A migrating electric complex of the canine small intestine

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The electric activity of the small bowel was studied in conscious, healthy dogs by the use of chronically implanted platinum electrodes. A caudad-moving band of large-amplitude action potentials (electric complex) starting in the duodenum and traversing the small bowel was identified. When one such complex reached the ileum, another was developing in the duodenum and proximal jejunum. Complexes were found only in fasting dogs. In six, the estimated mean velocity of caudad migration of the complex ranged from 6.2 to 3.5 cm/min in the proximal bowel and 1.9 to 1.2 cm/min in the distal bowel. The duration of the complex at all levels of the bowel ranged from 7.0 to 4.8 min, and its calculated length from 36.5 to 25.0 cm in the proximal bowel to 12.0 to 6.0 cm in the distal bowel. It appears that the function of the electric complex is to produce a caudad migrating band of rhythmic segmentation which moves the interdigestive contents down the small bowel and into the large bowel in preparation for the next meal. It is concluded that the motor complex it induces is the interdigestive "housekeeper" of the small bowel.

PREVIOUS STUDIES on the motor activity of the human (6) and canine (4, 5, 7, 8, 10) small intestine have demonstrated the occurrence of migrating motor complexes. The observations, however, were confined to short segments of the bowel, and the electric events responsible for the motor complex were not studied. The purpose of this report is to describe a migrating electric complex that occurs in fasting dogs. The complex is composed of a consecutive series of slow waves, on each of which is superimposed a burst of large-amplitude action potentials that distinguish it from other electric activity in the small bowel of fasting dogs. The complex develops in the upper small bowel and then migrates caudad to the ileum; as it terminates there, another starts in the duodenum or upper jejunum, and the recycling continues. A correlation is made between these findings and those relating to migrating motor complexes observed by others.

The term electric complex will be used when referring to the migrating bursts of action potentials. It is not meant to signify an electric event that is different from the action potential and slow wave. Rather, it is used to indicate a pattern of electric activity in which action potentials occur in rhythmic sequence with every slow wave of a series and the caudad migration of this pattern along the small bowel.

MATERIALS AND METHODS

Seven healthy, female, mongrel dogs (10-12 kg) were used. In three dogs, the electric potentials were detected by 15 unipolar and 5 bipolar platinum electrodes, and in four dogs, they were detected by 11 unipolar electrodes.

The construction of the electrodes and the connector used to unite them to a recorder was patterned after those described by Allen, Poole, and Code (1). The unipolar electrodes consisted of one platinum wire which protruded 0.5 mm from the Teflon disk. The bipolar electrodes consisted of two platinum wires separated by 5 mm, the tip of each protruding 0.5 mm from the disk. With the use of surgical aseptic technique (no premedications were used) while the dog was under pentobarbital anesthesia (30 mg/kg, intravenously), the electrodes were implanted at equal or very nearly equal distances, the first being placed on the duodenum and the last on the terminal ileum. The five bipolar electrodes, used in three dogs, were always the most distal and were oriented so that their detecting tips were at right angles to the long axis of the bowel.

Ten days after the operation, recording sessions were begun, and these were continued periodically for 3-6 months. The dogs were conscious and healthy and were trained to lie quietly in a sling during periods of recording. The observation sessions lasted for a minimum of 3.5 hr, during which the electric potentials were registered on an 8-channel recorder (Brush Mark 200) with a rectilinear inkwriting system using a time constant of 1 sec. Unipolar potentials were obtained between the electrodes on the bowel and a platinum needle electrode placed subcutaneously in the right thigh. Bipolar potentials were obtained between the electrodes on the bowel separated by 5 mm. If the slow wave in the ileum originated in the transverse plane as in the duodenum (2) then, theoretically, bipolar recording should cancel the slow-wave signal. In practice, however, slow waves were obtained, and the recordings were more stable and contained fewer movement artifacts than the unipolar recordings from the same region. An explanation might be that the recording tips of the bipolar electrodes were not perpendicular to the longitudinal muscle fibers, for when the electrodes were implanted, no particular precautions were taken to ensure that they were exactly perpendicular. Most experiments were done
when the dogs had fasted for 21 hr. A few observations were made 1–4 hr after the dogs had eaten the regular kennel meal.

