OBSERVATIONS ON THE MOTILITY OF THE DUODENUM AND THE RELATION OF DUODENAL ACTIVITY TO THAT OF THE PARS PYLORICA

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In an earlier paper, in which the relation of motility in the antrum to motility in the pyloric sphincter was discussed, attention was called to the observation that certain alterations occurring in these parts were associated with duodenal activity (1). The experiments here reported bear specifically on the relation of duodenal motility to the motor activities of the stomach.

Methods. The observations presented herein are based on graphic observations made on 23 dogs. In addition to these experiments, direct observations were made upon 3 dogs the viscera of which had been exposed in a warm saline bath. Graphic records were obtained from both anesthetized and conscious animals at various intervals of time following the operation for the placement of apparatus. Ether anesthesia was used throughout operative procedures. In 3 dogs a morphine narcosis (10 mgm. per k. subcutaneously) was employed and ether used only during the actual preparatory operation.

Briefly, the operations consisted of placing the chambers of a compound enterograph (1) in the first portion of the duodenum and in the antrum or pyloric canal through an opening in the fundic portion of the stomach. After securing the apparatus in position the openings in the stomach and abdomen were closed separately about the small, heavy rubber tubes leading from the chambers (balloons) of the enterograph. Aseptic precautions were observed in all cases in which the animal was permitted to survive for a period longer than 12 hours. In two experiments a simple, rigid pylorograph, previously described (2), was placed in the lumen of the sphincter and in the first part of the duodenum a free balloon, the conduit from which was brought out through the walls of the duodenum and abdomen. This procedure was abandoned by
reason of the immobility of the duodenum resulting from the trauma incident to operative methods.

The various types of apparatus used in obtaining graphic records are modifications of the pylorograph (2) and double-chambered enterograph (1). These enterographs consist of chambers (modified balloons) which, when in position, occupy the first portion of the duodenum and either the lumen of the antrum or the pyloric sphincter. Triple-chambered enterographs also were constructed for the purpose of obtaining synchronous readings of the activities in the antrum, sphincter and first part of the duodenum. The details of construction of these devices are illustrated diagrammatically in figure 1. The chambers of the

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![Fig. 1. Diagrams of various types of enterographs. 1, Double-chambered, semi-rigid enterograph used in obtaining synchronous antral and duodenal tracings. P, Sloping surface spool for sphincter fixation. Fixation was further secured by a ligature around the base of the spool stitched into the antral musculature. 2, Rigid, double-chambered enterograph used in obtaining synchronous readings of sphincteric and duodenal activity. The large flange on the gastric side of the sphincter chamber acts as a barrier to the passage of the apparatus into the duodenum. Fixation was further secured by stitching the ligatures about the bases of the sphincter chamber into the musculature of the gastric and duodenal walls. 3, Flexible, triple-chambered enterograph used in obtaining synchronous readings of antral, sphincter and duodenal motility. The vents leading from the three chambers are heavy rubber tubes. The disadvantage of this device is that pressure on the distended chambers tends to lengthen their long diameter. 4, Rigid, triple-chambered enterograph constructed so that pressure on the chambers can only result in the diminution of their cross diameter. Fixation of this apparatus is similar to that used for the double chambered enterograph. D, Duodenal chamber; P, pyloric chamber; A, antral chamber. V, Vents connected by heavy rubber tubing to water manometers. Chambers D and A are covered with condom rubber; P, with a section of finger cot. Portions shown in solid black are made of hard rubber.](image-url)
enterograph are connected by means of heavy-walled rubber tubing with manometers carrying from 5 to 30 mm. of water pressure for balloon distention. Piston, bellows and tambour recorders were used for the graphic registration of motility. Save for the water manometers, air transmission was used entirely.

Graphic records were obtained from stomachs recently emptied and from those containing various amounts of food; starved animals were not studied.

Results: Direct observations on the exposed duodenum. Motility in the duodenum, exposed in a warm saline solution, arises as a constriction band on the hepatic surface approximately 2 cm. distal to the pyloric ring, or in the terminal portion of the so-called "duodenal cap" in man. This primary contraction is immediately followed by the contraction of increasing numbers of fibers until finally a considerable portion of the duodenum is in a state of high contraction. This phase is followed by rapid relaxation which, beginning at the point of primary contraction, passes down over the previously constricted area. Such motor phenomena at times appear rhythmically, the positive phase of the cycle in the duodenum following immediately the positive phase of the cycle in the antrum. The duodenum may demonstrate a high degree of tonicity (contraction) and active segmentation from the distal portion of the "cap" to a point 2 inches distant.

The rhythmic segmental activity of the small intestine, so well described by Cannon (8), is readily discernible in the duodenum; however, there often appear in this region of the gut movements which do not conform to the segmental type of motility. Of this more will be said in the discussion of our graphic findings. A given portion of the duodenum often executes rhythmic contractions of equal strength (segmental contractions) for a considerable period of time. At other times the same portion of intestine may show groups of contractions, the first of which is powerful, followed by from one to four contractions of varying intensity, such a series of variations being similarly and successively repeated. At no time was segmental action seen in the "cap" region; however, this part of the intestine showed alterations in size which apparently depended upon the degree of force with which material was delivered into and withdrawn from it.

