Constrictions move contents by changing the configuration of the isolated cat stomach

KONRAD SCHULZE-DELRIEU, ROBERT J. HERMAN, SIROOS S. SHIRAZI, AND BRUCE P. BROWN

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Schulze-Delrieu, Konrad, Robert J. Herman, Siroos S. Shirazi, and Bruce P. Brown. Constrictions move contents by changing the configuration of the isolated cat stomach. Am. J. Physiol. 274 (Gastrointest. Liver Physiol. 37): G359–G369, 1998.—To understand how constrictions move gastric contents, we measured, in isolated cat stomachs, the effects of constrictions on gastric length, diameters, pressures, and emptying. Movements of the stomach and of gastric contents were monitored by video camera and ultrasound and were related to mechanical events. Based on pressures, we defined the following four phases of constrictions: 1) $P_o$, a steady pressure associated with tonic contraction of proximal stomach; 2) $P^*$, a pressure wave during which the constriction incises the gastric body; 3) a pressure nadir while the constriction lifts the gastric sinus toward the incisura; and 4) a second pressure wave, $P^*$, as the constriction advances through the antrum. In open preparations, liquid output and shortening of the greater curvature are larger during $P_o$ stop during $P^*$, and resume with $P^*$ Constrictions generate higher pressures when gastric volume is held steady. Constrictions increase wall thickness and decrease gastric diameters at sites they involve and have opposite effects at remote sites. Constrictions move the incisura and hence red the border between gastric segments and shift volumes back and forth within the gastric lumen. Constrictions furthermore stir, compress, and disperse particulate beans without moving them to the pylorus. We conclude that gastric constrictions 1) reverse changes in gastric length that occur during gastric filling, 2) move gastric contents directly through local contact and indirectly by changing the configuration of the stomach, and 3) interact with structures such as the incisura in retaining and breaking up solid gastric contents.

gastrectomy fibers; incisura angularis; pylorus; gastric sieving and trituration

THE MECHANISMS BY WHICH the stomach simultaneously empties liquid contents and retains and breaks down particles are only partially understood (4–11, 14–17, 20, 22–25, 27, 28). We have recently proposed that the configuration of the stomach plays a role in discriminating between liquid and solid contents (5). Solids appear to be trapped by the dependent part of the stomach opposite the gastric incisura, known as the sinus (5, 11, 36). Meanwhile, the stomach decants liquid contents over the brim formed by the pylorus. This view was based on our ultrasonographic observation that beans settle along the dependent part of the greater curvature of upright humans; broth flows over the beans and out through the pylorus. These studies were limited to observing the movements of the gastric antrum (5).

To record movements of the entire stomach under controlled conditions, we used isolated preparations of cat stomach. These preparations produce virtually identical constrictions and emptying in vitro as in situ (7, 13, 32, 34). We related visual parameters of gastric constrictions to their effects on gastric pressures and gastric emptying. We again used ultrasound to observe patterns of flow inside the gastric lumen and to measure the thickness of the gastric walls during contractions. Specific issues we wished to address here were 1) What are the relationships between movements of the gastric walls, gastric pressures, and emptying? 2) How do gastric constrictions affect the configuration of the stomach as represented by its length and diameters? and 3) What movements of solid contents do gastric constrictions cause?

METHODS

Twenty cats weighing 6–8 lb each were anesthetized with 300 mg intraperitoneal pentobarbital sodium. Their stomachs, including segments of the esophagus and the duodenum, were removed through a midline abdominal incision. Stomachs were cleaned in Ca$^{2+}$-free Krebs solution, and cannulas were tied into the cardia and proximal duodenum. Preparations were mounted in a transparent bath containing 15 liters of Krebs solution at 36.5°C aerated with 5% CO$_2$ in O$_2$ (the composition of the Krebs solution was, in mol/l, 240 NaCl, 9.66 KCl, 2.61 NaH$_2$PO$_4$·H$_2$O, 2.39 MgSO$_4$·7H$_2$O, 4.90 CaCl$_2$·2H$_2$O, 5.55 CsH$_2$O$_6$, and 12.5 NaHCO$_3$ + carbococh at 10 $^{-8}$M).