In each of six dogs, recordings of five migrating electric complexes were analyzed. For comparing results between dogs, the total length of small bowel of each dog was set as equal to 100 and electrode positions calculated as parts of 100; the gastroduodenal junction was considered as 0. Measurements of the velocity, duration, and length of the electric complexes and its effects on the frequency of the slow wave before, during, and after its passage were made at all electrode sites in each dog. However, to simplify the presentation of the results, only data are presented from those electrode sites spaced by distances representing approximately 10% of the length of the small bowel. The omitted data alter neither the description nor the conclusions. The velocity of propagation of the complex was calculated by determining the elapsed time between its termination under consecutive electrodes. This value was divided into the distance between the electrodes, yielding the velocity of propagation in centimeters per minute. The value for the velocity was always assigned to the orad electrode of the pair. The terminal or orad end of the complex was selected for this definition because it was sharper than the caudal or advancing face of the complex. The duration of the complex at each electrode site was determined by direct inspection of the record. The length of the electric complex (LEC) was estimated by multiplying the velocity \( v \) by the duration \( d \) of the complex:

\[
LEC = v \times d,
\]

Although the electrode distances of autopsy verified the electrode distances measured at the time of the operation, the values for velocity and calculated length are estimates since the exact distances between electrodes during the recording sessions were not known.

For determining whether the electric complex affects the slow wave, the frequency of the slow wave was determined at each electrode site 3 min before, 3 min during, and 3 min after passage of the complex.

RESULTS

General description of complex. The precomplex electric activity of the duodenum and jejunum was characterized, first, by slow waves without action potentials, then by a period of randomly occurring bursts of action potentials superimposed on slow waves, with the burst becoming more frequent and the action potentials larger in amplitude (Figs. 1 and 2). The duration of the period of random and diffuse action potential activity varied from 15 to 40 min. The period terminated when, as every slow wave displayed action potentials of large amplitude, a group of them amalgamated into a recognizable complex extending over the duodenum and proximal jejunum, which then migrated in an orderly fashion caudad (Figs. 2 and 3). The complex occurred as it migrated. The time required for the complex to pass a point in the bowel was the same in the proximal and distal portions, ranging from 4.8–7.0 min (Table 1).

No consistent changes in the duration of the electric complex occurred as it migrated. The time required for the complex to pass a point in the bowel was the same in the proximal and distal portions, ranging from 4.8–7.0 min (Table 2).

In all dogs, the calculated length of the electric complex (LEC) shortened as the distance from the gastroduodenal junction increased (Fig. 10). In the orad 10% of the small bowel, the mean calculated length ranged from 6.2 to 3.5 cm/min, whereas in the caudal 10% the range was 1.9–1.2 cm/min. In all dogs, the caudal migration of the complex slowed more markedly within the first half of the small bowel than in the last half.

The mean total time (+sn) necessary for the electric complex to traverse the entire small bowel of each of the dogs varied between 115 (+12.9) and 183 (+9.3) min (Table 1).

Such a migrating electric complex was regularly seen during fasting in six of the seven dogs. In the exception, they occurred only occasionally. During a period of 3 weeks, this dog lost weight, became debilitated, and died from peritonitis. The data derived from it were therefore not included in any of the calculations.

During this study, 37 electric complexes were recorded in the six dogs. All complexes originated in the duodenum and proximal jejunum and were propagated caudad. Thirty complexes reached the terminal ileum. The remaining complexes expired after traversing 75% of the small bowel. In these instances, the amplitude of the action potentials became smaller and the complex was less well defined as the distance from the gastroduodenal junction increased.

The period of recording over the entire small bowel was continued in 12 tests after termination of one complex to determine when another started. In each instance, when one complex reached the ileum, another was developing in the proximal small bowel (Fig. 8).

These electric complexes were seen only in fasting dogs. For example, no complexes originated in 4 hr of recordings obtained in each of six dogs, starting 1 hr after a meal.

Details of electric complex. In all dogs, the velocity of the electric complex slowed as the distance from the gastroduodenal junction increased (Fig. 9). In the orad 10% of the bowel, the mean velocity ranged from 6.2 to 3.5 cm/min, whereas in the caudal 10% the range was 1.9–1.2 cm/min. In all dogs, the caudal migration of the complex slowed more markedly within the first half of the small bowel than in the last half.

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The validity of the formulation LEC (cm) = \( v \times d \) was checked by comparing the calculated LEC to the LEC obtained by visual inspection of the tracings. For example, in Fig. 2, the electric complex is terminating under electrode 3 just as it is appearing under electrode 5, 42 cm away. The velocity of the complex between electrodes 3 and 5 was 7 cm/min and its duration...
ELECTRIC COMPLEX OF SMALL BOWEL

FIG. 1. Precomplex electric activity of duodenum and jejunum 15 min and 5 min before initiation of complex. Fifteen minutes before the complex, there were no action potentials. Five minutes before its initiation, random and diffuse action potential activity occurred irregularly under each electrode. In this and subsequent tracings, distance of each electrode from the gastroduodenal junction is indicated on left.

FIG. 2. Initiation of complex activity under electrodes 1 and 2 and its caudal progression past electrodes 3 through 5, 5 min after precomplex activity present in Fig. 1.