Graphic observations on duodenal activity. The most constant type of motility in the first part of the duodenum, as indicated by our graphic methods, is rhythmic segmentation (8). The segmental contractions occur at the rate of 3 to 5 per antral cycle, i.e., 15 to 25 a minute. An
individual segmental action, as has been shown by previous investigators, is characterized by a contraction and a relaxation phase.

Graphic records obtained by us usually showed changes which corresponded to alterations in intra-abdominal pressure incident to respiration. Before proceeding further we wish to discuss briefly these changes both because they were unavoidably recorded and because in some instances at least they might be confused with the motor activity of the gut itself.

These respiratory markings are especially well defined or even exaggerated in cases where duodenal activity and tone are diminished. When, on the other hand, the duodenum is highly active, respiratory movements affect the recording apparatus only slightly and appear as negligible irregularities on the duodenal curves. The influence of these respiratory changes in an animal demonstrating reduced duodenal motility is shown graphically in figure 2. Here, during the completion of one sphincter cycle, \( Y \), there occur eight acts of respiration superimposed upon what appear to be three and one-half feeble duodenal contractions. In contrast to this marked effect it will be noted that on the sphincter trace, \( C \), the same respiratory movements produce only slight irregularity during the relaxation phase. The same eight respiratory movements are shown on the duodenal tracing, \( A \), as definite two-phased curves. That the difference in respiratory influences upon these duodenal and sphincter records is due to a difference in tone of the viscus rather than to a difference in the thickness of wall or some other factor, is well illustrated by figure 3. Here is shown the record of an active duodenum on which the respiratory variations appear as relatively slight peaks or irregularities upon the segmental contractions. In such traces respiratory movements are of minor or negligible importance except during the relaxation phase of duodenal activity at which time they may so alter the curve as to suggest the presence of a phase of inhibition in the duodenal musculature preparatory to a following contraction. That such is not the case is shown in figure 3, and trace 3 of figure 4, by the relation of such apparent inhibitions to the respiratory phases.

Irrespective of respiratory influences, segmental actions of the duodenum show peculiarities in the phases of the individual contractions and in the relation of these contractions to each other. This work deals specifically with those types that recurred commonly enough to be considered normal activity. The more constant types of graphic records obtained by us are as follows: \( a \), Segmental contractions re-
curring at a fairly uniform rate and rising from a nearly constant tone level (figs. 3, insert A and 4, trace 3); b, groups of contractions, 3 to 5 in number, in which the individual contractions show variations in their height, the rate and tone level remaining nearly constant (fig. 3, insert B); c, groups of segmental contractions, 3 to 5 in number, in which the contraction remainder itself varies in such a manner in the group as to give the impression of a tone wave upon which the segmental contractions are built. Such tone waves recur more or less rhythmically (fig. 4, traces 1 and 2); and d, modifications in tone level associated with variations in the appearance of segmental contractions.

Fig. 2. Synchronous tracings of duodenal, pyloric sphincter and blood pressure activities; experiment 19; January 22, 1920. Ether used throughout the experiment. Records begun immediately following operative procedures. A, Trace showing the relation of changes in intra-abdominal pressure on duodenal motility; B, blood pressure tracing showing respiratory waves; C, sphincter contractions. The perpendicular lines from X and Y approximately indicate the relation of respiratory movements to blood pressure, and to actions of the duodenal and sphincteric musculature.
Fig. 3. Graph showing synchronous tracings of sphincter and duodenum and the influence of changes in the intra-abdominal pressure on the sphincter and duodenum. Experiment 42; May 3, 1920. Ether used throughout the experiment. S, Phyloric sphincter; X, respiration; D, duodenum. Time in seconds. Numerals indicate synchronous points. R, Relative point in the duodenal trace at the moment of greatest reaction in the intra-abdominal pressure.

