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Chapter

Biomechanics of the Small Intestinal Contractions

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Abstract

The small intestine is a part of the gastrointestinal segment comprising of the duodenum, jejunum, and ileum. They help to process the gastric contents for further digestion, which involves mixing with duodeno-biliary-pancreatic (DBP) secretions to facilitate the chemical digestion, and homogenization of the luminal contents through contractions of the circular and longitudinal smooth muscle fibers of the intestine. The contractions of these smooth muscle fibers develops the mechanical forces at the mucosal wall, which as a consequence, transfers its momentum to the underlying fluid to develop the fluid flows, suggesting relevance of mechanics in physiology. The resulting flows are what drive the digestion. Changes in contractility of wave shapes of circular and longitudinal smooth muscle contractions and fluid rheology are known to affect the digestive process through generation of various flow patterns that differ in luminal pressure, peak velocity, extent of shearing/mixing, volume of mixing, and flow rate. Recent studies indicate that the digestive process can be very specific such as to cause lipid digestion through segmental contractions and transport by eliciting propagating contractions, suggesting that the intestine manages to digest a variety of food in an efficient manner by eliciting appropriate contractions.

Keywords: small intestine, small intestinal motility, peristalsis, circular contraction, local longitudinal shortening

1. Introduction

The human small intestine is a part of the gastrointestinal tract which extends from end of the stomach to the inlet of large intestine. They form the visceral organ of our body which helps in processing the food at various levels such as mixing, digestion (mechanical grinding and chemical breakdown), and transport. They are arranged in a complex 3D manner, having numerous folds (convolutions) and flexures. The small intestine is functionally divided into duodenum, jejunum, and ileum; each of which has a specific physiology function to play in the digestion. They enable the digestion of meal in these compartments through coordinative effort. The small intestine elicits a complex series of motility patterns depending on the nature of meal to help (1) mixing with duodeno-biliary-pancreatic (DBP) secretions to facilitate the chemical digestion, (2) homogenization of the luminal contents of intestine, (3) regulation of pH in the duodenum, (4) mechanical disintegration, (5) absorption, and (6) transport. Since the generation of such motility patterns are highly variable and regulated by neurohormonal cues, the process of digestion has been a challenge, hitherto, to explore the mechanisms involved.

The mechanical relevance to digestion dates back to the classical study performed by Cannon on cat's intestine using X-ray [1]. The observations made by Cannon reports, The constrictions causing the segmentation thoroughly mix the food and digestive juices, and bring the digested food into contact with the absorbing mecha*nisms* [1]. Even after a century has passed, the digestion still remains to be mystery; probably due to the multifaceted dimensions of the digestive process. In the recent past, there has been growing literature on the involvement of the mechanics in the digestion. Studies indicate that the mechanics of peristalsis is intertwined with physiological function of the intestine and still remains to be explored. The idea that the mechanics play a key role in the intestinal physiology is best described by Costa and Brookes which reads, The discovery of the presence of multiple neurochemicals in the same nerve cells in specific combinations led to the concept of "chemical coding" and of "plurichemical transmission." The proposal that enteric reflexes are largely responsible for the propulsion of contents led to investigations of polarized reflex pathways and how these may be activated to generate the coordinated propulsive behav*ior of the intestine* [2]. We learn that the digestion system include highly complex organ which manages, *in house*, the enteric controls that are mediated through intramural reflexes (short and long range reflexes), and centralized control mediated through the central nervous system (involving higher nerves centers to process the information relating to gut sensing and relay through efferent nerves). While it has been a mystery for many decades as to how the digestion occurs in the gut, especially the mechanical breakdown, mixing and transiting over the long distance of the bowels, recent studies on mechanics are providing clues pertaining to the mechanisms that may contribute towards an understanding of the process involved at the level of mechanical digestion and their interaction with upstream and downstream players.

In this chapter, we present the current state of art in the area of intestinal biomechanics addressing various aspects of digestion through clinical, mathematical, and computational studies performed so far. This chapter is organized as follows: Section 2 describes the mechanics and physiology of the small intestine. Section 3 provides details as to how the small intestinal motility leads to the development of flows inside the lumen causing mixing and transport. The details of flow resulting from circular contraction are discussed in Section 4. In Section 5, the relevance of the local longitudinal shortening is explored followed by the physiological relevance of motility in Section 6. Since the nature of forces also affect the molecular biology of the cell, the basic principle behind the mechanotransduction is addressed in Section 7. The conclusions are drawn in Section 8 followed by the future scope of the work in Section 9.

2. Mechanophysiology of the small intestine and the small intestinal digestion

2.1 Anatomy

The small intestine is the part of the gastrointestinal tract which connects to the stomach at one end through pylorus and the large intestine at the other end through ileocecal valve (**Figure 1**). The anatomy of the small intestine segments, that includes duodenum, jejunum, and ileum, are discussed in the following.

2.1.1 Antrum

The antrum is a distal part of the stomach which is highly muscular having a thickness of $5.1 \pm 1.6 \text{ mm}$ (depends on degree of distention of antrum [3]), which

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Figure 1.

Anatomical details of the stomach and duodenum showing three layers of muscles—oblique muscle layer (OM), circular muscle layer (CM), and longitudinal muscle layer (LM).

is higher than proximal stomach [4]. Its musculature helps the antral segment to undergo rigorous peristalsis to perform the grinding of the food. They also help regulating the gastric emptying and duodenogastric reflux (DGR).

2.1.2 Pylorus

The pylorus (at L1 level or Lumber region 1) is a muscular tissue that connects the stomach at one end to the small intestine or more specifically the duodenum at the other end. Due to its musculature they contract radially to close or open the valve to cause the flow across the stomach and duodenum. It functions like a valve whereby it can regulate the flow of gastric content into the duodenum.

2.1.3 Small intestine

The small intestine is a muscular and convoluted tube that extends from pyloric region to the ileocecal valve that connects to the large intestine. It is approximately 7 m long and 2–4 cm in diameters and divided into the duodenum, jejunum, and ileum.

