Flow fields generated by peristaltic reflex in isolated guinea pig ileum: impact of contraction depth and shoulders

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Jeffrey, Brian, Holavanahalli S. Udaykumar, and Konrad S. Schulze. Flow fields generated by peristaltic reflex in isolated guinea pig ileum: impact of contraction depth and shoulders. Am J Physiol Gastrointest Liver Physiol 285: G907–G918, 2003; 10.1152/ajpgi.00062.2003.—The guinea pig ileum responds to distension with characteristic wall movements, luminal pressure gradients, and outflow (the peristaltic reflex). To date, little is known about whether the peristaltic reflex generates flow events other than laminar flow. Here we used a numerical method to solve for the flow generated by moving walls to assess occlusive contractions (case 1), nonocclusive contractions (case 2), and contractions with steep shoulders (case 3) for which visual parameters of wall movements are published. We found that all three contraction cases produced pressure differentials across the coapting segment, downstream and reverse flow, and vortical flow patterns that redistributed particles and mixed liquids. Contractions generated pressures and shear stresses, particularly along the moving section of the wall. The nonocclusive contraction was much less effective than the occlusive contraction with the steep shoulders; the occlusive contraction with flat shoulders had an intermediate effect. Our analysis shows that even peristaltic contractions produce not only laminar flow but also many flow events likely to promote digestion and absorption. The visual patterns of contractions impact the patterns of luminal flow, and precise definition of wall movements is critical to quantify the fluid mechanical consequences of intestinal contractions.

The isolated ileum of the guinea pig responds to distension with a complex contraction sequence known as the peristaltic reflex. The reflex is characterized by sequential movements of the intestinal wall, luminal pressure waves, and clearance of the lumen. Like others (5, 24), we have recently performed a temporal and spatial analysis of the intestinal wall movements during the reflex. Our laboratory has specifically showed how the depth and the length of the coapting segment and the slope of its shoulders adjust to the volume and composition of the bolus and to outflow resistance (7, 18).

Besides producing net luminal transit, intestinal contractions are thought to enhance digestion and absorption (1, 2, 9–12, 14, 16, 25). The fluid mechanical events that effectively mix nutrients with secretions or deliver them to sites of epithelial uptake remain poorly understood. Previous models of intestinal flow used simplifying assumptions regarding the contraction patterns and flow characteristics to make the flow calculations tractable. Thus the upstream and the downstream ends of intestinal contractions were assumed to propagate at the same times and the same speed, or contractions were assumed to reduce the lumen in a concentric manner. Wall shapes during contractions were idealized as propagating linear segments and sinusoidal waves (2, 9, 25). Such fluid mechanical analyses are likely to be flawed.

Here we used precise data on intestinal wall movements to calculate flow and pressure fields and to assess other fluid mechanical consequences of the peristaltic reflex. We employed a well-tested Eulerian–Lagrangian computational technique to analyze flow in the presence of moving boundaries (21, 23, 27). We selected three prototype contraction patterns (7, 18) to address the following issues.

First, it is known that contractions progress in time and in space along the segment of ileum. How then do pressure and flow fields within the segment compare at specific time points of a given contraction?

Second, vortical patterns derived from flow reversals are a powerful mechanism for mixing of luminal contents. Does reverse flow occur during peristaltic contractions in the isolated guinea pig ileum, and how effective is it in mixing two separate fluids or in redistributing particles?

Finally, experimental conditions such as bolus size and outflow resistance influence contraction patterns as defined by visual parameters. How do visual parameters such as the depth of the contraction and the slope of its shoulders affect its fluid mechanical consequences?