Insert A: Experiment 3; December 22, 1919. Trace showing rhythmic segmental contractions of the first part of the duodenum following the administration of morphine, 10 mgm. per kg. The irregularities in the waves represent the effects of respiratory movements. Insert B: Experiment 28; February 21, 1920. Trace of duodenal activity in a dog two weeks after the production of a gastric fistula. Tracing obtained on conscious animal.
Fig. 4. Experiment 42; May 1920. Ether used throughout experiment. Records begun immediately following closure of the abdomen; $D$, duodenum; $S$, sphincter. Time in seconds. Traces 1 and 2 show the relation of segmental contractions of the duodenum to the cycles of the pyloric sphincter. In $D$ of trace 2, a line is shown drawn to connect the points of greatest relaxation. It shows a close relation to the phases of the pyloric sphincter. Trace 3 shows duodenal segmental contractions as obtained on a fast drum. $X$, time occupied by complete sphincter cycle; $A$, crest of sphincter cycles; $R$, points corresponding to respiratory changes.
a. Rhythmic segmentations of the duodenum in which the two phases of the individual contractions are equal appear to bear no functional relationship to gastric motility. Duodenal contractions of this nature occur during an interval of constant tone level and may continue for a considerable period of time without showing essential alterations either as to rate or intensity (figs. 3 and 4, trace 3). This particular type of motility was observed in the three dogs which had received morphine prior to or after operative procedures. Similar activity was observed, though less frequently, in etherized dogs and following the administration of small doses of pilocarpine. When larger doses of pilocarpine were used the duodenum usually entered upon a state of maintained contracture or tone during which segmental activity was either diminished or abolished. This latter condition was also observed preceding the act of vomiting.

b. At times segmental contractions, although arising from a nearly constant tone level, show marked alterations in the height of the individual contractions. For instance, in the insert B of figure 3, it will be noted that segmental contractions tend to become grouped in such a manner as to suggest periods of increased and decreased strength recurring with a certain rhythm. Such groupings, as will be shown more fully below, are more or less definitely associated with phases of motility in the pars pylorica.

c. In the third type of duodenal activity the individual segmental contractions, as stated above, are so grouped that a line connecting their points of greatest relaxation forms a definite wave. The duodenal trace of figure 4, trace 1, greatly resembles that of figure 2, previously described. However, in the present case the individual curves represent segmental activity and are not the result of respiratory changes; the latter show as slight irregularities of the individual contractions. The duodenal trace of figure 4, trace 2, shows beautifully this grouping into waves of segmental contractions. The dotted line which connects roughly the points of greatest relaxation will serve to bring out clearly the rhythmic alterations in “contraction remainder” that is under discussion. This type of duodenal activity was observed by us both in animals while under the influence of ether and those that had been permitted to recover from the influence of the anesthetic. Such tracings were often obtained over relatively long periods of time irrespective of the reception of material from the stomach.

d. Under experimental conditions duodenal toneicity was found to vary greatly, such changes being associated with alterations in rhythmic
segmentation. Immediately following the operation for the placement of an enterograph the duodenum usually showed an absence of all motility; however, motility usually reappeared within less than an hour following the completion of operative procedures. Frequently it was possible to initiate duodenal activity and states of high tonicity immediately following closure of the abdomen by moderate, but suddenly applied, distention of the duodenal balloon. A rapid and vigorous distention of the duodenum invariably resulted in the onset of retching or vomiting. Considerable fluctuation in the tone level occurred during the course of an experiment.

The tone levels at which rhythmic segmentations occur in the duodenum appear to bear a definite relationship to the activities in the pars pylorica. As may be noted in figure 5, both the extent of the individual segmental contractions and the level of their occurrence bear a close relationship to antral and sphincter actions. Furthermore, the tracings of this figure show that periods of increased duodenal motility are associated with periods of increased tonicity in the pyloric sphincter. On the other hand, periods of duodenal inactivity and loss of tone, although not associated with actual cessation of rhythmic sphincter action, do occur at times during which the tonicity of the sphincter is low. This relationship is not always present; the duodenum may show marked alterations in tonicity and the height of the individual segmental contractions independently of the sphincteric action. However, since this last type of relation between the sphincter and duodenum was seen by us only following rapid distention of the duodenal balloon, we wish simply to call attention to it. An analogous condition probably does not occur normally.

Tonicity of the duodenum appears to bear a relation to the activity in the antrum which is the reverse of its relation to the activities of the sphincter. As shown in traces 1 and 2 of figure 5, periods of elevated duodenal tonicity are associated with marked reductions in the height of the antral waves while periods of low duodenal tonicity are associated with increased antral contractions.

The type of duodenal activity that we wish to consider especially in its relation to the pars pylorica is that characteristic grouping of segmental contractions, as described in section c, which when taken together form definite waves (figs. 6 and 9). For the present we will refer to these as duodenal x-waves. Whether such waves represent simple tone changes or the passage of a peristaltic wave will be considered following the presentation of further data. Special attention is called
to the fact that our duodenal tracings were obtained from the first 3 or 4 cm. of the duodenum or, as previously stated, just below the region corresponding to the "cap" in man. The activity of the duodenum by which these x-waves were produced was by far the most constant type of motility demonstrated by our graphic methods. As will be shown presently, these waves bear a definite relation in their sequence to the activity of the pars pylorica.

Fig. 5. Tracings showing the relation of tone changes in the duodenum to the activities of the pars pylorica. Trace 1, experiment 15; January 9, 1920. A, Duodenum; B, sphincter. Trace 2, experiment 26; February 14, 1920. No anesthesia used during registration of graph. A, Sphincter; B, duodenum; C, antrum. Trace 3, experiment 4; December 26, 1919. Conscious animal 15 hours after placement of enterograph. A, Sphincter; B, duodenum.