FIG. 3. Caudal progression of complex past electrodes 5 through 8. Tracing is continuous with that in Fig. 2. At electrode sites caudal to complex in both figures, precomplex activity occurred. Once complex passed an electrode site, only slow waves were present.

was 5.5 min. Thus, the calculated LEC was 38.5 cm. In most instances, there was good agreement between the calculated LEC and the actual LEC.

In Table 3, the grand means (+SEM) for velocity, duration, and length of 30 electric complexes (5 in each of six dogs) are listed.

The passage of the electric complex past an electrode site caused measurable changes in frequency of the slow wave. In general, the frequency of the slow wave was faster after passage of the complex than before its arrival, and these changes occurred uniformly over the entire small bowel. Because the observed changes were not related to the level of the bowel from which they were made, the \( \Delta_{EA} \) change \( \Delta_{EA} = (\text{frequency of slow wave after passage of electric complex}) - (\text{frequency before its arrival}) \) was determined at each electrode site for three different electric complexes in each of six dogs, and the results were pooled. In 127 of a total of 144 observations, the \( \Delta_{EA} \) change was positive, in 6 it was negative, and in the remaining 11 it was zero. In the cumulative frequency distribution for positive \( \Delta_{EA} \) (Fig. 11), the median increase in the slow-wave frequency after passage of the electric complex was 0.8
slow wave/min. Since the smallest increase in $\Delta_{A-B}$ was 0.1 slow wave/min and the largest was 3.4, then in one-half of the observations, $\Delta_{A-B}$ was between 0.1 and 0.8 slow wave/min and in the other half between 0.9 and 3.4 slow waves/min.

No consistent changes were observed when the frequency of the slow wave during the electric complex was compared to that before passage of the complex. The $\Delta_{n-B}$ change [$\Delta_{n-B} = (\text{frequency of slow wave during motor complex}) - (\text{frequency of slow wave before complex})$] was positive in 66 observations and negative in 49. No change in $\Delta_{n-B}$ was noted in 25 other observations.

DISCUSSION

All complexes were propagated caudad. As the distance from the gastroduodenal junction increased, the velocity became slower and the length of the complex shorten. The reduction of the calculated length of the electric complex (LEC) as it moved caudad was dependent on velocity.
ELECTRIC COMPLEX OF SMALL BOWEL

FIG. 7. Caudad sequence of complex in distal small bowel. Progression of complex past electrodes 16 through 19.

FIG. 8. Simultaneous termination of one complex in ileum and initiation of next in duodenum and proximal jejunum.

FIG. 9. Relation of estimated mean velocity of propagation of complex to percentage distance from gastroduodenal junction in six dogs. Each point is mean velocity of five complexes.

TABLE 2. Relation of duration of electric complex to distance from gastroduodenal junction

<table>
<thead>
<tr>
<th>Dog</th>
<th>Mean Duration of Complex, min*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10</td>
</tr>
<tr>
<td>1</td>
<td>6.1</td>
</tr>
<tr>
<td>2</td>
<td>5.2</td>
</tr>
<tr>
<td>3</td>
<td>3.3</td>
</tr>
<tr>
<td>4</td>
<td>5.8</td>
</tr>
<tr>
<td>5</td>
<td>6.9</td>
</tr>
<tr>
<td>6</td>
<td>7.0</td>
</tr>
</tbody>
</table>

* Standard error of mean ranged from 0.8 to 0.1 min; majority was 0.3 or less. N = 5 for each dog

because the time required for the complex to pass an electrode was similar at all levels of the bowel in every dog.

Eighty-one per cent of the observed electric complexes were propagated the entire length of the small bowel. When a complex reached the ileum, the electric activity of the duodenum and proximal jejunum was either of the precomplex or complex type. This recurrent sequence between the duodenum and the ileum would prescribe that only two electric complexes could occur simultaneously on the small bowel and that, in fasting dogs, a complex should always be present somewhere in the bowel.

It appeared that both prescriptions were correct. When-
FIG. 10. Relation of calculated length of complex (LEC) to percentage distance from the gastroduodenal junction in six dogs. Each point is mean length of five complexes.

TABLE 3. Characteristics of electric complex

<table>
<thead>
<tr>
<th>Percentage Distance From Gastroduodenal Junction</th>
<th>Velocity, cm/min</th>
<th>Duration, min</th>
<th>Length of Electric Complex (LEC), cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>5.3±0.4</td>
<td>6.1±0.3</td>
<td>32.0±1.9</td>
</tr>
<tr>
<td>20</td>
<td>5.5±0.5</td>
<td>5.5±0.2</td>
<td>29.5±2.3</td>
</tr>
<tr>
<td>30</td>
<td>4.0±0.4</td>
<td>5.5±0.3</td>
<td>22.0±0.0</td>
</tr>
<tr>
<td>40</td>
<td>2.6±0.2</td>
<td>5.5±0.2</td>
<td>13.9±0.8</td>
</tr>
<tr>
<td>50</td>
<td>2.1±0.1</td>
<td>5.5±0.2</td>
<td>11.6±1.1</td>
</tr>
<tr>
<td>60</td>
<td>1.6±0.1</td>
<td>5.6±0.1</td>
<td>9.0±0.7</td>
</tr>
<tr>
<td>70</td>
<td>1.6±0.2</td>
<td>5.6±0.2</td>
<td>9.2±1.7</td>
</tr>
<tr>
<td>80</td>
<td>1.5±0.1</td>
<td>5.7±0.2</td>
<td>7.6±0.8</td>
</tr>
<tr>
<td>90</td>
<td>1.5±0.1</td>
<td>5.9±0.3</td>
<td>8.7±1.1</td>
</tr>
</tbody>
</table>