MATERIALS AND METHODS

Experimental Conditions and Visual Parameters on Which Analysis is Based

We based the current numerical analysis on our laboratory’s published visual data of the wall movements generated by peristaltic contractions (7, 18). Briefly, in those studies, we combined on videotape the luminal pressures, outflow, and wall movements of isolated segments of guinea pig ileum. Segments at rest were cylindrical tubes of 10-cm length and 5-mm diam.
eter. Segments were filled with boluses of physiological saline through the upstream stopcock, which was then closed. The right (downstream) end was attached to an outflow stub that dripped into a reservoir 3 cm above the intestine. Segments responded to the bolus with the characteristic peristaltic reflex contraction. This started as an upstream indentation of the upper (antimesenteric) wall. As contractions deepened and broadened, they narrowed the lumen of up to one-half of the segment of ileum (the occluding or coapting segment). The contraction produced outflow during its first couple of seconds as the coapting segment expanded downstream. In the subsequent seconds, the contraction propagated by a downstream movement of its upstream end. This led to bulging of the receiving segment at the downstream end of the intestine. As the coapting segment approached the downstream end of the intestinal segment, it flared open as it merged with the receiving segment. The total duration of the contraction was ~5 s.

The contraction generated a characteristic luminal pressure transient that peaked as the contraction achieved its maximum length (7, 18). Backflow was observed through the transparent walls of the ileum and recorded on the videotapes. The initial backflow flowed because rates of outflow were less than that of bolus transit. The later backflow returned fluid pooled in the receiving segment and equalized diameters throughout the length of the segment of ileum.

We defined contractions in space and time by objective visual parameters like the depth, length, and location of the coapting segment and by the length and slopes of its shoulders (18). The length of the coapting segment, for instance, increased with bolus size and, over the course of the contraction, increased and decreased virtually in parallel with the luminal pressure. For the present analysis, we simulated three prototype contraction patterns: 1) contractions that reduced the luminal diameter from its original 5 mm to 1 mm, called occlusive contractions (case 1); 2) contractions that reduced the lumen only to 2 mm, called nonocclusive contractions (case 2); and 3) contractions that virtually occluded the lumen and whose shoulders remained 0.5 cm long during the entire course of the contraction. These are henceforth called contractions with steep shoulders. (In the first two cases, the shoulders made up one-third of the contraction length, were fairly shallow, and changed their length over the course of contractions.) All three contraction patterns had in common that the coapting segment reached a length of at least 5.0 cm and propagated over at least 5 cm. All contractions were modeled at rates of lumen reduction and changes in length and velocity of the propagation derived from experimental data (18). The present analysis focuses on time points that represent the entire course of contractions, from the initial indentation, through the peak of the contraction as it reaches maximum occlusion length, to its waning. Pressure and flow fields were calculated in relative units from the documented wall movements and not specifically referenced to experimental data on luminal pressures and outflow. The mixing of fluid boluses and the transport of particles were, similarly, flow patterns derived from experimental data on wall movements. Such simulations of relative pressure and flow fields are state of the art for solving problems involving moving boundaries. The techniques are documented for a wide variety of systems and have been, in recent years, validated against numerous experiments and other numerical simulations (2, 3, 9, 13, 15, 17, 21, 23, 27).

Conversion of Observed Visual Parameter Data Into Functional Forms

The visual parameters recorded and reported in Ref. 18 were converted into functional forms to provide geometrical inputs to the fluid flow solver. Wall position and velocity variation with time were represented as continuous functions of time. Linear regression curve fits were performed using Microsoft Excel. Figure 1 shows the discrete experimental data (symbols) and curve fits (polynomial curves) for 1) diameter reduction (wave amplitude), as measured (18) at the midpoint of the coapting segment (also indenting or occluding segment); 2) contraction length; and 3) the axial velocity of the midpoint of the contraction. The first peak represents propagation of the downstream end of the contraction, the second peak the propagation of the upstream end.