Stomachs were mounted semivertically in the bath with the lower esophageal sphincter held by the esophageal cannula $<$2 cm below the water surface and the pylorus held by the duodenal cannula $<$3 cm below the water surface. The esophageal cannula served to fill the stomach and to admit a probe connected to a pressure transducer (Gould Statham model P231D). The transducer and probe were filled with bubble-free water and repeatedly flushed but not perfused during the experiment. Pressures were recorded from the gastric cavity 2 cm below the lower esophageal sphincter (Fig. 1A). The duodenal cannula emptied through a plug in the wall of the bath into a cup outside of the bath. The cup was suspended on a calibrated force transducer (Grass force displacement transducer model FT03C) to continuously monitor gastric output. The duodenal cannula was designed to minimize obstruction of the lumen; it was 17 mm wide to fit the fully expanded duodenum. The cannula tapered down to 13 mm at the end over which the duodenum was tied (Fig. 1B).

Stomachs were filled for 1 h with 30 ml Krebs solution and then evacuated and filled through the esophageal cannula with 100 ml (closed preparations) or 150 ml (open preparations). Filling was performed at a rate of 1 ml/s, and the esophageal cannula was closed at the end of filling.

In the first set of experiments, we studied how constrictions affect gastric pressures, emptying, and gastric size. We filled six stomachs with 150 ml of solution and, after 3 min, opened the duodenal cannula while recording pressures, output, and...
movements on videotape. For determination of gastric size, we measured the length of the greater and lesser curvatures between the gastroesophageal junction and the pylorus.

In a second series of experiments, we examined how the configuration of the stomach changes when it contracts around a steady volume. For this, we filled six stomachs with 100 ml and recorded pressures and gastric diameters for contractions, which occurred a minimum of 3 min after the end of filling. Diameters represented the width of the fundus, body, incisura to sinus, and antrum, respectively. (The specific sites used to measure diameters are given below.) We also measured by ultrasound the thickness of the greater curvature wall of the fundus and antrum.

In a third series, we compared isotonic and isovolumetric contractions by filling and emptying stomachs repeatedly. After individual contractions, stomachs were allowed to empty for 5 min, and residual fluid was aspirated through the duodenal cannula. Stomachs were refilled as before, and a minimum of six sequences of contractions was recorded in all.

Ten grams of canned garbanzo beans were quartered and replaced 10 ml of Krebs solution in these experiments. The pH of the gastric contents and effluent was sampled throughout the experiments and never fell below 7.0.

Gastric movements were imaged simultaneously by video camera (DAGE-MTI series 67) and by ultrasonographic scanning (Sonolayer Vssa-90a; Toshiba). Images were combined (Image Labs model MPS-551I) on videotape (Fig. 1A) with the analog tracings of gastric pressures and output using a VGA-NTSC link (Visionetics). The computer time-stamped all entries on the videotape. All transducers were connected to a Hewlett Packard HP75000 series B VXI bus. Their signals were recorded as ASCII files using data acquisition software written in Quick Basic by R. Herman and I. Barnes, Department of Surgery, University of Iowa. The sampling rate for each channel was set at 10 Hz. The program generated both numerical data and an analog tracing of the physiological parameters. To condition the input signal, a second-order Butterworth anti-aliasing low-pass filter with one-half power frequency of 2 Hz was used. The filtered analog signal was digitized using a 5.5-digit low-noise integrating, 13-kHz high-speed sampling analog-to-digital converter (HP E1326B autoranging 5.5-digit multimeter).

Recordings were analyzed for pressures, volume output, and visual parameters of contractions. Only contractions that occurred singly and propagated through the length of the stomach were analyzed; they constituted more than one-half of all contractions recorded. Gastric cavity pressure was calibrated to 0 mmHg after mounting the empty stomach in the bath. Pressures recorded in the gastric cavity are given at their peaks and in sequence as \( P_0 \), \( P_8 \), and \( P_9 \); the duration of pressure waves is also given. Volume data included stroke volume, the amount of gastric outflow produced by a single contraction, and cumulative gastric output, the volume emptied during a 5-min recording period. Visual parameters include 1) the length of the greater curvature and of the lesser curvature between the cardia and the pylorus, 2) gastric wall thickness, and 3) gastric diameters. [To use consistent sites for diameter measurements, we divided the curvatures of the stomach into the fundus, body, incisura to sinus, and antrum, respectively.]
The wedge-shaped segment, which forms the transition between the proximal and the distal stomach, is called the gastric sinus; the sinus points at the incisura and has a sector of $-90^\circ$. At the incisura, the lower gastric slings, formed by the third layer of the muscularis propria, radiate toward the greater curvature, and insert in the walls of the sinus (11, 30, 31, 33, 36). All data are given as means ± SE. Comparisons were made using the t-test, two-tailed distribution, and two-sample unequal variance; $P < 0.05$ was considered significant.