2.1.3.1 Duodenum

Duodenum is the shortest segment of them all and is approximately 20–25 cm long and 2.5 cm in diameter. They are responsible to mix the chyme with DBP secretions, cause homogenization and pH transition from acidic to slightly alkaline. The process occurs inside the segment that is divided into four parts as follows: (1) the first part or par superior or duodenal bulb is about 5 cm long which begins its journey somewhere at the pylorus region and ends at the neck region of the gall bladder. Pars superior is the most movable region of the duodenum. (2) The second part or pars descendens is about 7–10 cm long and extends from the neck region of the gall bladder or L1 (lumbar region 1) to the upper border of L4 region. The common bile duct and the pancreatic duct together join and open at the major duodenal papilla into the medial side of this segment at approximately 7–10 cm distance from the pylorus. The minor duodenal papilla, if present, lies above the major duodenal papilla. (3) The third part or pars horizontalis is about 5–7.5 cm long and travels

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across the inferior vena cava and aorta above the upper border of the fourth lumbar region with the superior mesenteric vessels (the vein on the right and the artery on the left) on its front. (4) The fourth part or pars ascendens is about 2.5 cm long and continues to ascend toward the left side of the aorta. At its terminus, it abruptly transforms to a jejuna-like feature, where it forms the duodeno-jejunal flexure. The duodeno-jejunal flexure is connected to the superior mesenteric artery and celiac artery by suspensory muscles of the duodenum also known as the ligament of Treitz (a connective tissue), which marks the anatomical distinction between the duodenum and the jejunum.

2.1.3.2 Jejunum

It forms second part of the small intestine that is roughly 1.5-3.5 m (two-fifth of the small intestine) in length. They are attached to the posterior wall of the abdomen by the mesentery. The interior wall of the segment contains of numerous microscopic finger-like structures known as villi that help increase the surface area of absorption for the jejunum. Most of the nutrients are absorbed in this part of the small intestine. By the time the intestinal contents are emptied into the next segment (ileum), around 90% of all the available nutrients in the food has been absorbed. It also helps to shape the rheology of the digesta by absorbing about 90% of the secreted water, $6-8 l day^{-1}$.

2.1.3.3 Ileum

It forms the last segment of the intestine that is roughly 2.5–3.5 m (three-fifth of the small intestine) in length and ends at the intraperitoneal pouch known as cecum (where undigested food settle down). The remaining parts of the nutrients that have passed through the jejunum are absorbed here (also absorbs vitamin B12 and bile acids). The segment contains numerous lymphoid follicles (forming Payer's patch; mainly function to survey and respond to pathogens). They are attached to the posterior wall of the abdomen by mesentery (giving flexibility to the bowels to adjust in the abdominal cavity during act of peristalsis and intestinal transit).

2.1.4 Ileocecal valve (ileal ostium)

The valve is a muscular tissue that separates the contents of the small intestine from those of the large intestine. They help in controlling the volume of flow occurring from the large intestine into the ileum and as a consequence of this, help in regulating the bacterial growth (involved in causing small intestinal bacterial overgrowth; SIBO) in the small intestine in conjunction with the small intestinal motility. It also helps in vitamin B12 absorption and collecting most of bile acid (terminal ileum) to replenish for the secreted bile for reuse (via entero hepatic circulation) [5]. They play a key role in preventing reflux of the bacteria-rich content from the large intestine into the small intestine; thus forming a barrier separating the two bowels.

2.2 Generation of smooth muscle contractions: the precursor to luminal flows

The intestinal musculature comprises of the smooth muscle fibers arranged in intertwined bundles; interconnected to the neighboring smooth muscle fibers through gap junctions. This enables two neighboring muscles to be electrical coupled. The gap junctions provide a way to propagate the electric potential (a wave of depolarization) from one fiber to the other, thereby spreading across adjacent segment of the intestine resulting in a muscular contraction (initiated as a consequence of

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depolarization above threshold) to traverse the segment. In physiology, the membrane of the small intestinal smooth muscle (especially the myogenic cells) cell shows rhythmic changes in their electric potential which is referred to as the slow waves (resting membrane potential of -50 to -60 mV). Slow waves are the waves of partial depolarization of the membrane having the transmembrane potential of 5-15 mV. They help in nominal depolarization of the membrane, but do not initiate a muscle contraction. It is only during the condition when the membrane potential of smooth muscle cell cross the threshold level, an action potential is triggered causing contraction of the smooth muscle fiber. The event of spiking is known to occur at the crests of slow waves. To initiate the spike potential, it is necessary that smooth muscles of the segment are in the charged condition; having the neurotransmitters released in the vicinity by neurons. The neurotransmitters are released in response to a variety of stimuli such as neural signaling form higher center of the brain (mediated through vagus nerve), and distention-induced signaling (locally mediated through intramural reflex).

2.3 Control of smooth muscle contractions through sensing

Before we discuss the factors affecting APD motility, it is worth considering the sensory-motor integration of the intestinal segments (**Figure 2**). Generation of motility patterns is in some way hardwired to the sensors present and it is because of this reason that the APD segment can show a wide variation in its motility patterns. Little is known about the neurohormonal control, chemical control (pH [6], osmolarity [6, 7], lipid (also ileum) [8, 9], carbohydrates, and proteins), and other factors like size of bolus [10] and allergic responses through jejunal dysmotility [11]. They control muscles in the APD segment (also present in jejunal and ileal



Figure 2.

A cartoon representing mechanophysiology of the APD segment; indicating (1) the bolus undergoes disintegration due to grinding activity of the stomach, (2) smaller pieces of food, (3) food in its finely disintegrated form and yet to be mixed with DBP secretions, and (4 and 5) homogeneous mixture.

segments), which help in regulation of motor patterns mediated by some kind of sensor mechanism. To support the relevance of sensory-motor integrity, let us consider the report by Peter Holzer who suggested that prevention of acid damage to the mucosal tissues are carried out by an *elaborate network of acid-governed mechanisms* that help in protecting the tissue from acidosis and maintaining homeostasis [12]. The pH distribution of the gut lumen follows a particular trend, having lowest at the stomach (pH 1–3) and then goes on increasing from duodenum (pH 1.7–5 at proximal duodenum and pH 5–6 at distal duodenum) to terminal ileum (pH 7–9) [13, 14]. On exposure of the duodenum to acidic contents they stimulate various defense mechanisms which include increase in mucosal secretions, bicarbonate secretions, and blood flow. Together with this, hormones also play a major role in acid secretion at the stomach which in turn may contribute to the overall homeostasis. The pylorus also plays its role in regulatory mechanisms which run across the terminal stomach to proximal duodenum and shares the neural tracts and the circular muscle layer with antrum and duodenum. Besides being a muscular tissue, it also has sensors embedded within its mucosal layers, which are involved in some control related activities that are relayed through enteric nervous system or local mediated reflex pathway. Digestive processes are driven by the peristalsis motion that grinds the food rigorously in the antrum, so as to grind into small pieces less than 3 mm, so that they can escape the pyloric channel. The remaining part of the digestion is driven by the intestinal peristalsis which together with chemical secretions facilitates the process of mechanical and chemical degradation of the chyme into macromolecules and further down to simpler molecules so they can be absorbed (Figure 2)—steps 3–5.