Note that periods of increased duodenal tone are associated with depressed antral and augmented sphincter activity.
Fig. 6. Tracing showing simultaneous activities in the antrum, sphincter and duodenum. Numerals indicate synchronous points. Experiment 22; January 30, 1920. Ether used throughout experiment. Simple, spindle-enterograph. \( S \), Sphincter; \( D \), duodenum; \( A \), antrum.

Note the relation of duodenal activities to those of the pars pylorica.
Relation of antral to duodenal activities. Joseph and Meltzer were the first to call attention to the fact that activity in the descending part of the duodenum in rabbits is associated with inhibition in the gastrium. They state in their brief report: "During each contraction of the pyloric part of the stomach the duodenum stops its rhythmic activity and loses its tone, only to resume both again as soon as the contraction of the stomach passes off" (3). The details of these experiments were not given and up to the present time have not appeared in the literature. However, Joseph informs us that their results were obtained by means of small balloons anchored in the antrum and descending duodenum respectively and that observations were made at intervals up to 30 days after the operations. No mention is made in their report of a possible relation between sphincter and duodenal activities.

The present investigation of the relation of duodenal to antral activity is one of the sequellae of our studies on the motility of the pyloric sphincter (1), (2). This work was begun and practically completed...
before our attention was directed to the above mentioned contribution. We take this opportunity to thank Joseph for his interest in the present investigation.

Simultaneous tracings obtained by the use of a double-chambered enterograph, one chamber of which occupies the antrum, the other the first part of the duodenum, show that the duodenal $x$-waves are intimately associated with the activity in the antrum. The specific re-

Fig. 8. Tracing showing the functional relation of the duodenum to the pars pylorica. Experiment 20; February 14, 1920. Records obtained on conscious animal. $A$, Antrum; $S$, sphincter; $D$, duodenum. Time in seconds. Numerals indicate synchronous points.

Note that the sphincter responds to each action of the duodenum.

relationship of these two portions of the gut is shown in figure 6 and diagrammatically in figure 9 which represents the average of a series (27) of tracings. For the sake of clearness and brevity, this relation between duodenal and antral activities may be considered from figure 9. In this drawing the period for a complete antral cycle, curve $A$, is shown as 18 seconds. Rhythmic segmental activity of the duodenum is shown by curve $DS$. Here the 5 complete segmental contractions,
A, B, C, D and E, each of which occupies approximately 3½ seconds, although the height of the individual contractions varies considerably, group themselves in such a manner as to suggest a wave. A line connecting the points of greatest relaxation (curve DP) in the series of segmental contractions describes an arc which, beginning at X, reaches its greatest height between points 2 and 3. From this point the curve gradually descends to reach the level of its origin (point I), which constitutes the level from which the individual contractions are initiated during the formation of the x-wave. The duodenal x-wave demonstrates

![Diagram showing the average relation of the sphincter to the antrum and duodenum. PS, Pyloric sphincter curve; DP, duodenal peristaltic curve; DS, duodenal segmental contractions; A, antral curve. Time indicated in seconds. C1, C2, C3, diagrammatic representation of the movement of chyme during its passage from the antrum into the duodenum. Note that the first segmental contraction of the duodenum, A, reaches its highest point synchronous with the sphincter and at a time of relaxation of the antrum. Also that the duodenum demonstrates its greatest degree of relaxation, X, after the antrum has ceased contracting and during the period of contraction of the sphincter. The maximal height of the peristaltic wave in the duodenum occurs while the antrum is relaxing prior to the wave of contraction, L.](http://ajplegacy.physiology.org/Downloaded from 10.220.33.5 on April 7, 2017)
least activity at this point; approximately one second after commence-
ment of relaxation in the antrum (point N). The ascent of the first
segmental contraction following maximal duodenal relaxation is rapid
and reaches its height, A, at a time of nearly completed relaxation
of the antrum (point P, curve A). The phase of relaxation of con-
traction A is interrupted at 2 by the appearance of contraction B.
The three remaining segmental contractions show a progressive diminu-
tion of intensity. In contractions A and B the relaxation phases are
not equal to the contraction phases while in curves C, D and E the
relaxation phase is the more pronounced. The duodenal activities, as
shown in this diagram, constituting what we have termed the x-wave,
is therefore composed of graded rhythmic segmentations which occur
from different levels in such a manner as to form a second or DP curve.
This latter curve or wave, forming immediately following the completion
of antral contraction, increases in height to cover a period of relax-
ation of the antrum and returns toward the base line—point of greatest
relaxation—as the antrum enters upon its positive phase. In other
words, the curves DP and DS, presented in figure 9, are the equivalent
of the statements of Joseph and Meltzer; namely, "During
traction of the pyloric part of the stomach the duodenum stops its
rhythmic activity and loses tone, only to resume both again as soon as
the contraction of the stomach passes off." Just what is meant by
"tone" in this quotation is not clear. If it means a reduction of the
level at which diminished segmental contractions occur then it would
appear to correspond to the differences in the height of the curve DP.
Whether curve DP constitutes simply a condition of tonicity or whether
it represents the passage of a definite wave (peristaltic) upon which
segmental actions are grafted is not at present evident. It is evident,
however, that the height of the segmental contractions do show marked
alterations which bear a definite relation to antral activities. For
instance in the duodenal trace of insert B of figure 3, the heights of the
individual segmental contractions tend to form graded series although
the apparent tonicity of the duodenum remains constant. On the other
hand, such alterations of height in the individual segmental contrac-
tions may be associated with incomplete phases of relaxation or form
weak x-waves. In either case the higher segmental contractions appear
following the beginning of relaxation in the antrum (fig. 6). From
this alone it might be argued that the duodenal x-wave represents
nothing more than a tone wave, that is, that increased tonicity permits
of segmental contractions of greater strength while reduced tonicity
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(within limits) results in a depression of segmental contractions. However, the tracings of figures 7 and 8 would seem to show that the duodenal x-waves are not tone waves. For instance, in figure 7 in which two x-waves appear, the second wave originates at a height (tone level) which is much greater than that of the first although the two waves bear the same relation to the activities of the antrum as shown by the synchronous points marked by numerals. In figure 8 rhythmic segmental contractions beginning in an inactive duodenum, show such changes in the level of their origin as to suggest an increased duodenal tonicity over a period of two complete antral cycles. However, it should be emphasized that segmental contractions in the duodenum may occur independently of either tone changes or x-waves, and even in the absence of both. It appears, therefore, that tonicity of the duodenum may vary considerably without altering the relation of the duodenal x-waves to motility of the antrum, and that simple segmental contractions, which are not associated with alterations in the antrum, can occur from a constant level.

