the adapted gastric band will send off a wave toward the pylorus. The wave will not travel in the opposite direction (towards the fundus), because the cardiac sac is too much stretched to respond; if it were not, it would itself be the site of the pulsating band.

In harmony with the preceding argument is the observation that when peristaltic waves are running on the stomach, their place of origin can be shifted towards the pylorus by increasing internal pressure, or almost to the fundus by decreasing that pressure. In the first procedure the overstretched region is extended and the pulsating circumference, having to meet a greater distending force, is moved to a region where the muscles are stronger and lie in a smaller ring. In the second procedure precisely the opposite occurs—the muscles of the cardiac end, gradually less stretched beyond their responding power, begin to contract and in consequence the pulsatile source of the waves is moved farther towards the area of weakest musculature and longest circumference.¹²

As the stomach empties, the mid-region becomes narrow. The waves then originate at the upper end of a gastric tube, at a pulsating ring which separates the tube from the cardiac sac. The ring forms a depression which has been repeatedly noted in *x-ray* photographs of the human stomach,¹³ and is observable also in the exposed stomach of lower animals. In radiographs this persistent constriction has been designated the

12. Cannon: *Am. Jour. Physiol.*, 1911, xxvii, p. xiii.

13. See Kaestle, Rieder and Rosenthal: *Arch. Röntgen Ray*, 1910, xv, 21-24.

"*incisura cardiaca*." The activity of this deepened ring can best be explained in the same terms that were used to explain the activities of the tonic constrictions of the colon.

Since the stomach when full has a conical shape, the formation of a gastric tube of fairly uniform diameter requires a greater contraction at the cardiac end of the tube than at the pyloric end. Because the cardiac incisure, at the extreme cardiac end of the tube is therefore more contracted than any other part of the stomach, it, like the tonic ring in the colon, is probably more easily distended than any other part. Distention by internal pressure causes the tonic ring to respond rhythmically. Each contraction sends off a wave towards the pylorus. And as the food is forced on into the intestine, the cardiac sac, by tonically pressing on its contents, provides more material for the waves, while helping to maintain the internal pressure necessary for the continuance of gastric peristalsis. Only after the contents, the medium for exercising internal pressure, have disappeared, does gastric peristalsis normally cease.

Distention of a tonically contracted neuromusculature explains not only the rhythmic activities of the stomach and colon, but also those of the small intestine. The contractions of the intestine can be increased, within limits, both in extent and vigor by an increase in the distending force, or if the contractions are absent they may be started by distention.¹⁴ When a distending balloon is introduced into the intestine, the contractions are most marked in the region of greatest tension.¹⁵ The violent segmenting activity in cases of obstruction¹⁶ also point to distention of the gut as a cause of rhythmic contractions. Indeed rhythmic segmentation itself is an excellent example of the response of the intestine to stretching, for the contraction each time occurs in the bulging region, about midway between two previous contractions.¹⁷

In the esophagus, the stomach, the colon, and the small intestine, the importance of tonus has now been explained. It is the prime condition for that tension, or stretching, which has long been recognized as the most effective means of rousing contraction in viscera with walls of smooth muscle. When that tension is developed, contraction results; and if the tension persists, the contraction recurs. It recurs as soon as the neuromusculature can recover from a previous contraction. The result is that *rhythmic* activity appears—the activity most obviously characteristic of all movements of the alimentary canal. Since, therefore, the tonic state underlies all these exhibitions of rhythmicity, it is important to consider the conditions under which tonus is developed.

14. Bayliss and Starling: Jour. Physiol., 1899, xxiv, 105.

15. Bayliss and Starling: Jour. Physiol., 1901, xxvi, 134.

16. Cannon and Murphy: Am. Surg., 1906, xliii, 522.

17. Cannon: Am. Jour. Physiol., 1901, vi, 256.

When the vagus nerves are cut, the movements of the esophagus and stomach are for some time in abeyance; and even when peristalsis reappears the constrictions at first are weak and relatively ineffective. On the other hand, repeated stimulation of the vagus nerves causes an increased and more permanent tonic contraction of the gastric wall, and as the tonus increases the peristaltic constrictions increase in vigor.¹⁸ We may conclude, therefore, that the function of the vagi is that of setting the neuromusculature in a tonic state, of making it exert a tension, so that in relation to the contents it acts as if stretched by those contents.

The evidence already adduced to show the importance of the tonic state for normal functioning is reinforced by the observation previously mentioned that when all extrinsic nerves are cut, the esophagus and the stomach develop in time, within themselves, a tonic state. Whether the vagi are present or not, therefore, the neuromusculature must be in tonus and in tension before response will occur. In all probability the vagi adapt the size of the stomach to the varying amount of food ingested. Thus, if the stomach were relaxed, these nerves might set the musculature into tension about a small amount of food which would not by itself produce any tension whatever. When these nerves are severed, however, and time is allowed for the development of an autogenic tonus, the autogenic tonus compensates by rendering the stomach so contracted that even if a small amount is swallowed the muscle is stretched and peristaltic activities are at once started.