![Fig. 1. Regression curves fit to experimental data (3). A: diameter reduction over time of contraction was fit to a polynomial. Diameter reduction is swift in the first couple of seconds. The reduction is reversed at ~4 s. The diameter used is at the midpoint of the coapting segment. For details on the objective visual analysis of contractions, see Ref. 3. B: regression curve fit to the length of the coapting segment. At the beginning of contraction, length increases and then decreases. C: curve fit to the axial velocity of the midpoint of the contraction. The first peak represents propagation of the downstream end of the contraction, the second peak the propagation of the upstream end.](http://ajpgi.physiology.org/)

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tion. The velocity of each point on the upper moving wall was supplied to the flow solver, and the no-slip and no-penetration boundary conditions on the solid surface were satisfied by the flow field. The contraction wave was modeled as composed of 1) the coapting segment, which is a flat section whose diameter was reduced and in which the stationary (lower) and the moving (antimesenteric) walls were strictly parallel; and 2) the shoulders (which connect the coapting segment with the noncontracting sections of the ileum). These were represented by cosine waves at the up- and downstream ends of the coapting segment.

Quantifying Fluid Mechanical Consequences of Contractions

All calculations were carried out for several stages in the progression of the peristaltic contraction. We quantified the following functional outcomes.

Flow field characteristics. The flow field defines the velocity at which fluid in the lumen is transported downstream or upstream. The pressure field is relevant to deformation of the luminal bolus and to the forces (3, 13, 15) that drive absorption.

Shear stresses along the mucosal surface of the moving wall. Shear stress represents the force of friction (dyn/cm²) between the fluid in the lumen and the mucosal surface. Shear is tangential to the wall: a positive shear force implies a downstream-directed force, and a negative implies an upstream-directed force. Shear stress is likely to facilitate absorption by increasing diffusion to the mucosa by mass transfer (4, 17, 26) and by reducing the unstirred layer (8, 26).

Fluid mixing. This was quantified by solving a species transport equation in the tube in tandem with the mass and momentum transport. A bolus of fluid was marked black (for a concentration value of 1.0). As shown in Fig. 2A, it was placed between 1.5 and 3.5 cm and surrounded by unmarked, white fluid (with a concentration value of 0.0). The deformation and transport of the black bolus was followed by solving a convection-diffusion equation for the concentration of the primitive variables (fluid velocities and pressure). The integral form of the nondimensionalized governing equations is solved by using a finite volume formulation (21). The computations require that the following two equations be solved in a consistent, coupled, and accurate manner.

The mass conservation law

\[ \oint u \cdot \hat{n} dS = 0 \quad (3) \]

and the fluid momentum equation

\[ \frac{\partial}{\partial t} \int u dV + \oint \hat{u}(\hat{u} \cdot \hat{n}) dS = -\oint \hat{n} p dS + \frac{1}{Re} \oint \hat{u} \cdot \hat{n} dS \quad (4) \]

where \( \hat{u} \) is nondimensionalized velocity vector, \( \hat{n} \) is a unit normal vector, \( dS \) is an area element, \( p \) is pressure, and \( Re = U_0 L / \nu \) is the Reynolds number, where \( L \) is the length scale, \( U_0 \) is the velocity scale, and \( \nu \) is the kinematic viscosity. In the above equations, the integral symbol \( \int \) denotes integration over the control volume, whereas the symbol \( \oint \) denotes integration over the surfaces bounding the control volume, and \( \hat{n} \) is a unit vector normal to the face of the control volume. The above equations are to be solved with \( \hat{u}(x,t) = \hat{u}_i(x,t) \) on the boundary of the flow domain, where \( \hat{u}_i(x,t) \) is the prescribed boundary velocity. In the present studies, we had the top wall (representing the antimesenteric border) of the segment of segregated species, as assigned in Fig. 1, \( \sigma^2 = 0.16 \). Note that, by definition, from Eq. 1, complete mixing corresponds to \( \sigma^2 = 0 \), because, under this condition, the concentration at each point in the tube will be equal to the average value.

Particle movement and mixing. Forty massless particles in a regular array in the intestinal segment at rest (Fig. 1B) were tracked during the progression of the contraction. In advecting the particles, the velocity of each particle was taken to be the local fluid velocity. Each particle’s new position was then determined by multiplying the velocity by the time step and adding the movement in the \( x \) and \( y \) directions to the particle’s previous position. This method essentially traces the motion of individual fluid elements and measures the forces experienced by them.