Relation of sphincteric to duodenal activity. Sphincter contractions, as shown in a previous paper, reach their highest point at a time when the antrum is rapidly relaxing or is completely relaxed (1). The first segmental contraction which occurs in an x-wave reaches its height simultaneously with that of the sphincter (fig. 9, A curve DS, and Z of curve PS); i.e., the duodenum and sphincter execute contractions which are maximal at the same moment although the duration of contraction of the sphincter is greater than that of the duodenum. The second individual contraction, B, usually reaches a greater intensity than the first but this and the subsequent contractions occur during the period of relaxation of the sphincter. The first segmental contraction, as previously shown, is initiated approximately one second after the beginning of relaxation of the antrum and from the point of greatest duodenal relaxation. On the other hand, the sphincter begins its contraction approximately 2 1/2 seconds prior to the first segmental contraction, A, or while the antrum is still at the height of its contraction phase. Hence the sphincter has reached a high degree of contraction before the antrum begins its relaxation phase and before the duodenum begins a new x-wave or at the time of completion of a previous wave. Therefore, the period of greatest duodenal relaxation from which the first segmental contraction, A, occurs coincided with the period of contraction of the sphincter. The second and third, B and C, segmental contractions occur from higher levels than the primary or first segmental
contraction; the remaining two contractions, D and E, are greatly reduced in height and occur from successively lower levels. Therefore, curves DP and DS (x-wave) reach the greatest degree of contraction between 3 and 4 seconds following completion of the sphincter's positive phase, or during the first portion of its period of relaxation. From this point the heights of the curves DP and DS gradually diminish to finally reach the point of greatest duodenal relaxation and inactivity, point 1. During this period of decline in the x-wave, especially curve DP, the sphincter is rapidly relaxing or quiescent while the antrum is entering upon its positive phase; i.e., a positive phase in the antrum begins during the relaxation phase in the duodenum and sphincter.

In other words, the duodenum demonstrates an inactive phase during the positive phase of the antrum and sphincter which reaches its greatest degree of relaxation (inhibition) immediately following completion of the positive phase of the antrum and when the sphincter has begun its positive phase (figs. 4, 6, 7 and 9).