2.4 Coordination among the small intestinal segments

The APD contractions are very much time synchronized and work in coordination. These neurally activated contractions push the luminal contents by transferring their momentum, which helps to facilitate mixing, grinding, and transporting of the food. Two kinds of pumping action take place here, one at the antral side and the other in duodenum which tries to push their contents to the other side. It is not well understood on how these two motor actions play their part in causing the transport, i.e., either gastric emptying or reflux of duodenal content back into the stomach. However, from a mechanics point of view, we know that the flow would result in emptying when the pressure at the antral side is higher than duodenal side (Figure 3). However, a reverse situation can exist, i.e., reflux when duodenal pressure becomes higher than antral pressure leading to a disease condition known as the duodenogastric reflux (DGR). The mechanism by which the transport across the pylorus occurs is not clear; however, it is known that the transport occurs by developing two kinds of pressure waves via pressure pump (common cavity pressure wave) and peristaltic activity [15]. Multiple studies have been performed for estimating gastric emptying in relation to the generation of intragastric pressures using manometric studies. Though little is known about the relationship between the pump mechanism (gastric pumping) and the coordinative muscle contractions, few researchers have reported that the process of gastric emptying is observed only during those occasions when the antral pressure (Pa) is higher than the duodenal pressure (Pd). Study also indicates that the base line pressure or the common cavity pressure is the major determinant of gastric emptying (GE) rather than the antral contraction-induced emptying [15]. This idea is supported by literature which demonstrates that alternations in pressure inside the proximal stomach correlate well with the varying rates of gastric emptying of different liquid meals [16].

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Figure 3.

A cartoon diagram depicting the antrum, pylorus, and the duodenal (APD) segments, respectively. The dashed line represents the APD axis, while the blue colored plot shows pressure profile along the axial direction indicating higher antral pressure (Pa) in comparison to lower duodenal pressure (Pd).

The local generation of high pressure and appearance of anterograde and retrograde flow patterns suggest that the geometry is closely linked to the way emptying proceeds. In addition to the complexity present in gastric emptying predictions, the gut works by intelligently sensing the food content and accordingly modulating the contraction patterns.

The coordination is established through neural feedback means; e.g., enterogastric, ileogastric, intestino-intestinal reflex, and vago-vagal reflexes. One of the well-known reflexes is the ileal brake. The ileal brake refers to the ability of the ileal segments to modulate the motility patterns upon exposure to the nutrients such as lipid through enteric reflex [17]. The intestinal segments communicate with each other through such reflex in process to regulate the digestive process such as regulating the flow at which the gastric contents enter into the duodenum by suppressing pyloric channel.

3. From small intestinal motility to flows to the digestion

A fluid is a substance which continually deforms under the application of a shear force. When an external force is applied to a solid object it undergoes whole body translation; whereas, fluid undergoes both translation and deformation. Transport of fluid can be better appreciated by considering an example of the flow through a cylindrical pipe, also referred to as the Hagen-Poiseuille flow (flow in a cylindrical pipe). Applying a relatively higher pressure force at left end of the tube, in comparison to right end, sets up a pressure gradient along the length of the tube. As a result of this, the fluid tends to move down the pressure gradient only if it has overcome the viscous resistance. In the case of viscous flow the fluid eventually gains inertia and reaches a steady state when the axial velocity profile becomes parabolic. In a similar fashion, we can draw some parallels between the Hagen-Poiseuille flows to those of intestinal flows. In physiological scenario, as the contraction (i.e., the circular constriction that appear around the periphery) propagate thorough the small intestinal segment, it imparts a part of the momentum to the fluid underneath, which as a consequence of having gained the momentum can now hit the neighboring fluid particle and transmits a part of its momentum; eventually developing the flow.

4. Mechanics of small intestinal digestion: mixing, transport, and absorption

4.1 Basic mechanics

4.1.1 Law of Laplace

We discuss the basic principles of mechanics as applied to the small intestine. The small intestine, as we know, is a muscular conduit having two types of muscle layers—circular and longitudinal muscles. When muscles undergo contraction (reduction in the length of the muscles) they happen to either close the lumen (circular contraction) or shorten the segment (longitudinal contraction). From mechanics point of view, such contraction develops forces by virtue of muscular activity. By applying basic principles of mechanics, we can deduce as to how the muscular contraction results in the generation of pressure forces and flows inside the lumen. In general, whenever the tissue undergoes contraction, we explain the principle that the reduction is caused by generation of forces per unit area or stress. Parameters of interest are the percentage reduction in the length or strain that is caused by the stress. So, there exists some relation between the stress and the strain of the material under consideration. This leads us to assess the elasticity of the material or modulus of elasticity that measures the ability of the material to resistance deformation when a stress is applied to it. The nature of resistance or wall stiffness can be visualized by referring to the stress vs. strain plots obtained by allowing the material to deform under various strains and measuring the stress. The stress-strain plot provides details relevant to the mechanical properties of the tissue.

For simple geometry such as intestine approximated as a uniform and circular cylinder, the relation between the stress and luminal pressure under the assumption of thin wall is given by Laplace's law. It says that, under equilibrium condition, the tensile stress developed in wall is proportional to the intraluminal pressure and the radius of the intestinal tube. Suggesting that if the pressure inside the intestine is increased by gas formation (fermentation), for a non-significant change in the radius to wall thickness, then there would be a corresponding increase in the tensile force of the wall.

4.1.2 Flow through the channel

Transport of fluid across narrow constriction can be better appreciated by considering a familiar example of flow through a cylindrical pipe, also referred to as the Hagen-Poiseuille flow. Applying a relatively higher pressure force at left end of the tube, in comparison to the right end, causes the fluid to move down the pressure gradient only if it has overcome the viscous resistance. In case of viscous flow, the fluid eventually gains inertia and reaches a steady state when the axial velocity profile is parabolic. Let us assume a straight channel that is static (i.e., no contractions), with occlusion at the center and applied pressure at the ends as if they were generated by the APD contractions. In steady state, the flow rate can be derived as $Q = \pi r^4 \delta P/(8 \ \mu l)$, which relates the rate of flow at the outlet to the pressure difference applied to the channel. Suggesting that, the flow rate is highly sensitive to the fourth power of the channel radius and inversely proportional to the channel length.