Work done in luminal transport. The effective work (W) that a contraction performs in transporting the luminal bolus was quantified as follows

\[ W = \int_0^T \int_0^1 \hat{F}_{wall} \cdot \hat{V}_{wall} dS_{wall} dt \quad (2) \]

where \( \hat{F}_{wall} \) is the force vector acting on the wall of the tube, \( \hat{V}_{wall} \) is the velocity vector, \( dS_{wall} \) is the length element along the wall, \( T \) is the total time taken for the passage of the wave, and \( L \) is the length of the top wall of the tube (which changes with time). The forces acting on the wall are determined from the fluid flow calculation (as the result of the wall pressures and viscous shear forces), whereas the velocities are specified according to the experimental data on visual parameters (18).

Computational Approach

Our numerical method is designed to solve a wide range of moving boundary problems. The flow field is solved in a domain that is enclosed by the walls of the segment on a fixed Cartesian mesh. The fractional step numerical scheme (27) is used for advancing the fluid flow solution in time. The Navier-Stokes equations are discretized on a Cartesian mesh by using a cell-centered collocated (nonstaggered) arrangement of the primitive flow variables (fluid velocities and pressure). The integral form of the nondimensionalized governing equations is solved by using a finite volume formulation (21). The computations require that the following two equations be solved in a consistent, coupled, and accurate manner.

The mass conservation law

\[ \oint u \cdot \hat{n} dS = 0 \quad (3) \]

and the fluid momentum equation

\[ \frac{\partial}{\partial t} \int u dV + \oint \hat{u}(\hat{u} \cdot \hat{n}) dS = -\oint \hat{n} p dS + \frac{1}{Re} \oint \hat{u} \cdot \hat{n} dS \quad (4) \]
ileum move at the velocity obtained in our experimental data (18). We held the bottom wall (mesenteric border) stationary.

To quantify the mixing behavior imposed by the contraction, we solved a species transport equation in a manner similar to Eq. 4. This equation takes the standard advection-diffusion form

$$ \frac{\partial}{\partial t} \int \phi dV + \int \phi (\mathbf{u} \cdot \mathbf{n}) dS = \frac{1}{Pe} \int \nabla \phi \cdot \mathbf{n} dS \quad (5) $$

where $\phi$ is the concentration, $Pe = (U_o L/D)$ is the Peclet number characterizing the ratio of diffusive transport to convective transport of the (marked and unmarked) bolus fluids, and $D$ is the mass diffusion coefficient of the two fluids. To model fluids that mix with minimal diffusion, the Peclet number was set to a very small value ($=0.001$) in the present calculations.

Computational Setup

The geometry of the model used for the present calculations as shown in Fig. 2A closely simulates that of isolated segments of guinea pig ileum in our experiments (7, 18). In the peristaltic reflex, only the antimesenteric (upper) border moves, whereas the lower wall remains stationary. Thus the coapting segment is not axisymmetric about the segment centerline. Accordingly, we moved the upper boundary of the segment at the velocity and waveform characteristics that we previously recorded for the peristaltic reflex (7, 18). We used 33 grid points to resolve for flow in the $y$ direction of the tubular segment. In preliminary studies, we determined that a mesh spacing of $dx = 0.015$ mm (corresponding to 33 mesh points across the lumen) produces reliable results for flow in the system considered. The maximum flow Reynolds number in the segment is computed using the expression $Re = V_{max} D/v$ is ~50, where $V_{max}$ is the maximum axial velocity of the contraction, $D$ is the diameter of the segment, and $v$ is the kinematic viscosity of the aqueous bolus. This is the nominal Reynolds number based on our experimental data on the axial velocity of the midpoint of the contraction. Much stronger convective effects are expected when fluid is squeezed at high velocities through the coapting segment.