### RESULTS

Gastric pressures and emptying in relation to the phases of gastric contractions. In open preparations, contractions cause flow of contents from the stomach. Stroke volumes approximate 30% of intragastric volumes on average (Table 1), but individual stroke volumes might exceed 50% (Fig. 2). During a 5-min collection period, ~75% of the original filling volume empties. The rate of outflow varies over time (Fig. 2 and Table 2). The rate declines as the contraction involves more distal gastric segments (Table 2). Outflow may cease temporarily while the contraction involves the gastric body and resume as the contraction moves into the sinus and antrum (Figs. 2 and 3A).

Contractions affect pressures in the proximal gastric cavity. The pressure profile recorded from inside the proximal stomach consists of the following four phases: 1) $P_o$, characterized by a fairly steady pressure that may last many minutes (the stomach generates this after accommodating volume as previously described; see Refs. 4, 13, 14, 16, 34); 2) $P'$, a comparatively large and long pressure wave intervening or superimposing on $P_o$; 3) a pressure nadir; and 4) $P''$, a second pressure wave, smaller and shorter than $P'$ (Figs. 2 and 3A and Tables 1 and 2). Luminal pressure drops once the contraction reaches the pylorus.

Contractions lead to characteristic changes in the size and configuration of the stomach. The filled stomach assumes a saccular shape with bulging curvatures; with emptying, the gastric curvatures flatten and the stomach becomes almost tubular. Changes in gastric configuration reflect both the changing site of the contraction and the decrease in gastric volume (Fig.

![Table 1. Pressures, stroke volumes, and cumulative output generated by gastric contractions](image)

<table>
<thead>
<tr>
<th>Amplitude of Pressure Waves, mmHg</th>
<th>Duration, s</th>
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<tbody>
<tr>
<td>$P_o$</td>
<td>$s'$</td>
</tr>
<tr>
<td>$P'$, isovolumetric (pylorus closed, $V_o=100\text{ ml}$)</td>
<td>5.3 ± 1.0</td>
</tr>
<tr>
<td>$P''$, isovolumetric (pylorus closed, $V_o=150\text{ ml}$)</td>
<td>2.1 ± 0.7*</td>
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<tr>
<td>$s''$</td>
<td>10.6 ± 1.0</td>
</tr>
<tr>
<td>$s''$</td>
<td>8.0 ± 1.1</td>
</tr>
<tr>
<td>$s'$</td>
<td>14 ± 1.0</td>
</tr>
</tbody>
</table>

Data are means ± SE; n = 6 preparations. $P_o$, steady pressure associated with tonic contraction of proximal stomach; $P'$, pressure wave during which contraction induces gastric body; $P''$, 2nd pressure wave as contraction advances through antrum; $s'$ and $s''$, duration of 1st and 2nd pressure wave, respectively. Stroke volume was 37.5 ± 4.5 ml. Volume emptied during 5-min recording period (cumulative output) was 114.7 ± 4.7 ml. *$P < 0.05$ between pylorus closed and open; $P''$ was significantly different from $P_o$ and $P''$ in both open and closed preparations.

![Fig. 2. Pressures, outflow, and changes in gastric length resulting from contraction of isolated cat stomach](image)
3A). The decrease in the size of the stomach is reflected in the shortening of the greater curvature. That curvature shortens by ~3 cm or 15% of its total length (Fig. 2 and Table 2). Shortening occurs primarily as the contraction moves through the gastric body (sites 1–2) and again as it moves from the sinus into the antrum (sites 3–4). Shortening of the greater curvature parallels gastric outflow. During P', there is no outflow, and the length of the greater curvature remains stable. The lesser curvature shortens little during contraction and emptying of the stomach (Fig. 2).

The pressure phases inside the proximal stomach reflect the advance of the contraction from the fundus to the body, sinus, and antrum. During P₀, the contraction tonically flattens both curvatures and narrows the very proximal stomach. During P', the contraction indents sequential points of the greater gastric curvature and moves the incisura toward the greater curvature. During the pressure nadir, the contraction moves the sinus and the incisura toward each other. During P'', the contraction moves rapidly through the antrum, and the incisura moves toward the pylorus (Fig. 3A).

Changes in gastric dimensions with stomachs contracting around a steady volume. As contractions propagate through the length of the stomach, they again produce characteristic changes in the configuration of the stomach (Fig. 3B). This is reflected in cyclic changes of the diameters of the fundus, body, sinus, and antrum. The contraction leads to greater diameter reductions the more distal it moves. Once the contraction moves beyond a segment, the diameter of that segment increases over resting levels (Fig. 4 and Table 3). Contents shift back into the proximal segment as seen by the direction of flow on ultrasound. Unlike in stomachs that empty, the greater curvature, if anything, becomes longer as the stomach contracts around a steady volume (Fig. 3B and Table 3).

