Spatial and temporal coupling between slow waves and pendular contractions

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Lammers, Wim J. E. P. Spatial and temporal coupling between slow waves and pendular contractions. Am J Physiol Gastrointest Liver Physiol 289: G898–G903, 2005. First published July 14, 2005; doi:10.1152/ajpgi.00070.2005.—In contrast to the mechanisms of segmental and peristaltic contractions in the small intestine, not much is known about the mechanism of pendular contractions. High-resolution electrical and mechanical recordings were performed from isolated segments of the rabbit ileum during pendular contractions. The electrical activities were recorded with 32 extracellular electrodes while motility was assessed simultaneously by video tracking the displacements of 20–40 serosal markers. The electrical activities consisted of slow waves, followed by spikes, that propagated in either the aboral or oral direction. The mechanical activity always followed the initial electrical activity, describing a contraction phase in one direction followed by a relaxation phase in the opposite direction. Pendular displacements were always in rhythm with the slow wave, whereas the direction of the displacements was dictated by the origin of the slow wave. If the slow wave propagated aborally, then the pendular displacement occurred in the oral direction, whereas if the slow wave propagated in the oral direction, then the displacement occurred in the aboral direction. In the case of more complex propagation patterns, such as in the area of pacemaking or collision, direction of displacements remained always opposite to the direction of the slow wave. In summary, the direction and pattern of propagation of the slow wave determine the rhythm and the direction of the pendular motility. The well-known variability in pendular movements is caused by the variability in the propagation of the underlying slow wave.

gastrointestinal motility; direction of propagation; electromechanical coupling; spikes

SEVERAL TYPES OF MOTOR PATTERNS have been investigated in the small intestine. Some of these, such as the peristaltic reflex, have been extensively studied, whereas others have not received much attention. One type of behavior, referred to as “pendular contraction,” “to-and-fro movements,” or “sleeve contraction,” (6, 20) has not been well described, although it has often been observed (1–4, 7, 11). Christensen (5), in an early review, sighed that “pendular movements are so poorly comprehensible.”

There have been attempts to record pendular movements (3, 8, 10). Bayliss and Starling described the first tracings of the “pendulum” movements in dogs (1) and rabbits (2). Melville et al. (16) traced the longitudinal displacement of spots of India ink on the opposum duodenum. More recently, Hennig et al. (9) placed sutures onto the longitudinal coat of the guinea pig small intestine, video recorded their rhythmic contractions, and plotted them in spatial-temporal maps. Pendular contractions have even been modeled to show that they would mix luminal contents (15, 16). The major conclusion from these studies was that pendular movements were caused by contractions of the longitudinal muscle layer.

In the present study, we simultaneously recorded the electrical and mechanical activities of an isolated intestinal segment during pendular contractions and described in detail their spatial and temporal relationships. With this analysis, we show that the slow wave drives the pendular contraction and that the direction of the slow wave determines the direction of the ensuing pendular movements.

METHODS

Mongrel rabbits (n = 14, 7 males and 7 females, average weight 1.2 ± 0.4 kg, mean ± SD) were used. The experimental procedure was approved by the Animal Research Ethical Committee, Faculty of Medicine and Health Sciences, of the United Arab Emirates University. After cervical dislocation, the abdomen was opened, and the small intestine was rapidly removed and placed in a dissecting dish containing cold Tyrode solution. A 10-cm-long segment of the ileum was dissected, gently flushed from the oral end, and transferred to a 250-ml organ bath. This custom-made tissue bath was made of Perspex sidewalls to allow a clear view for video recording. The preparations were superfused at a rate of 100 ml/min with a modified Tyrode solution [composed of (in mM) 130 NaCl, 4.5 KCl, 2.2 CaCl2, 0.6 MgCl2, 24.2 NaHCO3, 1.2 NaH2PO4, and 11 glucose] saturated with carbogen (95% O2-5% CO2) and kept at a constant pH (7.35 ± 0.05) and temperature (37 ± 0.5°C). The oral end of the tubular segment was connected to an infusion pump (Harvard Apparatus; 1 ml/min, infusion of Tyrode solution), whereas the distal end was attached to a short silicone tubing. The level of the outflow in the experiments was kept at the same level as the preparation to avoid distension of the preparation and initiate related contractions.

Electrical activities were recorded using a row of 32 extracellular electrodes (Teflon-coated silver wires, 0.3 mm diameter, 1 mm inter-electrode distance). The tips of the electrodes were connected to 32 alternating current preamplifiers (gain 4,000), and the recorded signals were subsequently filtered (2–400 Hz), digitized (8 bits, 1 kHz sampling rate/channel), multiplexed, and stored.