4.1.3 Longitudinal shortening

Using high-frequency ultrasound, Nicosia et al. were able to calculate the percentage reduction in the length of the longitudinal muscles [18]. As discussed in the later section, using the principle of mass conservation, the authors were able to quantify local longitudinal shortening as the ratio of longitudinal length after contraction relative to the initial length as inversely related to the ratio of cross-sectional area of the muscle after contraction relative to the initial area; $L/L^* = 1/(A/A^*)$.

4.2 Modeling small intestinal contractions

Unlike the gastric contractions, the small intestine motility patterns are not regular. In preprandial state, the small intestine enter into the interdigestive phase showing distinct patterns of activity every 90–120 min⁻¹ (also known as Migrating motor complex or MMC) which include (1) a period of quiescence with no contractions (Phase I), (2) a long period of unsynchronized contractions (Phase II), and (3) a burst of strong and regular contractions (Phase III) [19]. Of these, phase III plays an important role in sweeping the undigested food particles (left over debris) and bacteria out of the small intestine and into the large intestine. However, after meal ingestion (postprandial), the small intestine switches to a more synchronized motility patterns.

4.3 Pyloric contraction

Pylorus plays a key role in mediating the flow across the stomach and the duodenum. It does by developing higher resistance to flow through closing of the lumen. They typically open and close the lumen at intervals of 20 s [20]. Flow through the channel is driven by generating a pressure gradient across the two ends of the channel and depends on luminal diameter, degree of opening, length of canal; thus, regulating gastric emptying (GE) or duodenogastric reflux (DGR) [21–26]. Both antegrade and retrograde flow have been reported in the literature to be normal; however, when the quantity of flow in the reverse direction leads to increased volume of reflux, then it leads to DGR disease. The flow is found to be pulsatile in nature [27–34]. The pylorus exhibits both tonic and phasic contractions [35–38], which develops a pressure of 10.8 \pm 4.5 mmHg at 1–4 min⁻¹ rates of phasic contraction [35]. In postprandial state, pylorus opens and closes with mean diameter 5.4 ± 1.0 mm [21]. Out of 193 pyloric closure events, 133 occurred in 2 s of the antral and duodenal contraction in a study carried out in patients. The pylorus was reported to be in closed position for 55.5% of 154 isolated duodenal contractions recorded. In porcine flow, pulses happen at 11.2 \pm 0.4 min⁻¹ frequency and occur between subsequent pyloric pressure events with each flow lasting for 3.5 ± 0.1 s with volumes of 0.3 ± 0.01 ml being release during the stroke. They occur 2.8 ± 0.7 s before pyloric pressure event, and 2.3 ± 0.5 s before antral wall motion [39]. Mealdependent effects of pyloric motility using clinical trials of intravenous injection of 20% dextrose solution indicated causation of pyloric contraction, suppression of antral contraction, and duodenal phase-3-like motility [40]. The duration and intensity of phasic and tonic contraction of the pylorus showed direct correlation with caloric content of dextrose solution been infused into duodenum. Increase in caloric content caused increase in isolated pyloric pressure waves and basal pyloric pressure [41]. Duodenal infusion of saline shows no change in motility patterns of APD; whereas, triglyceride and fatty acid infusion suppresses antral contractions, but enhances pyloric phasic and tonic activity and delays gastric emptying [42, 43].

4.4 Intestinal peristalsis

Contractions of the intestine are a mix of elementary contractions such as stationary (SW), antegrade (APW), or retrograde propagating wave (RPW). A literature survey of the motility patterns indicate frequency of 15–18 wave min⁻¹, velocity of propagation of 0.1–0.4 cm s⁻¹, and higher propensity to develop

propagating contraction in the intestine in comparison to stationary contraction [44]. Retroperistalsis have been linked to the reflux of duodenal contents and trigger the development of DGR diseases. Standing contractions are the non-propagating contractions they are confined over a particular segment (12 waves min⁻¹). They are known to be involved in the mixing process. Contractions appearing on one side of the channel are known as sleeve contractions. It involves longitudinal muscle for generating contraction [45] and help in mixing and churning of luminal contents [46]. Pendular movements are the longitudinal contraction of the muscles, which develops motility patterns involving to-and-fro motions of segmental shortening and extension. In physiology, the contractions occur as a mixture of the basic contractions, as discussed above. It is a well-known fact that upon nutrient infusion of duodenum, the duodenal motility patterns changes from propulsive to a segmental contraction that traveled only for a short span. Such contractions form segmental contractions or cluster contractions, which can be stationary or non-stationary [47].

4.5 Flow due to circular muscle contractions

Flow due to circular contraction were investigated by the author by approximating the flow for a Newtonian liquid meal with viscosity 1000 cP and density 1000 g cc⁻¹ inside the APD segment [44]. The rationale for choosing such an assumption was—(1) for a liquid meal intake the meal mixes with gastric and duodeno-biliary-pancreatic secretions giving a mixture that is also a liquid; (2) the rheology of the contents present inside the duodenum is not yet known; therefore, a Newtonian approximation was made; (3) modeling a semi-solid meal increases the complexity, therefore, a liquid meal was considered to simplify the development of the APD segment. Further, the APD segment was assumed to be a rigid wall to simplify the flow model.

There is a formation of recirculation eddies near the occlusion zone (with velocities reaching its peak at its center) and occurrence of a local transport at the pyloric region (arising due to the pressure difference across it) (**Figure 4**). Results indicate that a retrograde moving wave cause pressurization at the head region of the wave in comparison to the tail region. As a result of this behavior, a steep pressure rise is developed to cause flow in the direction that is downward the steep. It was also found that this wave generates a pressure difference across the pylorus, that is, higher pressure on the antrum side in comparison to a lower pressure on proximal duodenum thereby causing reflux.

To understand the impact of variations in the intestinal peristalsis, the author performed a parametric study by varying the geometry and wave parameters of the contraction. Based on literature, a hypothetical range was considered for these parameters presuming that this range falls within the physiological regime.