By ultrasonographic measurement, the thickness of the wall of the proximal stomach is less than that of the distal stomach. This agrees with anatomic data (13, 31, 36). The wall of the fundus thickens, whereas the proximal stomach contracts during P' and thins when the antrum contracts, during P''. Conversely, the thickness of the antral wall increases with the contraction there and decreases while the proximal stomach contracts (Table 3).

Movements of solid gastric contents (garbanzo beans) by contractions. Particles move during all phases of gastric contractions (Fig. 5). Movements are complex and change the position of particles in relation to each other and the gastric walls. Even though particles repeatedly move toward the pylorus, they do not reach it and are not noticeably closer to it after than before the contraction.

The tonic contraction of the proximal stomach presses the sediment into the sinus, which bulges. When the contraction involves the distal gastric body during P', the beans are heaped up (Fig. 5, A and B). Particle movements are increasingly rapid and complex when the contraction involves the incisura and the sinus (Fig. 5, C–G). 1) As the wall of the greater curvature folds in and points at the incisura, it stirs up the particles in the sinus. 2) As the fold advances toward the pylorus along the greater curvature, it imparts a tumbling motion on the particles. 3) The incisura moves down and across the particles, pounding, shearing, and retaining them. The movements of the incisura and of the contraction along the greater curvature are accompanied by currents and countercurrents at the interface between liquids and particles. Currents carry along some particles or disperse them through jets (Fig. 5D). The jet disperses everything in its trail all over the proximal stomach. Particles are sent on trajectories of differing lengths and directions; as their momentum fades, they shower back into the sinus. Visible particles never collected in the duodenal cannula, but gastric effluent became turbid after repeated filling and multiple contractions.

Comparison between open and closed preparations. Open and closed preparations respond with similar mechanical activity to filling. Tonic contractions of the proximal stomach give rise to rhythmic contractions. These propagate from the gastric body through the gastric sinus into the antrum and pylorus. Contractions cause higher pressures and last longer in closed than in open preparations (Table 1).

**DISCUSSION**

We studied in isolated gastric preparations how contractions affect the configuration of the stomach, its pressures, and its emptying. Our approach differs from most previous studies (6, 9, 15, 17, 20, 22–25, 27) in that we quantified the visual, mechanical, and fluid mechanical parameters of contractions over the course of single contractions. To do this, we combined recordings of gastric pressures and output with imaging of gastric configuration by video camera and by ultrasound. Mechanical data were recorded digitally on-line, and visual parameters were digitized off-line. Correla-

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**Table 2.** Gastric pressures, flow rates, and greater curvature length in response to contractions involving sequential gastric segments

<table>
<thead>
<tr>
<th></th>
<th>Baseline</th>
<th>Fundus</th>
<th>Body</th>
<th>Sinus</th>
<th>Antrum</th>
<th>Beyond Pylorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pressure, mmHg</td>
<td>8.2 ± 1.6*</td>
<td>4.2 ± 1.2</td>
<td>4.0 ± 1.4</td>
<td>3.6 ± 1</td>
<td>2.6 ± 1.5</td>
<td>2.3 ± 1.4</td>
</tr>
<tr>
<td>Flow rate, ml/s</td>
<td>0.0</td>
<td>5.0 ± 0.9</td>
<td>4.6 ± 0.9</td>
<td>2.9 ± 0.4</td>
<td>2.5 ± 0.6</td>
<td>1.7 ± 0.5</td>
</tr>
<tr>
<td>Length change, cm</td>
<td>20.5 ± 0.6*</td>
<td>-0.5 ± 0.2*</td>
<td>-1.1 ± 0.2*</td>
<td>-0.1 ± 0.3*</td>
<td>-1.4 ± 0.4</td>
<td>-0.5 ± 0.4*</td>
</tr>
</tbody>
</table>