RESULTS

**Fluid Mechanical Consequences of Contractions**

All contractions produced pressure pulses, shear forces, and flow reversals with fluid mixing, in addition to net downstream flow.

Figure 3A shows the pressure contours at select time points during progression of the occlusive contraction (case 1). Pressure is initially high on the left (upstream) end of the segment, but, as the coaptation reaches its maximum at $3.2 \, \text{s}$, pressure becomes higher on the downstream end. Thus the contraction produces a pressure pulse that moves faster and farther than the contraction: it starts upstream, moves under and through the contraction, and ends downstream. The pressure differential across the coapting segment, along the segment of ileum, and across its wall (from inside to outside) peaks as the coapting segment reaches maximum length.

Figure 3B shows the flow fields that result from the same contraction. During the initial seconds where the length of the coapting segment increases, the contraction produces laminar flow downstream and out of the ileum. As the entire contraction moves downstream, it generates rapid reverse flow through the narrow lumen of the coapting segment. Reverse flow continues as the coapting segment flares open and the contraction recedes.

The mixing of liquids produced by the contraction is shown in Fig. 3C. A bolus of black liquid was placed where the contraction first indents the lumen (Fig. 2A). The lumen upstream and downstream contained white liquid. As the contraction starts, the black bolus is stretched, and its tip is moved downstream. At maximum coaptation, the bolus is broken up into a core, which remains black, and into layers of gray fluid, which advance far downstream. As the contraction recedes, a small black core remains attached to the stationary wall. This is surrounded on all sides by layers of fluid that are all shades of gray.

The displacement and redistribution of particles by the contraction is studied in Fig. 3D. The breakup of the downstream rows of particles starts with the initial indentation. Downstream and radial movement of particles peaks with maximum coaptation and is reversed only in part as the contraction recedes. The contraction changes the position of these particles relative to each other, to the cross-section, and to the long axis of the intestines. Particles from the most downstream row are trapped between the walls of the coapting segment.
where they would be exposed to large pressure and shear forces. The four upstream rows of particles remain essentially stationary over the progression of the contraction, indicating that the flow field is very weak there.

Mixing of liquids and redistribution of particles is critically dependent on the occurrence of vortical flow patterns, due to changes in flow direction. As shown in Fig. 4, the fast reverse flow in the coapting segment sets up vortices upstream from the contraction. However, the mixing is not vigorous, because the vortices are transient in nature and appear when flow reverses.

The pressure profile generated by the nonocclusive contraction (Fig. 5A) is similar to that of the occlusive counterpart (Fig. 3A), but pressure differentials are much lower over the course of the contraction. Flow velocities (Fig. 5B) are decreased compared with Fig. 3B, but not as drastically as the pressures. This is because the propagation velocity of the contractions is the same. Figure 5C shows deformation and mixing of the black and white fluids similar to Fig. 3C. Figure 5D shows less displacement and redistribution of particles than Fig. 3D.

Figure 6 shows the flow fields and mixing caused by the contraction with steep shoulders. The pressure profile in Fig. 6A is similar to that caused by the contraction with flat shoulders (Fig. 3A), but the pressure differentials are much larger. In the flow field contours of Fig. 6B, axial velocities are increased over those in Fig. 3B. In Fig. 6C, mixing of black fluid is enhanced over that in Fig. 3C, and particle redistribution involves more rows of particles in Fig. 6D than in Fig. 3D.

Quantitative Impact of Contractions

Figure 7 depicts the mixing of black and white liquids. Judged by the variance defined in Eq. 1, the three cases of contractions mix to a similar degree. Three phases of mixing can be discerned. In the first phase (up to ~2 s), little mixing occurs as the black bolus is stretched (compare Figs. 3C, 5C, and 6C). Mixing accelerates in the second phase as maximum coaptation is reached. A downstream portion of the bolus is further stretched, whereas the black core is diminished in size and shifted upstream and toward the stationary (lower) wall of the ileum. Layers of fluid that represent the gray scale from black to white replace the sharp borders between black bolus and white fluid. In the third phase, mixing continues as recession of the contraction produces more reverse flow. The black core is much reduced in size, and the most downstream lightly mixed fluid returns from the downstream half of the ileum to its upper half.