Each value is the grand mean±SEM (N = 6).

FIG. 11. Cumulative frequency distribution of increase in slow-wave frequency after passage of electric complex (ΔA-R). ΔL,R = slow wave frequency after passage — before passage. Only those ΔA-R which were positive (127) were used to construct this distribution. From such a distribution, smallest, largest, and median increase in slow-wave frequency can be read directly. Rank location (percent of 127 observations) for any ΔA-R can be obtained by projecting a vertical line for any point on abscissa to graph line, and then projecting horizontally to ordinate.

During propagation of the electric complex, the slow-wave frequency at all levels of the bowel was greater after the passage of the complex than before. This indicates that the complex interferes with the influence of oral pacemakers on intestinal segments distal to it. Although we are not certain how the interference is accomplished, it is most likely related to the effect of the intensive action potential activity of the complex on the ability of the smooth muscle cells to generate or conduct the slow wave. It has been previously shown that the frequency of slow waves is reduced during periods of spontaneously occurring action potentials (11) and during periods of action potential activity initiated by a cholinergic stimulus (12). Others (2, 3) have shown that intense action potential activity initiated by morphine sulfate can obliterate slow waves.

Although this is the first description of an electric complex propagated over the entire length of the small bowel, others have recorded migrating motor complexes over short segments of the small bowel in the dog and the human (4–8, 10). For example, Castleton (4), Douglas and Mann (5), and Grindlay and Mann (7) found that, in Biebl loops of the canine small bowel, periods of quiescence lasting for 105 min were interrupted by periods of irregular segmentation which ended with a 3- to 5-min burst of rhythmic segmentation. Both Hiatt et al. (8) and Reinke et al. (10), although using different methods, recorded caudal-progressing bands of contraction in the small bowel of dogs. From their published records, the velocity and duration of the band of contraction was calculated. In Hiatt and associates' publication, the velocity was 2.5 cm/min and duration 4–4.5 min, and in Reinke and associates' they were 1.3 cm/min and 4 min, respectively. These agree with calculations for the velocity and duration of the electric complex for similar regions of the small bowel. Similarly, Foulk et al. (6) have observed that in the upper small bowel of humans, a prolonged period of type I contractions ended with a 3- to 6-min period of basic rhythm (rhythmic segmentation) superimposed on a base-line pressure change (type III contraction) and that these bursts of intensive rhythmic segmentation were followed by periods of quiescence. All of these results taken together indicate that the motor correlate to the prescomplex electric activity is likely irregular segmentation (type I contractions when recorded by balloons and basal-type contractions when recorded by strain gauges) and that the motor correlate to the complex activity is a burst of rhythmic segmentation in caudad sequence (type III contractions or burst-type contractions).

The function of the migrating electric complex remains speculative. The motor activity it induces, however, would mix the residual contents (for example, cellular debris) with interdigestive secretions and move these caudad. Hoelzel (9) noted in his own stomach that gastric secretions accumulated during motor quiescence but that less than 10 ml had been left after a period of vigorous gastric motor activity. Reinke et al. (10) observed that expulsion of mucinous secretions from a duodenal cannula coincided with coordinated bursts of activity in the stomach and duodenum. In terms of the entire small bowel, it is suggested that the function of the complex is to move the interdigestive

ever a dog was placed in the stand, an electric complex could always be located somewhere along the small bowel. Because the dogs had fasted 21 hr when the recording session began and because each recording session lasted 3.5 hr, the electric complexes were certainly recycling in these dogs after fasting for 24 hr. How long the recycling would continue with prolonged fasting is unknown.
contents down the small bowel and into the large bowel in preparation for the next meal. The complexes may, therefore, be regarded as the interdigestive "housekeeper" of the small bowel.

I am grateful to Dr. C. F. Code, who encouraged me to pursue this investigation and for many helpful suggestions including the proposal that the complex is the interdigestive housekeeper of the small bowel. I thank Dr. A. Rosenbaum, who participated in some of these experiments, and Mr. P. Schmalk and Mr. J. Miller for their technical assistance.

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