Data are means ± SE; n = 6 open preparations. *P < 0.05 (compared with following site).
Fig. 3. Changes in the configuration of the isolated cat stomach produced by a single contraction. A: contraction empties gastric contents. Pressure and outflow data are on bottom. Stomach was filled with 150 ml solution at −180 s. Duodenal cannula was opened at 34 s, and contraction was recorded between 34 and 58 s. The 1st diagram in A, top, gives an overview of how the gastric outline changes from a globular configuration upon being filled at 180 s, through the pressure wave $P_8$ at 43 s, and to an almost tubular configuration after ~60% of contents have emptied at 58 s. The sinus (dependent part of the greater curve opposite the incisura) shifts upward and distally. The 2nd diagram provides details of the tonic contraction between 34 and 37 s. The proximal greater curvature flattens while gastric outflow surges. The 3rd diagram details the peristaltic contraction of the gastric body responsible for $P_8$. Pressure declines as the contraction reaches the gastric transition zone at the incisura and sinus. At 46 s, the incisura deepens and moves toward the greater curvature, which folds up. The 4th diagram shows the peristaltic contraction of the antrum responsible for $P_9$. The incisura opened and flattened as the contraction passed it. B: isolated cat stomach contracting around a steady luminal volume. Pressure curve resulting from the recorded contraction can be seen in bottom. Again, the stomach was filled at −180 s and originally assumed the shape shown in the 1st frame in A. The 1st diagram in B, top, is an overview of the changes in gastric configuration produced by a contraction that starts at −43 s and ends at −61 s. Again, the sinus pulls up toward the incisura during the pressure nadir at 57 s. Along the greater curvature, the contraction produces a discrete indentation, first in the middle of the gastric body. Along the lesser curvature, the incisura is the only consistent indentation moving with the contraction. (Thus the contraction produces sequential changes in the position and angle of the incisura and in the degree to which segments of the lesser curvature bulge.) The 2nd diagram shows how the tonic contraction of the proximal stomach shifts volume distally. The dependent part of the greater curvature opposite the incisura, the sinus, bulges. The 3rd panel tracks the contraction as it moves from the distal body into the sinus. While the contraction lifts the sinus toward the incisura, luminal pressure drops to a nadir at 55 s. The 4th diagram shows the passage of the contraction from the sinus into the antrum. Along the greater curvature, the contraction sequentially indents the sinus at 57 s, the proximal antrum at 61 s, and the midantrum at 65 s. Along the lesser curvature, the incisura flattens and moves toward the pylorus. The gastric body bulges along the greater curvature after 57 s and along the lesser curvature after 61 s. Intragastric pressure remains low and falls off further before the contraction reaches the pylorus.
Gastric diameters, length of greater curvature, and wall thickness corresponding to pressure phases

When the stomach is inflated, the antrum accommodates. In response to distension, the antral walls produce a pressure wave as a discrete indentation forms along the greater curvature and propagates from the middle to the distal gastric body. In the third phase, a pressure nadir occurs as the antral walls pass through the antrum, generating a second pressure wave. In the stomach in situ, vagovagal reflexes mediate receptive relaxation, a short-lived inhibition of muscle tone in response to swallowing, and adaptive relaxation, a prolonged inhibition in response to gastric distension, and vagal reflexes enhance antral contractions in response to distension of the corpus, the corporoantral reflex (1, 12, 30). Adaptations in antral wall tension by mechanoreceptors are thought to control gastric diameters in response to the viscosity of luminal contents (24, 28). We did not specifically study to what extent neuronal reflexes controlled the mechanical activity of our preparations, but previous work leaves little doubt that many if not all gastrogastric reflexes for which a vagovagal pathway has been demonstrated are also mediated by intramural pathways. Similar to the stomach in situ, the isolated stomach accommodates. In response to filling, muscle tension in the proximal stomach is inhibited, the stomach accommodates. In response to distension of the corpus, the corporoantral reflex (1, 12, 30). Adaptations in antral wall tension by mechanoreceptors are thought to control gastric diameters in response to the viscosity of luminal contents (24, 28). We did not specifically study to what extent neuronal reflexes controlled the mechanical activity of our preparations, but previous work leaves little doubt that many if not all gastrogastric reflexes for which a vagovagal pathway has been demonstrated are also mediated by intramural pathways. Similar to the stomach in situ, the isolated stomach accommodates. In response to filling, muscle tension in the proximal stomach is inhibited, the stomach accommodates. In response to distension of the corpus, the corporoantral reflex (1, 12, 30). Adaptations in antral wall tension by mechanoreceptors are thought to control gastric diameters in response to the viscosity of luminal contents (24, 28). We did not specifically study to what extent neuronal reflexes controlled the mechanical activity of our preparations, but previous work leaves little doubt that many if not all gastrogastric reflexes for which a vagovagal pathway has been demonstrated are also mediated by intramural pathways. Similar to the stomach in situ, the isolated stomach accommodates. In response to filling, muscle tension in the proximal stomach is inhibited, the stomach accommodates. In response to distension of the corpus, the corporoantral reflex (1, 12, 30). Adaptations in antral wall tension by mechanoreceptors are thought to control gastric diameters in response to the viscosity of luminal contents (24, 28). We did not specifically study to what extent neuronal reflexes controlled the mechanical activity of our preparations, but previous work leaves little doubt that many if not all gastrogastric reflexes for which a vagovagal pathway has been demonstrated are also mediated by intramural pathways. Similar to the stomach in situ, the isolated stomach accommodates. In response to filling, muscle tension in the proximal stomach is inhibited, the stomach accommodates. In response to distension of the corpus, the corporoantral reflex (1, 12, 30). Adaptations in antral wall tension by mechanoreceptors are thought to control gastric diameters in response to the viscosity of luminal contents (24, 28). We did not specifically study to what extent neuronal reflexes controlled the mechanical activity of our preparations, but previous work leaves little doubt that many if not all gastrogastric reflexes for which a vagovagal pathway has been demonstrated are also mediated by intramural pathways. Similar to the stomach in situ, the isolated stomach accommodates. In response to filling, muscle tension in the proximal stomach is inhibited, the stomach accommodates. In response to distension of the corpus, the corporoantral reflex (1, 12, 30). Adaptations in antral wall tension by mechanoreceptors are thought to control gastric diameters in response to the viscosity of luminal contents (24, 28). We did not specifically study to what extent neuronal reflexes controlled the mechanical activity of our preparations, but previous work leaves little doubt that many if not all gastrogastric reflexes for which a vagovagal pathway has been demonstrated are also mediated by intramural pathways. Similar to the stomach in situ, the isolated stomach accommodates. In response to filling, muscle tension in the proximal stomach is inhibited, the stomach accommodates.