Figure 8 illustrates the shear stress along the moving (upper or antimesenteric) wall. Shear stresses are high within the coapting segment and peak at maximum coaption at 3.2 s. Between the beginning of the contraction and the maximum coaption, shear stress changes direction abruptly from downstream to upstream. The nonocclusive contraction generates the lowest and the contraction with the steep shoulders generates the highest shear stress. Because its coapting segment is long, the surface exposed to high shear stresses is longer for the contraction with steep shoulders than the others. The profile of the shear stress varies between contraction cases somewhat at the beginning but not systematically during much of the contraction.

Figure 9 analyzes the pressures along the moving wall of the segment. Pressures increase abruptly within the coapting segment. Contractions with steep shoulders lead to the largest wall pressures over the longest section. The pressures exceed those of the flat nonocclusive contraction by an order of magnitude. Occlusive contractions produce higher pressures than nonocclusive contractions. Similarly, the pressure differential that the coapting segment generates between the up- and downstream ends of the ileum is highest with the steep shoulders, least with the nonocclusive contraction, and intermediate with the occlusive contraction with flat shoulders.

Figure 10 assesses the work done in transporting the fluid bolus. Work in the initial 2–3 s (when downstream and flow out of the segment is generated) is quite low for all contractions. The nonocclusive contraction persists in performing little fluid transport work. For the occlusive contractions, work increases as fluid needs to be moved at ever-increasing pressures and velocities through the coapting segment. Both the pressure and the tangential (shear) forces increase with the degree of coaptation. Pressure forces predominate in the current situation over the shear forces.

Fig. 5. Pressure and flow fields for nonocclusive contraction (case 2). A: pressure differentials generated are much smaller than those generated by the occlusive contraction. B: axial velocity contours. The flow-field contours are similar to those of case 1, with a modest reduction in flow velocity. C: deformation of black fluid bolus and mixing with white fluid. D: particle redistribution. Fewer particles are moved by the nonocclusive contraction than by the occlusive contraction.
DISCUSSION

We computed the profiles of luminal pressures and flow, luminal mixing, and shear stresses for three prototype intestinal contractions. This shows that the peristaltic contraction of the guinea pig ileum generates fluid mechanical effects beyond unidirectional laminar flow and net luminal transit. Flow effects include pressure pulses and shear forces. Reverse flow occurs and triggers vortical flow and mixing of fluid and the redistribution of particles. These flow processes are likely to enhance digestion and absorption of nutrients. Our analysis also shows that their depth and shoulders greatly affect the fluid mechanical impact of contractions. The work done by pressure forces was found to dominate that of the shear, as should be expected for the flow at moderate Reynolds numbers encountered in the segment.

One important function of contractions is to move luminal contents downstream. Our calculations show that, as the contraction gathers depth and length, it indeed generates laminar flow in the receiving segment and flow out of the downstream end of the segment. This fits well with our experimental data, where outflow occurred in the first couple of seconds and ceased as the contraction reached maximum occlusion (7, 18).

Our calculations show that the contraction furthermore generates a pressure differential along the gut. A pressure pulse moves from upstream, into the coapting segment, and then downstream. This corresponds to luminal pressure gradients recorded during the peristaltic reflex in isolated segments of guinea pig intestine (7, 18, 19).