The study demonstrated that higher degrees of occlusion and higher velocity for the propagatory contractions have a profound effect on the flow rate across the channel (**Table 1**). Although, for APWs, the emptying rate increases with occurrence of multiple waves, they also induce reflux when occurring in four numbers spread across the duodenum and centered at 8 cm away from pylorus. The effect of multiplicity in the RPW shows an increasing trend in reflux. In general, it can be interpreted that the APW type contractions lead to emptying while RPW lead to reflux.

Standing contractions (SW type) of closing type were found to be reflux inducing. However, they occur at less than one-tenth of a magnitude for variations in distance, wavelength, and degree of occlusion in comparison to the APW and the RPW contractions. They also show an increasing level of reflux with increasing values of parameters except for distance. When multiple standing waves occur they result in significant increase in the reflux. *Biomechanics of the Small Intestinal Contractions* DOI: http://dx.doi.org/10.5772/intechopen.86539



Figure 4.

Flow due retrograde wave traveling toward the pylorus. Arrows indicate velocity vector over the local region and colors indicate the magnitude.

On overall comparison of the reflux levels caused by the elementary contractions, it is clear that the SW of higher frequency and the RPW of higher occlusion (70%), higher velocity and occurring in multiple numbers dominate the list of reflux inducing contractions of the duodenum.

The APW and RPW contraction show mixing at higher intensity that is typically of the order of hundreds that is ten times those of SW. Variations in distance and wavelengths of the APW and RPW type contractions show similar levels of mixing (**Table 2**). Contractions cause higher degree of mixing with increasing occlusions and are highly sensitive to the velocity, wherein a change from 1 to 4 cm s⁻¹ can lead to a ten-fold increase in I_{mixing} . Further, it was seen that multiple waves can cause significant rise in mixing. However, the standing contractions show negligible mixing that are typically of the order of tens and are highly sensitive to frequency and multiple waves. While I_{mixing} shows extent of mixing in the whole duodenum,

Contraction type	Distance (†)	Wavelength (↑)	% Occlusion (†)	Velocity (cm s^{-1}) or frequency (\uparrow)	Multiple waves (†)
APW	Negligible	Negligible	1	\uparrow	1
RPW	Negligible	Negligible	1	1	1
SW*	\downarrow	1	1	1	1

*For SW, frequency is considered. APW, antegrade propagating wave; RPW, retrograde propagating wave; and SW, standing wave.

Table 1.

Effects of duodenal pumping on transpyloric flow rate (GE or DGR) studied for various parameters of APW, RPW, and SW type of contractions.

Contraction type	Distance (†)	Wavelength (↑)	% Occlusion (†)	Velocity (cm s^{-1}) or frequency (\uparrow)	Multiple waves (†)
APW	↑ or ↓	Ļ	1	↑	↑ or \downarrow
RPW	Negligible	1	1	1	1
SW	Ļ	1	1	1	1

Table 2.

Effect of APD contractions on intensity of mixing.

Contraction type	Distance (↑)	Wavelength (↑)	% occlusion (↑)	Velocity (cm s ⁻¹) or frequency (†)	Multiple waves (†)		
APW	Negligible	Negligible	1	1	1		
RPW	Negligible	Negligible	1	1	1		
SW	Negligible	Negligible	Negligible	1	Negligible		

Table 3.

Effect of APD contractions on volume of mixing.

we also wanted to quantify the region over which the mixing or the volume of mixing is significant (computed as the volume of duodenum that has mixing index above 1.005). Changes in distance and wavelength of the peristaltic waves showed no major change in volume of mixing; however, it was sensitive to occlusion to some extent and highly sensitive to velocity and multiple waves. Standing contractions, on the other hand, showed zero or negligible volumes of mixing, except for a frequency of 6 Hz where they showed some mixing (**Table 3**).

5. Significance of the longitudinal muscles

5.1 What is LLS?

Contractions of the longitudinal muscles, when occurring over short range of the gut segment, are referred to as the local longitudinal shortening. In literature, longitudinal shortening have been investigated as if they are advancing with the contraction, which we define as the advancing LLS and those that are stationary or stationary LLS are rarely considered. During LLS, the longitudinal muscles contract to shorten the segment along the axial direction only.

5.2 Learning from esophageal studies of LLS

LLS studies of the intestinal segments have been rarely considered. In order to understand the mechanophysiology of the LLS in intestine, we resort to the LLS studies of the esophageal segment.

One of the classical studies of LLS was the study of esophageal peristalsis during feline. By using a widely spaced metal clips clamped to the esophageal mucosa (four tantalum wires that were imbedded in the outer esophageal wall), Dodds et al. [48] captured the longitudinal shortening of the esophageal segment which varies with their relative position. The study demonstrated the existence of a wave of local longitudinal shortening that moves in conjunction with the bolus. They also found that the relative displacements of the markers vary from one location to the other

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location suggesting that the LLS is effective over a given segment of the esophagus (especially the distal most esophagus). Subsequent studies, using widely spaced metal clips attached to the esophageal mucosa, support the contractive nature of the longitudinal muscles in the local regions of the esophageal wall during peristalsis [49–51]. Measuring local longitudinal shortening was, however, a challenge using the mucosal clip studies; given the large spacing of 3–10 cm. Nicosia et al. provided a more accurate method of determining the LLS and their coordination with CC using the high-frequency ultrasound transducer [18]. By employing the principle of law of mass conservation, the changes in the cross-sectional area with the temporal variation in local longitudinal shortening was made; which were compared with the luminal pressure measured using high resolution manometry. Following relation was derived: cross-sectional area during rest phase/cross-sectional area during contraction = length of the segment during contracted state/length during rest. Key observations were as follows: (1) during luminal filling (with bolus entry), the esophagus distends reducing the effective thickness of the muscles, (2) the wave of longitudinal shortening was followed by the circular contraction, (3) contraction of the longitudinal muscles were found to nearly coincide with the peak luminal pressure, (4) longitudinal shortening overlaps the CC and occur prior to CC and ended after CC, and (5) lastly, the strength of LLS directly relates to the generation of higher luminal pressure. Further clinical studies by the investigators also indicate the prior contraction of the longitudinal muscle during onset of distal esophageal peristalasis [18, 49, 50]. Such fine coordination the contraction of two muscles fibers provides for a mechanical advantage of gathering the neighboring circular muscle fiber closer to ensure that the circular contraction occurs at ease [52]. The coordination of CC and LLS is managed by the enteric and central nervous system. The delay in the onset of contraction is due to the existence of a gradient of latency of contraction along the length of the esophagus [53].