Table 3. Gastric diameters, length of greater curvature, and wall thickness corresponding to pressure phases

<table>
<thead>
<tr>
<th>Pressure Phase</th>
<th>Greater Curvature, cm</th>
<th>Thickness of Fundus, mm</th>
<th>Thickness of Antrum, mm</th>
<th>Diameter Changes of Sequential Gastric Segments, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Fundus</td>
</tr>
<tr>
<td>P_0</td>
<td>19.2 ± 0.3*</td>
<td>2.6 ± 0.2*</td>
<td>4.3 ± 0.3</td>
<td>-1.6 ± 1.3*</td>
</tr>
<tr>
<td>P’</td>
<td>20.0 ± 0.2*</td>
<td>3.1 ± 0.2*</td>
<td>4.0 ± 0.3</td>
<td>-0.4 ± 1.1*</td>
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<tr>
<td>Nadir</td>
<td>19.3 ± 0.2*</td>
<td>2.6 ± 0.1</td>
<td>4.0 ± 0.2*</td>
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<tr>
<td>P”</td>
<td>18.5 ± 0.1*</td>
<td>2.3 ± 0.2</td>
<td>5.4 ± 0.3</td>
<td>0.5 ± 0.9</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td>Body</td>
</tr>
<tr>
<td>P_0</td>
<td>20.0 ± 0.2*</td>
<td>3.1 ± 0.2*</td>
<td>4.0 ± 0.3</td>
<td>0.4 ± 1.1*</td>
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<td>Sinus</td>
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<tr>
<td></td>
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<td>Antrum</td>
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<td>P_0</td>
<td>20.0 ± 0.2*</td>
<td>3.1 ± 0.2*</td>
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</tbody>
</table>

Data are means ± SE; n = 6 closed preparations. Wall thickness of antrum is significantly greater than fundus at all pressure phases. All changes in diameter are significantly different between sinus and antrum. P < 0.05 compared with next pressure phase (*), when P’ compared with P” (†), and compared with preceding site (‡).
ach enlarges, and its luminal pressure rises little (13, 31, 33, 34). The corporeoantral reflex is mediated at least in part by intramural pathways, and it is likely that intramural pathways mediate adaptive relaxation as well. However, little is known about the role of these reflexes during the dynamics of individual gastric contractions or over the duration of gastric emptying (20). Adaptations are not necessarily all mediated by nervous reflexes; the adaptations of fiber length of the proximal gastric musculature are largely mediated by myogenic mechanisms (33).