The results of graphic methods, as described above, show that a fairly definite relation exists between the rhythmic grouping of segmental contractions in the duodenum and the phases of motility in the pars pylorica. An interpretation of these x-waves and of their functional relation to the stomach must, at present, be guarded for the reason that the impression now prevalent concerning the independence of gastric and duodenal activity offers no support to our findings (4). As already pointed out, it is difficult to explain these waves in the duodenum upon the assumption of tone changes. Moreover, if they are tone changes it becomes necessary to explain the origin of such tone changes. *A priori*, there is no reason to assume that the duodenum undergoes tone changes which have the same rate as peristaltic waves in the stomach, and at the same time bear no intimate relation to such waves, especially when material is not permitted to reach the duodenum from the stomach. The character and constant time relation of the x-waves to the acts of the pars pylorica is such as to suggest a continuance of the contraction process which passes over the antrum and sphincter. If these x-waves are to be considered modified segmental contractions then they must be differentiated from the usual segmental contractions of the duodenum because they require a greater period of time for their completion than is commonly thought to be covered normally by rhythmic segmental contractions. Moreover, during the passage of the contraction process over the first portion of the duodenum, rhythmic segmentation continues although the phases of
the individual contractions are markedly altered. At times rhythmic segmentations occur unassociated with alterations in height and without being grouped into rhythmically repeated cycles. Consequently two fundamentally different factors are operative in the production of the x-waves. If rhythmic segmentations can occur unassociated with alterations in intensity and tone level, and if these same rhythmic segmentations can be so altered as to form rhythmically appearing groups of contractions because of activities of the stomach, then it must either be assumed that the appearance of the factor which causes this grouping of segmental contractions excites all types of motor responses, thereby causing alterations in segmental phenomena, or that increased segmental activity gives rise to the formation of x-waves. This latter assumption appears untenable for without the appearance of the factor which causes the production of the x-waves the segmental contractions remain of uniform height and occur from a constant level. Therefore we may assume, at least tentatively, that the factor which causes the grouping of segmental contractions in the first part of the duodenum is a peristaltic wave which has passed into it from the stomach or that the duodenum has been excited because of gastric motility.

As suggested above, rhythmic segmentation may occur independent of, or intimately associated with, gastric contractions. It has been shown that periods of greatly increased tonicity associated with heightened rhythmic segmentations are also associated with a depression in the height of antral contractions and a marked increase in the tone level at which the sphincter demonstrates its rhythmic contractions. Not infrequently the pyloric sphincter responds more or less to each duodenal motor activity. Hence not only may the activities of the duodenum be influenced by the stomach, but also may the activities of the stomach be influenced by those of the duodenum. If, for example, in an exposed preparation, the finger is placed within the lumen of the pyloric sphincter, one notes that with the initiation of a positive motor phase in the duodenum—outer portion of the "cap" region—there is a decided compression on the finger because of the sphincter's contraction. Direct observation at such times shows that the sphincteric contraction occurs immediately following the first dimpling on the greater curvature of the duodenum. Similar results may be obtained graphically by placing a pylorograph in the lumen of the sphincter and noting, at a time of inactivity (complete relaxation), the effect of strong stimulation of the duodenum along its greater curvature. In such an experiment stimulation of the duodenum invariably excites the sphincter to demonstrate motor phenomenon, the period of contraction of which
is short, the phase of relaxation more or less maintained. Three such responses of the sphincter to duodenal stimulation are shown in figure 6, page 136, of a previous paper (1), all of which were obtained from a quiet stomach and duodenum immediately following operative procedures for the placement of a pylorograph. Similar motor relations between the sphincter and duodenum may be seen during the synchronous registration of motility in the antrum, sphincter and duodenum. Such a condition is well shown in figure 8. Here the contractions of the sphincter are of varying height and duration. Prior to the appearance of duodenal activity the sphincter demonstrates only movements which bear the usual relation to the antrum. The same relation is continued throughout the trace as indicated by points 4, 8, 1, however, following the appearance of duodenal activity the sphincter is seen to respond to each duodenal contraction occurring during the inactive phase of the antrum, points 6 and 9, i.e., the sphincter responds not only to the reduced antral contractions but also to the individual duodenal contractions. Here two complete antral cycles are associated with four complete sphincter and duodenal cycles, that is, the appearance of duodenal activity is such as to cause an extra sphincter response during an antral cycle (curves 6 and 9). These extra sphincteric contractions are usually less pronounced than those bearing the usual relation to antral activity although the maximal height of contraction of the duodenum occurs synchronously with the point of maximal contraction of the sphincter in each case. However, this relation between sphincter and duodenum seems to bear some relation to the degree of activity in the antrum; usually antral contractions are reduced in height although they occur rhythmically.

In figure 7 the duodenum demonstrates two complete waves of action, each wave being associated with three segmental contractions, each of which in turn is associated to some degree with alterations in the sphincter, although such alterations occur as minor modifications of the response to the antrum. In this trace a second wave of the duodenum and the corresponding sphincter wave occur from a higher level than the one just preceding or the two immediately following. This condition is analogous to the more marked duodenal-sphincter relation shown in figure 5. With the development of a constant repetition of peristalsis in the duodenum and an active antrum the irregularities in the sphincter curve become greatly reduced or abolished (fig. 6). It therefore appears that a relatively quiet antrum may occur during active duodenal motility, also that periods of increased duodenal activity may be associated with increased motor activity of the sphincter.
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DISCUSSION

Mering, 1893, (5) advanced the theory that the filling of the small intestine reflexly retarded the emptying of the stomach. This view was shared by Schicker in 1911 (6). Marbaix, 1898, (7) contended that it was the duodenum which exerted the influence for the replete intestine on the closing of the pylorus. According to Cannon (9), the degree of gastric acidity determines the reflex opening of the pylorus. Cole (10), from his radiographic studies of the human stomach and duodenum, concluded that the duodenal-sphincter reflex from the replete intestine affects not the pyloric sphincter as believed by Marbaix (7) but the the contractions which withdraw the chyme from the "reservoir cap." This process Cole considers is similar to the one by which the duodenum is replenished from the stomach.