5.3 Effect of advancing LLS on flows

Like the peristalsis waves (which are modeling as trains of periodic sinusoidal waves traversing the muscular tube at certain velocity), the LLS is modeled as a sinusoidal wave whose amplitude relates to the local shortening (l/l_0) and propagates with the CC. As shown in **Figure 5**, LLS brings together the neighboring tissues through generation of a localized wave of shortening. As a result of this, the circular muscles become denser giving its advantage to compress the lumen at ease. We consider that the longitudinal contraction is in relative motion to the CC; hence, we define them as LLS of advancing type.

As the LLS traverse the intestine with CC, the intestinal wall undergoes deformation. Such change in the wall generates wall momentum which acts as a source of energy to push the fluid and develop flows. The details of the wall motions are provided in the form of a local wall velocity in **Figure 5**. Circular contractions are wall motions that appear as ripples traveling over the surface of water. As the circular muscles contract, the wall moves radially inward; however, as the wave moves at certain velocity they appear to close the head region of the wave leaving behind the tail end to relax or open (outward velocity vector; first panel in **Figure 5**). For advancing LLS, a wave of localized shortening occurs which travels at certain speed. During such activity, the surface of the intestinal wall appear to move forward but recoils back to its original position after the disturbance has traverse the segment. This generates a net forward velocity, as shown in second panel of **Figure 5**. Superimposing both the waves result in a summation of the two velocity vectors (third panel in **Figure 5**). We may summarize that the introduction of LLS results in an axial displacement of the wall and CC in radial displacement.



Figure 5.

A cartoon diagram illustrating the circular (CC) and longitudinal contractions (LLS) in the intestinal wall. L is the length and R is the radius of the intestine. CC is characterized by the wavelength (λ) and the percentage occlusion of the lumen (p_{occ}). Peak value of LLS is given by the peak l/lo ratio which is spaced at a relative distance (δ) from the peak CC or the point of maximal occlusion.

Considering no-slip condition (fluid particle at wall moves with the same velocity with which the wall moves), we also learn that there is an effective axial displacement of the fluid adjacent to wall and helps to drag the peripheral part of the food along with it (**Figure 6**).

Rheology plays an essential role in regulating the transport of the digesta from stomach to duodenum (gastric emptying) and duodenum (duodenogastric reflux). For a meal that is highly viscous, the mixing and transport can be a difficult task to be performed by the enteric system when compared to low viscous digesta. Since the mechanical processes taking part in intestine correlates to the rate at which absorption takes place and determines the serum glucose levels, the subject matter is of high relevance to satiety, indigestion, and other digestive disorders of the gut.

Let us estimate the flow regime of water, juice, and honey. We consider an intestinal geometry with diameter 2.5 cm (2.5–3 cm), and wave traveling at a characteristic velocity of 2.5 cm s⁻¹ (2.5–5 cm s⁻¹) for short and long wavelength of one and ten times the diameter. Assuming a fluid density of 1 g cc^{-1} and fluid viscosities of 1 cP (water), 0.65P (juice), and 33P (honey) and substituting into the formula ($Re = \rho v D/\mu$) we determine Reynolds number as 625, 9.615, and 0.189. As per the long wavelength approximation [54], we perform viscous scaling by a factor (=diameter/wavelength of the wave) to get an approximate Reynolds number. At one-tenth of scaling, the Reynolds number is found to be 62.5, 0.9615, and 0.0189. At higher Reynolds number, the inertial forces of the fluid are much higher than viscous resistance and as a result lead to turbulence flow. We speculate that a fast moving contraction of the intestine help in pushing the fluid to a higher extent that it leads to turbulence and upon interaction with air leads to borborygmus (a rumbling, growling or gurgling noise of the intestine). The studies of the bowel sounds (auscultation) were pioneered by Cannon in the early twentieth century. However, due to technical challenges, the method appears to be of some hope to clinicians in diagnosing GI disorders through bowel sound computational analysis (BSCA) [55]. At low *Re*, the flows are laminar and silent.

Flow details of the intestinal peristalsis have been recently reported in the literature [56]. When a wave of contraction propagates along the intestinal wall, they develop peripheral forces that can be directed radially inward, axially oriented,



A snapshot of a simulation study indicating the wall velocity (blue line) along the radial direction (CC) and no shortening (LLS, red line) (first panel). Study involving LLS (approximated by sinusoidal waveform) without CC; the wall is pulled toward the point of peak LLS (second panel). Effect of CC and LLS on wall velocity.

or inclined depending on the nature of contraction (CC and/or LLS) (**Figure 7**). As a result, the head region develops a higher pressure relative to the tail end. While at the tail end, development of low pressure field results from the retraction of the wall as if they were to open the channel. As a result the development of differential pressure forces across the segment, a pressure gradient which acts as a driving force to propel the luminal contents from a region of higher pressure to the lower pressure (retrograde flow). Flow due to advancing LLS is less prominent due to generation of low fluid velocity and low shear stress. Since they develop axial velocity at the wall, the advancing LLS, through viscous behavior, drags the neighboring fluid to move along with the wall creating a whirlpool-like motion in the region of contraction.



Figure 7. Effect of simultaneous circular and longitudinal contractions on flow.

The advancing LLS and CC lead to the generation of pressure field and shear stress of similar trend. Local variations in the pressure along the axis indicate a linear variation in the non-contraction region and a nonlinear variation in the contraction region; zero at the center and boundaries—inlet and outlet of the intestinal segment. The pressure peaks at an offset from the center and shows symmetry about the axis for a contraction wave at the mid-segment. The wall shear stress shows a peak at the center of the contraction region and reduces to lower value at the either end of the wave and remains constant throughout the non-contraction region. Axial variations in the pressure and wall shear stress are similar for fluid of pseudo-plastic, Newtonian, and dilatants type. The study also reports that the pressure developed is higher for shear thickening fluids in comparison to shear-thinning fluid (**Table 4**). In a similar manner, wall shearing is highest for the dilatants. Shear stress in the lumen is highest at the wall and reduces linearly to the lowest value

Parameter (†)	Pressure	Shear stress	Flow rate	Peak luminal velocity	Physiological relevance
Viscosity	¢	1	No change	No change	Extent of viscous behavior
Flow behavior index	¢	¢	Ļ	ţ	Captures the rheology of diverse fluids
LLS spacing (about optimal)	ţ	Ļ	↑ or ↓	↑ or ↓	CC and LLS coordination
Wavelength	↑ or ↓	\downarrow	↑	↑	Effect of motility
Occlusion	1	1	↑	↑	Effect of motility

Table 4.