Inhibition of tension of the proximal gastric musculature during accommodation leads to characteristic changes in both the size and the configuration of the stomach (11, 31–33). In particular, as the greater curvature lengthens, gravity makes it sag below and distal to the lesser curvature. Thus the gastric sinus opposite to the gastric incisura is formed. Despite its location aborad from the gastric corpus/fundus segment proper, the sinus appears to function as a reservoir; in our ultrasonographic studies on seated men, particulate beans seemed to settle in the sinus. The opening or even bulging of the sinus changes the shape of the antrum from resembling a tube to resembling a funnel that points toward the pylorus (5). Similarly, in dynamic scintigraphic studies on seated humans, large boluses of the nuclide meal accumulated in this distal reservoir (37). These findings might be taken as visual evidence for the priming of the antral pump postulated by Ehrlein and Akkermans (10).

As seen here, gastric contractions effectively reversed the elongation of the greater gastric curvature that occurs during volume accommodation (11, 30, 31, 33). Emptying of liquids occurred while stomachs shrank in size and the greater curvature shortened. We propose therefore that contractions empty volume from the proximal into the distal stomach and hence into the duodenum by reducing the size of the stomach. Volume shifts occur under largely isotonic conditions and peak when the contraction reduces first the size of the fundus (thereby further “priming the antral pump”) and again when the contraction reduces the size of the sinus, virtually lifting and inverting it. Our current interpretation is consistent with the importance many investigators attach to tonic contractions of the proximal stomach to gastric emptying (3, 7, 17, 20, 23, 26). However, tonic contractions might not have to generate a “back pressure” or positive pressure differential for flow to occur. We favor the view that much flow occurs as the gastric musculature shortens its fiber length (33); consequently, the size and the configuration of the stomach change, and the borders between various segments are redrawn. Large volume shifts occur without generating high pressures. Whenever high pressures occur, they presumably trigger renewed accommodation and hence delay gastric emptying. Such a mechanism was explicitly considered by Miller et al. (26) to explain why increases of gastric pressures as set by barostat do not result in quite the expected increase in gastric cavity pressures or gastric emptying. The same mechanism might explain why we observed cessation of gastric outflow at times when cavity pressure in the proximal stomach rose. A problem with the current interpretation is that our methodology makes it impossible to determine to what extent decreases in gastric size are a cause or a consequence of gastric emptying.

This might be taken to imply that high luminal pressures are more likely to compact, break down, and disperse particulate gastric contents (17, 22, 23) rather than to empty gastric contents. [Our observation does not exclude that pressures generated by the distal stomach are important to gastric emptying. Considerable evidence suggests this to be so (9, 14–16, 25, 27, 28). However, most findings pertain to the net result of pressure activity over the course of digesting and emptying a meal.] Investigations of duodenal outflow produced by individual contractions appear to agree that this peaks when the contraction is at a site fairly orad to the pylorus (10, 28), with the exception that we have called the sinus what Ehrlein and Akkermans (10) termed the proximal antrum.

Along the greater curvature, the contraction produces sequential shortening and an indentation that increases its depth the more it moves distally. This is consistent with the results of previous investigators (7, 8, 10, 11, 28). Indeed, our observations on the interactions between movements of the gastric walls and contents resemble those made by Urbain et al. (10) that contractions along the lesser curvature manifest primarily as changes in the angle and the position of the gastric incisura. The mechanisms by which the stomach retains and breaks up particles are poorly understood (4, 5, 10, 23). As summarized by Ehrlein and Akkermans (10), contractions of the terminal antrum and pylorus enhance retropulsion and grinding, particles are held back by the narrow pylorus while liquids are squirted forcefully through it, and particles are crushed through compression of the thick walls of the distal antrum (5, 8, 9, 15, 17, 22, 23, 25). In previous ultrasonographic studies on seated human subjects, we suggested that retention and grinding are likely to occur also in the gastric sinus; while liquids emptied freely through the pylorus, particulate beans rarely advanced to the pylorus. Only once beans were reduced to paste did they move into the terminal antrum, where bits of paste were carried off with the liquid (5).