The observations and conclusions of Cole seem to us worthy of note, both because of their clinical and theoretical aspects. It seems logical to assume that the degree of receptivity of the small intestine is as great a factor in the emptying of the "cap" as the motility of the stomach is in filling this region. By way of illustration we may cite the observation that one dog starved 18 hours emptied its stomach of an 8-ounce barium mixture in 80 minutes, while a second meal of the same amount was not completely removed at the end of 2½ hours. Analogous results were observed in human subjects.

The results of our present and previous work show that the acts of opening and closing of the pyloric sphincter are to a great extent dependent upon the motility of the structures lying on either side. That is, the sphincter acts as a functional link in the chain of forward conduction of material from the stomach, thereby aiding both gastric and "cap" evacuation. Our graphic results are in agreement with the radiographic findings of Cole regarding the relation of the sphincter to the duodenum. That is, the "reservoir cap" receives the chyme during the active phase of the antrum, material being held in this region at the time of relaxation of the antrum because of contraction of the sphincter. The duodenum, just beyond the "cap," demonstrates its greatest degree of relaxation (loss of tone) at the close of the positive phase of the antrum and at a time of rapid contraction of the sphincter. However, following this period of maximal depression, the duodenum develops a positive phase as evidenced by the appearance of an x-wave the first segmental contraction of which reaches its maximum along with that of the sphincter or at a time of marked relaxation in the antrum. Thus the positive phase of the duodenum is well initiated at
the moment of beginning sphincter relaxation. Therefore, this positive phase in the duodenum associated with a powerful initial segmental contraction, both of which are initiated during the period of sphincter contraction, act in such a manner as to supplement the activity (positive phase) of the sphincter.

For the sake of clearness let us suppose that a single bolus of food is presented to the region of the sphincter during the positive phase of the antrum, also that the antrum, sphincter and duodenum constitute a tube similar to any portion of the intestine demonstrating peristalsis; then, according to the law of the intestine there should be a state of relaxation in the pre-antral region (behind the constricting band), inhibition of the sphincter and lower segments and a positive band of constriction behind the bolus or in the antrum proper. Inasmuch as peristalsis is a progressive phenomenon, the bolus would be expected to pass the sphincter and enter the portion below, namely, the duodenum, the sphincter closing as the result of the positive phase of the peristaltic wave reaching this structure. The antrum and sphincter would now demonstrate their inactive phases while the positive wave would pass over the first part of the duodenum.

Such a hypothetical case as the one just given finds experimental substantiation in our results. The main difference between the hypothetical case and the results of experimental methods is that in addition to the passage of a peristaltic wave over the duodenum there is associated with it the phenomenon of rhythmic segmentation. A further discrepancy appears in that the sphincter not only responds as a functional unit in the progressive movement of a peristaltic wave but also, at times, to each rhythmic contraction in the duodenum. This, however, does not disprove the above statement for, as will be recalled, a true peristaltic wave is one which involves contraction above the food mass and relaxation—inhibition—below.

If the duodenal musculature, because of excitation or because of distention, responds as any other portion of the gut, i.e., inhibition at point of excitation and contraction cranialward, then a band of constriction should appear in the portion next higher, that is, in the sphincter, because this is the first definitely contractile portion behind the bolus in the “cap” region. That the sphincter may respond to individual, rhythmic, duodenal contractions has already been shown. That the sequence of actions in the duodenum as related to gastric motility is not the result of distention of the duodenum because of material delivered to it is evidenced by the fact that this same relation holds
for the motility of the empty stomach and duodenum and also for preparations in which material is prevented from leaving the stomach because of the presence of an enterograph.

If, as contended by Cole, duodenal receptivity controls the evacuation of the "cap" through duodenal peristalsis rather than the evacuation of the stomach through a pyloric sphincter, then it would appear as though the sole function of the sphincter and antrum, as far as motility is concerned, is to assure the filling of the cap. However, the statements of Cole are reconcilable with the present work. Granting that the "cap" is evacuated by duodenal peristalsis—a statement we agree with—such peristaltic movements would of necessity force material back into the antrum save for the checking influence of a contracting sphincter. As shown above, this duodenal wave of peristalsis which withdraws material from the "cap" arises, as far as the duodenum is primarily concerned, in the outer portion of the "cap" along with a powerful segmental contraction at a time when the sphincter is rapidly mounting to the height of its positive phase. Once the peristaltic wave (x-wave) is formed in the duodenum there is no apparent reason for assuming that the sphincter need continue its positive phase. Hence it may be assumed that the sphincter aids not only in the processes which fill the "cap" because of gastric evacuation, but also in the processes which fill the duodenum from the material in the "cap."