Reverse flow increases as the contraction propagates and sets in motion vortical patterns of flow at the upstream shoulder of the contraction. Such vortical flow patterns are critical to mixing of luminal contents (4). Mixing of fluids is preceded by deformation of the bolus at the site of the contraction. The bolus is stretched at its downstream end, and its core is reduced as layers of partially mixed fluids form around it. The small interfaces separating the two fluids along the length of the intestine are replaced by many large interfaces across and along the intestinal lumen. Particles are initially carried along and trapped by the contraction. As the contraction ceases, it releases the particles to locations that differ both in the cross-sectional and the axial profile from their sites of origin. Shear forces are generated along the moving wall and peak with maximum coaptation.

The coapting segment encloses a sample of contents and exposes them to swift reversal shear stresses. The concentration gradient of the contents is high, which, by itself, could impact absorption.

Large shear forces along the surface and residence times, which are prolonged by flow reversals, promote uptake of easily diffused smaller molecules. Shear will reduce the diffusional resistance to transport of nutrients from the lumen to the wall. Shear and pressure-induced effuxes can increase diffusion and subsequent absorption according to the Darcy model (3, 8, 13, 15). The pressure contours demonstrate pressure differentials across the coapting segment and show that transmural pressure differentials would be particularly high in the coapting segment. Large transmural pressure differentials favor the uptake of macromolecules through porous membranes (13, 26), but whether they reduce the epithelial or the much larger luminal resistance to absorption (as defined in Ref. 8) is unclear.

For a nutrient to be absorbed by the intestine, it needs to be brought, first, into contact with the brush border of the mucosal epithelium and, second, to be transported across the epithelial cell. Absorption is accordingly described as a two-step process, where a nutrient has to pass through a preepithelial (luminal) and an intraepithelial diffusion barrier. The cross-epithelial transport is well studied for most nutrients and, with perfusion of nutrients, constitutes much less a barrier to absorption than the preepithelial barrier.

Two models have been proposed to describe the absorption of nutrients from intestinal lumen into...
and across the mucosa during intestinal perfusion. The classic “unstirred layer” model divides luminal contents into a perfectly stirred core layer and an unstirred boundary layer (26). The laminar flow model assumes a laminar flow profile where flow velocity increases parabolically from zero at the mucosal boundary to high-axial flow in the core (8). In this model, mixing occurs only along the longitudinal but not the radial (cross-sectional) axis. Analytic studies with laminar flow models show that the luminal resistance barrier to absorption becomes intolerably high, as the boundary layer is rapidly depleted of nutrient (8).

Several flow processes illustrated here are likely to reduce the luminal resistance barrier (8, 10, 12, 25, 26). We found that even the peristaltic contractions studied here produced reverse and vortical flow patterns. These followed, in place and in time, the laminar flow. Reverse flow would improve axial mixing over laminar flow. Vortical flow produces cross-sectional mixing. Cross-sectional stirring should effectively replenish the nutrient concentration at the boundary, facilitate contact between nutrients and brush border sites, and hence reduce the preepithelial diffusion barrier.

The mixing of fluids and the rearrangement of particles would ensure adequate exposure of contents to digestive secretions. The period of bolus stretch may favor absorption because nutrients in the bolus would be forcefully exposed to both the
moving and stationary walls. Large fluid-to-fluid interfaces may promote the interaction of digestive enzymes with substrates. Lipid digestion, for instance, occurs at the interface of lipases carried in aqueous secretions and of triglycerides (22).

Both the depth of the lumen occlusion and the slope of the shoulders have profound effects on fluid dynamics. This demonstrates that seemingly minor details in the configuration of intestinal contractions have profound fluid mechanical consequences. On most accounts, the occlusive contraction with steep shoulders proved more effective than the contraction with shallow shoulders, especially the nonocclusive type. The pressures and shear stresses in the coapting segment are increased dramatically by steep shoulders, and this would likely enhance absorption. The increased pressure and shear forces require, however, significantly more work. Steep shoulders have little effect on mixing. Mixing is enhanced by the presence of vortical flow, particularly in the phase following maximum occlusion when the receding contraction causes a reverse flow in the segment through the occlusion.