Our current observations indicate a role for the incisura in conjunction with the sinus in retaining particulate contents. Furthermore, we suggest that the incisura exerts forces that pound and shear the solid contents of the sinus. Fluid currents at the solid-liquid boundary, countercurrents, and jet effects appeared to be intimately linked to movements of the incisura and are likely to further contribute to particle dispersion.
Fig. 5. Movements of solid luminal contents (garbanzo beans) during gastric contraction and emptying. A–G, left, are ultrasonographic scans of the sinus and its contents with hand-drawn renderings of the scan at bottom; A–G, right, show video images of the isolated stomach with pressure and output profiles at bottom. Arrows in the profiles show points in time at which the videos and scans were captured. A: contraction of the proximal stomach pushes the beans into the bulging sinus of the greater curvature opposite the incisura. B: beans are heaped up as the contraction lifts the sinus toward the incisura. C: fluid ahead of the contraction fills the bulging antrum, and duodenal outflow resumes. Beans are trapped upstream from the liquid. D: beans are compressed between the incisura and the greater curvature. At the surface of the beans, fluid generates crosscurrents and retrograde jets. Incisura cuts through the beans and pushes their largest fraction along the lesser curvature back into the gastric body. E: as the contraction accelerates toward the pylorus, it imparts a tumbling motion on the beans and leaves them behind. Outflow stops. F: as the contraction reaches the distal antrum, all beans are still far from the pylorus. G: as the stomach relaxes, the beans settle again along the greater curvature of the sinus. (The sequence recorded here is the 1st during which gastric effluent turned cloudy; the previous 2 contractions had emptied >50 ml of the 150-ml original volume, but the stomach remained tonically contracted with an elevated baseline pressure.)
Particle movement and dispersion in our observations is not limited to the period of the terminal antral contraction and retropulsion, as implied by Ehrlein and Akkermans (10). Also, according to Ehrlein and Akkermans, the balance between propulsion and retropulsion of antral contents was determined by the respective luminal diameters of the antral and pyloric contraction (10, 28), with the indentations produced by contractions in the antrum growing deeper the more liquid the gastric contents. Contrary to this observation, we previously found that the amplitude by which contractions indented the human antrum changed little over the course of a meal but that the baseline diameter of the antrum decreased over the same time, bringing about more intimate contact between pasty contents and antral walls (5). Also somewhat differing from Ehrlein and Akkermans (10), we observed that backflow of luminal contents began while the contraction was passing into the sinus and was not necessarily produced by the terminal antral contraction. Rather sudden and massive retrograde fluid movements appeared to be mediated by widening and shortening of the antrum as the incisura moved out of the sinus.

The present study was limited by our difficulty in quantifying intragastric volume shifts. We inferred volume shifts from changes of diameters and length. Methodological improvements are required to truly quantify these changes. One solution would be three-dimensional reconstruction. As reviewed by Malagelada and Azpiroz (20), this would require at least two planes of imaging. Another way might be volumetric assessment with the barostat (1, 30). A somewhat related problem is that our methodology did not allow us to determine whether a segment that enlarged did so because it relaxed because of neurogenic inhibition or because it was passively distended. We have reviewed above gastogastric reflexes through which distension of one segment of the stomach affects the mechanical activity of another segment.

Our observations were made on preparations that differed in many aspects from the intact stomach. Their extrinsic nervous controls were severed, they were not in continuity with the small bowel, they did not secrete acid in sufficient amounts to lower the luminal pH, and they did not contain a gastric air bubble. The contractions and flow described by us are most likely to resemble those occurring during the initial phases of emptying of the in situ stomach when control is exerted by gastric mechanoreceptors (10, 26). Our preparation would not do justice to the linear, steady-state phase of gastric emptying occurring after enterogastric feedback mechanisms become operative (19, 23, 24, 27, 29).

Vagotomy has many ill effects on the motility and emptying of the stomach in situ (1, 2, 12, 35). Yet isolated preparations display contractions and outflow similar to that of the innervated stomach. Indeed, most investigators have found no apparent difference in the motility patterns or emptying rates of stomachs in vitro compared with in situ (7, 13, 32, 34). One reason for this apparent paradox is that acute vagotomy reduced cholinergic tone (2, 12, 18). Chronic vagotomy is followed by chronic changes in the gastric musculature and enteric neuronal networks (2). Isolated preparations taken from chronically vagotomized animals show motor abnormalities similar to those of the vagotomized stomach in situ (18). The vagus nerves also process sensory input from various parts of the stomach and the intestine, which alters the activity of the stomach in situ (3, 12, 20, 38). Of course, no such influences would be operative in our preparation.

In summary, we studied the effects that contractions have on gastric pressures, flow, and the dimensions of gastric segments. Contractions that empty the stomach shorten the greater curvature and reverse changes in gastric configuration from gastric filling. When contractions involve a certain gastric segment, they reduce its diameter and increase the thickness of its wall. Thus contractions move gastric contents by their local impact and by changing the capacity of various gastric segments. The progression of contractions from gastric fundus to antrum is reflected in characteristic phases of pressures in the proximal gastric cavity; contractions increase luminal pressure most while involving the gastric body and least while passing the gastric transition zone around the gastric incisura. Contractions impact complex movements on particulate beans in the gastric sinus. Movements of the gastric incisura appear to contribute to processes that lead to the retention, compression, and dispersal of particulate gastric contents.

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