Soot markers (~20–40) were placed on the serosal surface of the segment facing the video camera (13). A digital video camera (SONY DCR-TRV10E) was positioned against one of the Perspex sidewalls for a clear view of the tubular segment and its markers (Fig. 1A). Video recordings (25 frames/s, 720 × 480 pixels) were performed simultaneously with the electrical recordings for periods of 1–5 min. To synchronize the electromyogram of the video signals, a digital stimulator (Neuro Data PG 4000) produced rhythmic pulses every 1 and 10 s, which were fed into one of the amplifiers and, converted in an auditory signal, recorded by the video camera. The resolution of the signals recorded in these experiments differ from each other; the electrical signals were sampled at 1 kHz (resolution of 1 ms), whereas...
the resolution of the motility signals was determined by the video frame rate (25 frames/s), resulting in a resolution of 40 ms.

After the experiment, the electrical signals were analyzed using custom-made software (SmoothMap, written in Delphi) (14). For every slow wave cycle, the direction and pattern of slow wave propagation and, in the case of uniform propagation, the time difference between the first and the last slow wave recorded at opposite ends of the electrode array were measured. The displacement of the markers was analyzed using custom-developed software (MotilityMap, written in RealBasic 5.0; Fig. 1B) (13).

RESULTS

The spontaneous displacement of a single marker during pendular contraction is presented in Fig. 2. As shown in Fig. 2A, the majority of the displacements occurred in the longitudinal direction with very little movement in the circular direction. In B, this displacement was plotted against time in the longitudinal (top trace) and circular direction (bottom trace). Three phases are recognizable in the longitudinal displacement: a contraction phase and a relaxation phase followed by a period of rest.

Fig. 2. Tracking and analyzing the displacements of the local markers. A: actual displacement of one marker during three successive cycles. The displacement occurred in a narrow loop with its major axis in the longitudinal direction. In B, this displacement was plotted against time in the longitudinal (top trace) and circular direction (bottom trace). Three phases are recognizable in the longitudinal displacement: a contraction phase and a relaxation phase followed by a period of rest.

Fig. 3. Pendular displacements during aboral slow wave propagations. Top: 32 electrogams recorded along the length of an intestinal segment showing three successive slow waves (SW1–SW3), propagating uniformly from oral to aboral followed, in many tracings, by numerous spikes. The slow wave propagation time from oral to aboral ranged from 1.10 to 1.21 s. Bottom: displacements of 16 markers that had occurred in rhythm with the slow waves. The locations of the original markers are depicted in the diagram to the left. Three vertical lines, drawn from the moment of the appearance of the first slow wave in lead 1 show that the displacements occurred after the initiation of the slow wave. The dashed arrows in the motility tracings represent the timing and direction of the slow waves superimposed on the motility tracings. The timing of the displacements in the first and last marker is indicated by the solid circles positioned halfway on the contractions. The displacements of the last marker occurred later than that of the first marker, although the time differences were less than those of the corresponding slow waves. In addition, the distal markers started to displace before the slow wave had actually reached that area (•).
tion. This is also evident when the displacements were plotted in time in the longitudinal direction, showing large excursions, and in the circular direction, demonstrating little change (Fig. 2B). In the longitudinal traces, the rhythmic displacements can be separated into three phases: 1) a resting phase, in which the tissue, after the previous contraction, moved back to its resting state; 2) a contraction phase, in which the markers displaced predominantly in the longitudinal direction; and 3) a relaxation phase, wherein the markers moved back.

Pendular displacements occur in synchrony with the rhythm of the slow wave. This is shown in Fig. 3, where the slow wave propagated uniformly in the aboral direction. Figure 3, top, displays the 32 electrograms recorded during 3 successive slow wave cycles. The conduction time between the first and last recorded slow wave was 1.1–1.2 s (~2.7 cm/s). Figure 3, bottom, presents the displacements of 16 markers during this period. The markers all moved in the oral direction, in rhythm with the slow wave. The onset of the displacement was somewhat later than that of the slow wave, as evidenced by the three vertical lines. In addition, pendular motility also showed some phase differences because oral marker 1 started earlier than distal marker 16. The difference in time between these two markers ranged from 0.64 to 0.52 s.

In the isolated intestine, spontaneous changes in pacemaker location and resulting direction of slow wave propagation often occur (14). Such events allowed us to analyze the ensuing patterns of pendular contractions. Figure 4 shows the situation in which the slow wave propagated in the oral direction. Three successive cycles are shown, with the electrical slow waves in Fig. 4, top, and the motility traces in Fig. 4, bottom. Again, there was synchrony between electrical activity and motility with the slow waves preceding the local displacements. The electrical slow wave propagated in the oral direction, and the local displacements occurred somewhat earlier at the distal than proximal end, while the differences in time are again smaller than that of the slow waves. The major difference between the motility traces during oral propagation compared with aboral propagation (Fig. 3) is that the markers displaced toward the distal part of the segment.