Effect of contractility and rheology (normalized values) on flow; based on semi-analytical method.

at the center. At region where the shearing is higher there is a more stirring of the fluid. CC and LLS coordination is found to affect the luminal pressure, shearing of the contents, flow rate, and peak velocity significantly.

6. Physiological relevance of intestinal motility

6.1 Mixing

Using imaginary tracers, the author was able to determine particle trajectories due to the peristalsis—CC and LLS [56]. Two kinds of flows were observed; one resulting in axial displacement of the fluid and other causing circulation of the fluids (eddies). The radial displacement brought the fluid from the core region to the periphery and vice versa; thus allowing for flushing of the fluid proximal to the mucosa. However, the particles were displaced when the wave traverses the segment. Particle motion is highly dependent on the type of intestinal motility. Positioning of the tracers at various depths of the lumen showed different trajectory and followed the wall; particles close to the wall tend to follow the wall, while those near the axis exhibited near circulation. The authors report that the radial dimension of the whorls is found to be higher when the particles were positioned close to the wall and least at the center. Suggesting that, the contractions are more effective near the wall since the particles experience most of the wall momentum and least at the center of the lumen. Such a behavior is indicative of the mixing of the contents; given that the shearing is effective near the wall with formation of eddies.

6.2 Transport

When contraction traverses at 50% occlusion, there is a higher tendency for the particles to undergo circulation; favoring mixing [56]. However, at 80% occlusion, the particles tend to under more of axial displacement and less of a radial displacement with no circulation; favoring transport. Particles positioned near the center were found to travel a longer distance in comparison to those near the wall. Such behavior reminds us the parabolic velocity profile in case of pressure driven flows in pipe. Previous studies corroborates with the understanding that the flows in occlusion regions tend to show a parabolic profile [44]. Rheological effects of the particle displacement suggest that the eccentricity of the particle trajectory for Newtonian fluid is more and undergoes a near complete circulation. Particle trajectory for dilatants showed formation of a complete circulation. For fluid having flow behavior index less than 1.0, following observations were made (1) particles tend to travel with higher velocity over longer distance and (2) particles showed more of a radial predominance. There were no significant changes in the flow developed by introducing the LLS; however, due to additional momentum along the axial direction they tend to suppress the radial displacement of the tracer leading to a more translocation. The transport has been linked to malabsorption of the nutrients and electrolyte concentration. Alternations in the intestinal transit can disturb the equilibrium of osmolality and intestinal absorption leading to diarrhea or constipation [57]. Knowledge of the intestinal transit of bolus is essential when design the drug. Orally administered drugs have to be tuned to the environmental conditions of the small intestine so that drug bioavailability can be maximized. Since the physical properties of the meal, such as viscosity can greatly influence the transport behavior, clinical preparation of the food can be administered to help manage the patient suffering from motility disorders.

6.3 Frictional advantage

Frictional effects of the intestinal wall have been attributed to a disadvantage when considering transport. By estimating the flow resistance, the author was able to assess the importance of the slowing down of the fluid flow and increase in the retention time of the fluid near the mucosa; providing more time to undergo chemical digestion and absorption [56]. The extent of friction offered by the intestine to fluid of different flow behavior index (n = 0.6, 1.0, and 1.4) suggests that the friction is highest for pseudo-plastics and decreases with increase in flow behavior index [56]. In addition to this, friction is found to be dependent on pressure gradient; showing increasing trend with increase in pressure. They are linearly related to the Reynolds number; higher the *Re* higher is the resistance. Since the friction is analyzed for a channel with smooth inner surface, we presume that the contribution resulting from plicae circulares would be much higher.

Friction is more at the occlusion center and drops significantly as one recedes away from occlusion center to the wave end. The friction due to mucosal layer of the intestine is a subject matter of interest to intestinal digestion. We may consider the problem similar to the flooding of the terrain occupied by numerous trees. At the flood end, where the fluid velocity is very high, the fluid particles tend to slow down upon interacting with the tree. Since the surface area of the tree is more, the effectiveness to slow the fluid particle is much higher. In physiology, such resistance to flow is provided by the intestinal folds of mucosa known as the plicae circulares or the valves of kerckring. The author speculates that these structures help in reducing the luminal transport and increase the time of retention of the fluid near the mucosa so as to allow for increased absorption of the nutrients. Depending on the flow regime, the flow may be highly agitated to flush the contents and allow for replenishment of the nutrient-rich contents. Such a behavior prevents the formation of trapped fluids and cause continuous flushing of the mucosa without stagnation. Such understanding is necessary to know the dynamics of nutrient transport near the intestinal mucosa and equilibration. While, stagnation of the acidic contents near the duodenum can have drastic impact on the mucosal layer leading to duodena ulceration.

6.4 Power demands of peristalsis

Contraction leading to flow is majorly determined by the muscular contractions of the circular and longitudinal muscle layers of the intestine. Although extramural pressure forces may contribute in the modulating the flow patterns, much of the mechanics is initiated and driven by the muscles. Efficiency to pump is defined as the ratio of energy due to pressure force to the energy spent by intestine through muscular contraction. The circular contractions are majorly known to cause the positive displacement of the fluid, and hence primarily responsible to transport. However, the LLS results in the developed for axial forces that are small in comparison to circular contraction and have minor contribution to efficiency at lower occlusions. LLS is advantageous at higher occlusion, where they primarily help to forcefully shrink the intestinal wall along the axial direction to concentrate more circular fibers. The energy spent on contraction can be reduce dramatically from 26.5 (CC along) to 22.5 units (CC with 0.65% LLS) approximately; a 15% reduction in energy spent by the intestinal motility to drive shear thickening fluid. However, in contrast to the above, we also identify that power advantage of LLS negatively correlates for shear-thinning fluid driven by CC with 0.65% LLS. Suggesting that rheology of the luminal contents shares some relation with the nature of LLS. This emphasizes an important observation as to whether such a correlation exists, and

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if so, how does the intestine senses the fluid rheology? Although there are no direct sensors to detect the rheology or viscosity of the contents, we speculate that the gut may use an indirect mechanism to serve the purpose of assessing the rheology through stretch sensors. Since this sensor respond to distension, we also speculate that the difficulty to pump highly viscous fluid are reflected in the form of stretch. The concept of mechanical sensing of the stretch in the intestinal wall was observed by infusing a larger bolus of isotonic saline directly into the intestinal lumen [58]. The study reported that a controlled distension of the intestine activates a subset of vagal sensory neurons. Perhaps, the sensors data are relayed to the higher centers of the brain or through the local reflex to trigger certain feedback controls. Somehow, the intestine is aware of the trade-offs between the power demands of peristalsis at a certain occlusion against the percentage LLS. It may not prefer to contract at higher LLS for circular contraction of lower occlusion; since it would be non-economical. However, on the contrary, it is economical to contract at higher LLS for circular contraction of higher occlusion; an optimal strategy in conserving the amount of energy it spends to perform the peristalsis.