Previous simulations of intestinal flow (2, 8–10, 12, 20, 25) were not backed by precise visual data on wall movements and are, therefore, not representative. It is often assumed that the upstream and the downstream ends of contractions progress at the same times and speed or that contractions reduce the lumen in a concentric manner.

We analyzed here the flow effects of single peristaltic contractions. This type of contraction propagates swiftly through a comparatively great length of the intestine and generates effective axial transport. It typifies the motor pattern encountered in the fasting state or triggered by boluses of physiological saline or cellulose gum (7, 14, 16). Nutrients such as oil, glucose, or complex meals trigger repetitive stationary contractions at multiple sites that generate intense to-and-fro movements of luminal contents (14, 16). Flow reversals, vortical flow patterns, mixing, particle redistribution, and reversal of shear forces described here for the single peristaltic reflex are thus likely to be intensified in the digestive state.

Our analysis applies strictly to the experimental conditions from which the visual parameters were derived (7, 18). The boundary conditions were such that no additional flow occurred into the study segment from upstream and that outflow through the downstream cannula was modestly restricted. As a consequence, part of the bolus propelled by the contraction failed to clear the cannula and pooled in the receiving segment. As the contraction waned, that fluid redistributed within the study segment. The boundary conditions that we chose to study are intermediate between extremes where the contraction either 1) fails to clear any of the bolus or 2) clears the bolus from both the study segment and the segment downstream from it. Under condition 1, which occurs when outflow resis-

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**Fig. 9.** Pressures (p) along the moving (upper) wall at height of contraction (at 3.2 s and maximal length of coapting segment). The pressure differential along the 10-cm-long segment of ileum is moderate with the occlusive contraction (case 1; A), small with the nonocclusive contraction (case 2; B), and large with the contraction with steep shoulders (case 3; C). Pressures are relative.

**Fig. 10.** Work done by contraction cases 1, 2, and 3. Steep shoulders dramatically increase work performed by the contraction (computed using Eq. 2; see MATERIALS AND METHODS, Work done in luminal transport).
tance is comparatively high, as it may be in front of the ileocecal valve, retrograde flow is even more prominent as the bolus escapes through the advancing contraction (18). Under condition 2, relaxation of the study segment would not lead to backflow because no bolus would be available. Flow patterns would also differ from the ones analyzed here if a bolus were available upstream. Presumably, all of these conditions exist at various points of time or place in the small intestine.

Our analysis suffers from several potential drawbacks. We limited our experimental and analytic data to contractions with minimal shortening and twisting. Some shortening and twisting is inherent in intestinal movements and is likely to impact fluid mechanics. Unfortunately, shortening and twisting interferes with imaging and with the recording of movement data. Our model assumed, furthermore, that the slope of the contraction remains constant over time. This is not truly the case (7, 18), and some flow phenomena may be misrepresented by our current calculations. Perhaps the most serious shortcoming of our model is that it analyzes the fluid mechanical effects of contractions in only two dimensions. We used analytic tools of flow in the presence of moving boundaries that are state of the art and have been well validated in a variety of systems (3, 13, 15, 17, 20, 21, 23, 27). Three-dimensional systems would be required to compare experimental data on fluid outflow to those calculated by the model. Three-dimensional modeling of flow in the presence of moving boundaries remains to be established and to be validated. It requires inordinate computing power and generates enormous quantities of data, which remain difficult to visually represent, to analyze, and to interpret.

In summary, we used state-of-the-art numerical methods to compute the fluid mechanical consequences of realistic prototype peristaltic contractions. Our analysis provides new insights into the flow and pressure profiles generated by contractions, tracks the mixing of fluids and particle movements, and quantifies shear stresses between wall and lumen. These data should improve the understanding of mechanics of intestinal digestion and absorption. A similar analysis of flow events generated by different contraction patterns in segments other than the ileum (6, 10, 14, 19) should be of interest.

James Fenton, then an engineering student at Iowa, was instrumental in setting up the current collaboration.

DISCLOSURES

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REFERENCES