This leads to a fundamental finding in this study. With pendular contractions, the tissue contracts first at the location from where the slow wave came from. This is due to the fact that the spikes, visible in the slow wave tracings in Figs. 3 and
Pendular contractions can become more complicated when other patterns of slow wave propagations occurred but are consistent with what was described with the previous uniform propagations. Figure 6 shows the situation in which a slow wave pacemaker was located in the middle of the segment, as shown during the first two slow wave cycles. The motility traces showed little displacements at the site of the pacemaker but increasingly larger displacements away from this site. Furthermore, the displacements occurred toward the area where the slow wave had originated. Therefore, both the oral markers and distal markers moved toward the center, in accordance with the rule presented earlier. The third cycle in this analysis happened to be an oral propagating slow wave with resulting displacements toward the distal end, similar to what was demonstrated before.

The opposite pattern occurred when two slow waves propagated toward each other, colliding in the middle of the segment (Fig. 7). The motility traces shown in Fig. 7, bottom, now show displacements toward the oral end for the oral part and toward the distal end for the distal part of the preparation, again in accordance with the fact that pendular displacements occur toward the direction from where the slow wave came from. The middle part of the segment hardly displaced at all, as it was more or less simultaneously pulled from both ends.
Pendular displacements are immediately affected by a change in direction of the slow wave. An example of this is shown in Fig. 8, in which a longer sequence of 12 slow waves and the resulting motility was analyzed. The dashed arrows, as before, were superimposed on the motility tracings, indicating timing and direction of the slow waves. Pendular displacements occurred toward the oral end with aboral slow wave propagation (Fig. 8, SW1 and SW12), whereas movements in the opposite direction occurred when the slow waves originated from the distal end (Fig. 8, SW7–SW10). More subdued and complex motility patterns occurred in the case of pacemaking (Fig. 8, SW2–SW6) and collision (Fig. 8, SW11). Changes in slow wave propagation are immediately reflected in changes in pendular displacements.

The experimental situation is artificial in the sense that the segments could have been stretched by fixation to the in- and outlets. To determine whether this had any effect on the occurrence of pendular displacements, an additional five experiments were performed in which the suspended segments were stretched or compressed to various degrees. As shown in Fig. 9, pendular displacements during various degrees of stretch. Pendular displacements were recorded when the segment was kept at its initial length (C), stretched by 8% and 28% (D and E), or when the segment was compressed by moving the in- and outlets toward each other (A and B), thereby somewhat buckling the tissue. In all situations, pendular displacements and phase differences between various sites occurred, although the amplitude was higher and the displacements were slightly more regular when the preparation was stretched.
Fig. 9, pendular rhythm was present at the resting length of the segment (C), when it was stretched (D and E), and even when the tissue was compressed (A and B).

DISCUSSION

There is a close and causal relationship between the slow wave and the ensuing pendular displacements. Pendular motility is determined by the initial site of contraction, which in turn is determined by the origin of the slow wave. The coupling between slow waves and pendular displacements is performed by the action potentials (=spikes) that are initiated by the slow wave and that induced local contraction. Because the slow wave takes time to propagate and because spikes occur fairly quickly after the slow wave depolarization (17, 19), contraction in the segment will occur earlier at one end than at the other end. This asynchrony in contraction initiates displacement of the segment toward the area where the slow waves originated from and where the first spikes had occurred.

This relation between slow waves, spikes, contraction, and displacements is stable, as it holds under a variety of conditions as evidenced by spontaneous changes in the direction of propagation of the slow waves (Figs. 3, 4, and 6–8). Furthermore, the system does not seem to have a long memory as spontaneous and sudden changes in slow wave propagation were immediately reflected in changes in the direction of displacements of the markers. This was shown, for example, in the third cycles in Figs. 6 and 7 and more extensively in Fig. 8. Because pendular swings reflect the direction of the propagating slow wave, recording the direction of pendular swings could be useful in determining the direction of the slow waves.

The limitations of this study must be clear. This is not a detailed mapping study of the electrical propagation of the slow wave as presented earlier (14). This was not possible, as the electrodes would then have to be in contact with the preparation and thereby impede their movements. However, as shown in this study and in a previous one (12), it is possible to record local electrical activities with the electrode tips located at a short distance from the surface of the preparation, albeit at reduced amplitudes as is evidenced in the signals in the electrical records. Furthermore, the preparation is moving during the recording with respect to the position of the electrodes, making an accurate spatial determination of the slow wave propagation not possible. This was, therefore, not attempted. However, from the electrical signals, it is possible and permissible to determine the direction of propagation of the slow wave and to correlate that with the movement of each pendular contraction.

Other limitations relate to the in vitro nature of the study, the use of a single species, and, indeed, of one part of the small intestine.

Within these limitations, the conclusions are clear in that it is the direction of slow wave propagation that determines the direction of the pendular movements. It is therefore, in retrospect, no surprise that pendular contractions, in contrast to other types of contraction, were deemed to be “incomprehensible” (5). They do not show a stereotypical pattern such as the peristaltic reflex (18). Instead, pendular contractions and pendular movements are determined and controlled by the slow waves. Because slow wave origins and propagations are not fixed but show continuous and spontaneous changes (14), the ensuing pendular motility reflects this inherent variability.

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GRANTS

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REFERENCES