Alvarez (4) states: "It is not generally known that there is a fairly complete connective-tissue barrier between the muscle of the antrum and duodenum. Ordinarily there are only a few bundles from the longitudinal coat which pass over. This explains the fact that gastric waves do not run over onto the duodenum. Graphic records show that some influences may pass over to start peristaltic rushes in the bowel, but the deep waves, visible to the unaided eye, certainly stop at the barrier" (p. 614). Again: "There is considerable evidence for the view that the rhythmicity of the primitive gastro-intestinal tube is graded downward from the pharynx to anus much the same as the rhythmicity of the primitive heart tube is graded from the venous to aortic end," however, "in mammals specialization in the functions of the stomach has been accompanied by specialization in the muscle and a loss in the rhythmicity." Possibly the differences between the slow rate of the antrum and the more rapid rate in the duodenum and at the incisurial angularis of the stomach are to be explained on the basis of this muscular modification.
The "connective-tissue barrier" between the sphincter and duodenum is not as extensive in the dog as the above statement leads one to believe. In this animal it is true there is considerable connective-tissue among the bundles of muscle fibers constituting the terminal antrum and sphincter; however, numerous muscle fibers are found connecting the antrum with the duodenum. That connective-tissue should be found in abundance in this region is not surprising in view of the fact that connective-tissue usually occurs in relatively large amounts where it is necessary to supply large blood vessels. The statement that "gastric waves do not run over onto the duodenum" save "to start peristaltic rushes in the bowel" appears to contradict itself. However, the latter statement would seem more logical than the first in the light of the author's own hypothesis. The apparent stoppage of the gastric wave at the sphincter may be assumed, as suggested above, to result because of the degrees of specialization of the musculature beyond this point. In the light of our work it must be assumed that the degree of specialization of the musculature in the sphincter and duodenum of dogs is not sufficient to cause cessation of a progressive movement over the stomach at the pyloric sphincter.

Our graphic results indicate that the factors exciting waves of peristalsis in the stomach are more or less directly responsible for peristalsis in the duodenum, the phases of which bear a definite relation to those of the stomach. Inasmuch as our graphic records show a progressive series of events in the antrum, sphincter and duodenum which bear a constant and definite time relation to each other, we believe that the activities of these three parts conform to the principle of the "law of the intestine." Therefore our results, if correctly interpreted, appear to lend considerable weight to the "gradient theory of the gastro-intestinal tube" as evolved by Alvarez inasmuch as they show a progressive series of events in the musculature of the stomach and the first part of the duodenum.

**SUMMARY AND CONCLUSION**

The outstanding features in the action of the duodenum in relation to those of the pars pylorica may be briefly summarized as follows:

1. The pyloric sphincter, like the antrum proper, demonstrates cycles of rhythmic motility. These cycles are of the same duration as those of the antrum; however, their phases are so placed that they functionally supplement the activities of the antrum. A phase of
inhibition (maximal relaxation) manifests itself during the height of antral contraction. Following this, and while the antrum is finishing its contraction, the sphincter begins its positive phase and reaches the height of its contraction when the antrum is rapidly relaxing or is relaxed. Following this the sphincter relaxes to ultimately reach its point of greatest depression preparatory to a second positive phase.

2. The rhythmic activities of the duodenum, as first shown by Joseph and Meltzer, like those of the sphincter, bear a definite and constant relation to the various phases of the antrum. Peristaltic waves in the duodenum are associated with groupings or segmental contractions the first of which usually has its origin at the same time the positive phase of a peristaltic wave reaches the duodenum, or better, perhaps the appearance of a contraction wave in the duodenum excites rhythmic segmental contractions in the region in which they were previously depressed or abolished because of a preceding wave of inhibition. The peristaltic wave begins in the duodenum approximately one second after the antrum has begun to relax and at a time of rapid contraction of the sphincter and reached its height during the phase of rapid relaxation of the sphincter and while the antrum is entering upon its phase of greatest depression.

3. The observations recorded above shown that the antrum, pyloric sphincter and first part of the duodenum in the dog each possesses definite rhythmic cycles which bear a constant relationship and show a dependence upon each other, that is, parts excited cranialward travel caudalward to excite lower segments. The three portions, therefore, show progressive motility which occurs in a definite sequence and in a manner which we may believe normally causes material to leave the stomach and to be delivered into portions of the gut below the first portion of the duodenum.

4. The sphincter may be excited to cover a phase of motility in the duodenum occurring during the inactive phase of the antrum. The sphincter, therefore, may act not only in relation to the antrum to aid in the propulsion forward of material from the stomach, but also as a barrier to the regression of chyme during the presence of a positive phase of the duodenum.

5. In conclusion, it may be assumed that the progressive nature of the cycles of events in the three portions of the gastro-intestinal canal studied demonstrate "the law of the intestine" i.e., a progressive band of constriction preceded by inhibition and followed by relaxation.
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