The question now arises as to the stage in the digestive process at which vagus influences affect gastric tonus. That impulses pass down the vagus nerves to the stomach during mastication and ingestion of food was proved by Pawlow's observation on the psychic secretion of the gastric juice.¹⁹ As already stated, repeated stimulation of the vagi results in an increased tonic state which is much more persistent than that which follows single stimulation. Since a tonic state is necessary for gastric peristalsis, and since, as we have seen, peristalsis does not appear if the vagi are cut shortly before food is eaten, the inference is that, just as there is psychic secretion, so also there is psychic tonus. At present, however, no direct evidence for this inference has been secured.

After digestion is well started, the vagus nerves can be severed without altering either the nature of gastric peristalsis or the rate at which the stomach empties itself. This statement is based on observations by means of *x*-rays, also on inspection, and on records of intragastric pres-

18. May: *Jour. Physiol.*, 1904, xxxi, 262.

19. Pawlow: *The Work of the Digestive Glands*, London, 1902, p. 50.

sure when the digesting stomach was exposed under salt solution. The initial tonus (psychic?) might be aroused while food was being ingested, and might continue for a period of some minutes thereafter. Then the tonic state must be maintained by other agencies. As the above evidence, together with observations on the excised stomach, shows, the tonic state, once established at the beginning of gastric digestion, is self-supporting. And again like the psychic secretion, it maintains itself by some local mechanism.

The small intestine is also supplied with "motor" impulses by the vagus nerves. Stimulation of these nerves, in the absence of the splanchnics, results in a brief inhibitory phase, followed by a rise of tonus and a gradual increase of rhythmic contractions to an extent above the normal.²⁰ In all probability, therefore, the vagi act on the intestine, just as they act on the stomach, to produce a tonic condition of the neuromusculature. In this connection it is interesting to recall Magnus' experience in studying isolated pieces of intestine, that the strips beat more actively when removed from a normally-fed animal than when removed from an animal that was not digesting.

The tonus of the colon is increased by the pelvic visceral nerves which belong to the sacral autonomic system. They are distributed especially to the distal part of the colon. Nevertheless, Elliott and Barclay-Smith report that stimulation of these nerves first increases the tone of the mid-region of the large intestine, and that then antiperistaltic waves may arise in the region of increased tone.²¹ Severance of these nerves causes evident disturbance of the movement of the colon. The loss of the tonic impulses results in accumulation of feces, and in weak and sluggish contractions just as is the case when the vagus impulses are removed from the esophagus and stomach.

Looking back over the evidence here adduced we see that double provision is made for the establishment of a state of tonic contraction in the alimentary neuromusculature. Almost the entire length of the digestive canal is supplied with extrinsic nerves which when stimulated cause an increase of tone and when destroyed leave the canal at first in a toneless state. And if the canal is entirely separated from the central nervous system it has a remarkable power of developing an independent tonic state. When thus isolated, the canal regains its characteristic movements only as it recovers tone. Tonus is therefore fundamental. It supplies the resiliency that causes the state of tension when the canal is filled, or establishes the state of tension when the canal is only partly filled. The state of tension is the occasion for the contraction of viscera which

20. Bayliss and Starling: *Jour. Physiol.*, 1899, xxiv, 131.

21. Elliott and Barclay-Smith: *Jour. Physiol.*, 1904, xxxi, 282, 283.

are walled with smooth muscle holding a nerve net. Refractoriness to stimulation during contraction, and gradually increasing irritability during relaxation, result in a rhythmic response to the condition of tension. The most characteristic feature of the movements of the alimentary canal, their rhythmicity, can thus be accounted for.

The view that tonicity of the neuromusculature of the alimentary canal is a fundamental necessity for the appearance of rhythmic movements harmonizes many diverse observations. It accounts for the failure of efficient motility in atonic states of the stomach and intestines. It gives a reasonable explanation for the existence and importance of extrinsic motor nerves. It is in agreement with the observation that tonic contraction and rhythmic peristalsis disappear together in cases of general bodily weakness, when the depleted central nervous system may be supposed to fail to deliver the necessary tonic impulses; it is also in agreement with the observation that worry, anxiety and distress stop gastro-intestinal movements, for such states, accompanied by splanchnic impulses, abolish tonus. It fits admirably with the fact that the stomach of hungry animals is strongly contracted, for then the tonic state makes the organ ready for instant action on swallowed food. Indeed I am inclined to believe, for reasons which time does not now permit me to develop, that the sensation of hunger results from tonic contraction of the empty stomach. These are only some of the conditions in which the importance of tonus for movements of the alimentary canal is manifested; doubtless other conditions will suggest themselves.

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