6.5 What is the optimal parameter space for contractility?

The intestine has its own ability to perform muscular contraction to an extent that can be mapped onto a phase space (multidimensional space in which each state variable represented by an axis is constructed to specify the state of a physical system at a given point of time). To derive such plots for intestine, we resorted to literature reports related to the clinical observations of the intestinal motility during fed and fasted state, and, normal and pathology condition [22]. The parameters of interest are: incidence of propagatory versus stationary contractions per min, percentage incidence of antegrade and retrograde propagating waves, frequency of the wave, wave velocity in mm/s, and duration of MMC (interdigestive contractions) cycle. The ability of the intestine to perform digestion optimally depends on how well it coordinates with neurohormonal system. Eliciting segmental contraction on duodenal infusion of fat or hydrochloric acid requires that the contents are mixed well with the biliopancreatic secretions to cause buffering and emulsification. Such motility patterns are known to transform the fat into droplets which help providing more surface area for lipase binding to take place and perform the digestion [59]. Previous study by the author shows intestinal preference to digestion especially extent of mixing, and volume of mixing, and to-and-fro motion of contents [44]. Since the peristalsis provides sufficient shearing forces to help cause the droplet formation, we learn that some correlation exist between the motility and emulsification. Similarly, transport of the contents requires forceful expulsion of the contents by through muscular contraction of the intestinal wall; which demands generation of sufficient forces or right motility patterns. Studies indicate that the intestine utilizes the LLS at its advantage to perform forceful contractions; with peak LLS not exceeding 65% [18, 52]. The optimal choice of wavelength at which the shearing attains its maximum value is equal to the intestinal diameter (1 unit); higher wavelength (1.5 units) is inefficient [56]. Similarly occlusive contractions show two functions—mixing at lower occlusion and transport at higher occlusion. The choice of occlusion is dependent on whether the meal needs further processing or not.

7. From wall shear and strain to influencing cell biology of the intestine

As a result of the mechanical forces arising from muscular contraction (CC, LLS, due to muscularis mucosa) or due to luminal contents (distension during

gasification), the intestinal tissues are remodeled in accordance to the nature of forces. The epithelial and non-epithelial cells undergo various types of mechanical forces during the physiology function. Contractions of the circular muscle leads to generation of a tangential force along the periphery (shear) and contraction of longitudinal muscle layer leads to axial force (shear). In reality, such contractions are highly irregular and occur in conjunction that varies in wave geometry and kinetics (velocity). Shear forces at the mucosal layer affect the villi structure which modulates the adsorptive function of the organ and strain in the intramural structure affect the tissue (intestinal wall) and its compliance. The responsive nature of the intestine comes from the fact that the intestinal walls have several mechanosensitive cell types that respond to various types of mechanical stimuli such as-epithelial enterochromaffin cells (ECL), enteric neuronal cells (intrinsic and extrinsic), smooth muscle cells, and interstitial cells of Cajal (ICC). These cells contain ion channels (stretch-activated ion channel) that respond to mechanical forces and in response to stimuli they generate ionic currents in the channel thereby affecting mechanotransduction process. In mechanotransduction, the mechanical forces such as shear, stretch, and pressure trigger a biochemical pathway (through conformation change) initiating the chain reaction (involving second messengers) to affect the gene expression, and protein synthesis. In vitro experiment involving the seeding of scaffolds with human umbilical vein endothelial cells (HUVECs) demonstrated that the mechanical stimuli provided in the form of a pulsatile shear stress (12 ± 4 dyne cm⁻²) leads to changes in the expression of the mechanosensitive genes (Pecam1, Enos) [60].

8. Conclusion

The digestive process of the intestine is complex and depends on multiple parameters such as rheology of food, chemical composition, motility pattern, and neurohormonal signaling. In this chapter, we have addressed the question as to how the mechanics play a key role in performing the disintegration of the partially digested food through shearing action of the peristalsis. Both circular and longitudinal contraction participate in the process in a way to optimally perform the digestion at ease; which otherwise would be uneconomical. LLS is advantageous when driving contents having shear thickening behavior, where the longitudinal shortening brings the circular muscles closer to reduce the tension in the individual fibers during peristalsis. LLS have no significant contribution in the development of the flows. In conclusion, biomechanical studies indicate that the flow is highly sensitive to the motility patterns (geometry and wave parameters), and in order to perform the digestion, the intestine elicits the right kinds of contraction to perform the physiological functions (such as preventing duodenal ulceration through segmental contraction, buffering of chyme in the duodenum, preventing duodenogastric reflux, and digestion of meal).

9. Future scope

Previous study involving the 3D computer simulations of the flow provided details of relevance to physiology. Contraction types analyzed so far include: (1) stationary contractions (contractions that close and open at a given location) (a) closure type, (b) Opening type*, (c) multiple contractions, (d) cluster/repetitive contractions; (2) propulsive contractions (contractions moving in either direction) (a) antegrade type, (b) retrograde type, (c) multiple contractions, (d) short distance traveling contractions*, (e) long distance traveling contractions*; and (3)

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Figure 8.

Compartment model of the APD segment showing various segments (1) stomach, (2) pylorus, (3) duodenal bulb, and (4) distal duodenum.

mixed (mixture of both stationary and propulsive contractions)*. The contractions marked with * could not be analyzed due to computational limitations. This gives us a huge opportunity to the biomechanical engineers to explore the mechanism as to how the motility leads to digestion. Literature suggests a compartmental model to describe the physiological relevance of antrum, pylorus and the duodenum (**Figure 8**). The jejunal and ileal segments still remain a mystery as to how they coordinate with each other and how they contribute to digestion.

Conflict of interest

There are no conflicts of interest.

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