THE PRINCIPAL OBJECTIVE of these experiments was to define the patterns of electrical activity in the muscular coat \( (\text{tunica muscularis}) \) of the stomach of the healthy, conscious dog during fasting, after distention of the stomach by a balloon, and after instillation of water and cottonseed oil into the stomach. A secondary objective was to correlate the electrical patterns with gastric contractions.

METHODS

Twelve healthy, mongrel, female dogs \( (10-14 \text{ kg in weight}) \) were used in the experiments. Monopolar, silver wire electrodes, similar to those used in this laboratory in the past \( (1) \), were employed for recording electrical activity. The tips of the electrodes, which had been electrolytically coated with silver chloride, projected 2 mm from one surface of a flat, “heart-shaped,” two-layered Teflon disc (Fig. 1). The electrode passed through one layer of the disc and was connected between the layers to a Teflon-insulated, copper lead 12 inches long. The entire disc, aside from the tips of the electrodes, was sealed with epoxy resin. Three holes were drilled in the disc and through these the disc was sutured to the viscus. The insulated lead from each disc was connected to a pin of a nine-pin tube socket mounted with dental impression material (Acrolite) in a metal cannula.

With sterile operating technique, nine electrodes were implanted in each dog during anesthesia with pentobarbital given intravenously. Eight of the nine electrodes were sutured in a serial fashion to the anterior serosal surface of the stomach midway between the greater and the lesser curvature (Fig. 1). The first electrode was placed at the orad extremity of the fundus, and the eighth, 1 cm orad to the pylorus. The other gastric electrodes were spaced at equal intervals (approximately 3 cm) between these two. The ninth electrode was sutured to the antimesenteric border of the descending part of the duodenum 7 to 10 cm distal to the pylorus.

The metal cannula containing the nine-pin socket to which the electrodes were attached was positioned in and sutured to the right anterior abdominal wall in the mid-clavicular line. After recovery from the operation the dogs were healthy, maintained their weight throughout the period of testing, and did not appear to be hampered by the presence of the electrical apparatus.

Recordings were begun 2 weeks postoperatively and were made one or more times a week for 3 months. The animals were fasted for at least 18 hr before each recording session. They were trained to lie quietly in a sling during the sessions. Insulated wire leads were attached to the pins in the cannula and connected to either a direct writing, Offner curvilinear pen recorder or a Brush Mark 200 rectilinear pen recorder. Alternating-current amplifiers with a time constant of 1.0 sec were employed. Differences in potential were measured between the visceral electrodes and an indifferent electrode placed subcutaneously in the right hind limb of the animal at each session. On some occasions potential differences between adjacent gastric electrodes were also recorded.

The pattern of electrical activity during fasting was identified in eight dogs. Recordings were obtained from each dog, from all of the gastric electrodes, for periods of 10 min on 10 different days. The occurrence and configuration of cyclical fluctuations in electrical potential \( (\text{the pacemaker potential, PP}) \) in the tracings from each electrode were noted.

The amplitude of the PP at each electrode was estimated by calculating the mean millivolts of the negative deflection from the isopotential line of six consecutive cycles. The site of origin of the PP was identified as the area between the most orad electrode from which the PP was recorded and the next orad electrode. The mean frequency of the PP at each of the recording sites was determined during 6 min and was expressed in cycles per minute \( (\text{cycles/min}) \).
FIG. 1. Design of silver-silver chloride electrodes (inset) and sites of implantation on canine stomach and duodenum.

The direction of propagation of the PP was investigated by changing from the monopolar recording technique to a bipolar technique in which the potential changes between adjacent gastric electrodes were recorded. The pattern of the bipolar tracings identified the direction of conduction.

The mean time required for conduction of the PP between adjacent electrodes for six consecutive waves was measured during a 2-min period of monopolar recording at rapid paper speeds of 1 cm/sec. The wavelength of the PP was calculated by dividing the velocity in centimeters per second (interelectrode distance assumed to be 3 cm) by the frequency of the PP per second, giving the wavelength in centimeters. The presence of action potentials in association with the cycles of the PP was always identified and the incidence of action potentials was calculated as the percentage of PPs with action potentials during a 6-min period.

Simultaneous electrical, mechanical, and cinefluoroscopic observations were made on five occasions in five dogs. Electrical activity was recorded as described. Changes in intragastric pressure were measured by means of a round, soft, thin-walled, spherical rubber balloon with a diameter of 1.0 cm, which was attached to a polyethylene (PE-240) catheter. The catheter was passed through the mouth and the balloon was positioned by fluoroscopy in the stomach beneath one of the antral electrodes. The tubing and the balloon were filled, but not distended, with a colloidal thorium dioxide suspension (Thorotrast). The tubing was connected to a Statham strain gauge and the output of the gauge to a recorder. Cinefluorographic recordings were made simultaneously. Waves of contraction indenting the balloon could easily be seen fluoroscopically and in the motion pictures. Their presence was recorded by a hand switch which activated one of the pens of the recorder. Thus, the electrical activity, the changes in intragastric pressure, and the contractions (seen cinefluoroscopically) in one area of the stomach were correlated.

Four additional experimental procedures were performed. In the first, recordings were made for 1 hr on five occasions in each of five dogs when the animals rested quietly in the stands and received no stimulus. These observations were made to provide suitable control data for the hour-long recordings made after performing the various test procedures described below. The mean frequency of the PP over a 6-min period and the mean time required for conduction of six consecutive PPs in the corpus and antrum were determined before and 10, 20, 30, and 60 min after the start of the 1-hr period. The mean wavelength of the PP in the corpus and antrum was calculated from the mean frequency and mean velocity. The mean incidence of antral action potentials over a 6-min period was also determined at these same intervals.

In the second procedure, in which a set of three experiments was performed on each of five animals, after a 10-min period of control recording, an oral-gastric tube capped on its far end was inserted to the level of the lower end of the pylorus. The balloon was then inflated with 500 ml of air. Changes in intragastric pressure were recorded simultaneously with electrical activity as described above. The balloon was distended to the point at which it began to indent the wall of the stomach, and observations were made on hourly intervals for 5 hr. The mean frequency of the PP over a 6-min period and the mean time required for conduction of six consecutive PPs in the corpus and antrum were determined before and 10, 20, 30, 40, and 50 min after distending the balloon. The mean wavelength of the PP in the corpus and antrum was calculated from the mean frequency and mean velocity. The mean incidence of antral action potentials over a 6-min period was also determined at these same intervals.
its gastric end with a large, pear-shaped balloon was passed
into the stomach and the balloon then filled with 500 ml of
water at approximately 37 C. After recording with the
balloon inflated for 30 min it was deflated and withdrawn,
and the recordings were continued for an additional 30 min.
Roentgenograms made with the balloon in place and filled
with 500 ml of air showed that it distended the fundus and
corpus and increased the distance between electrodes in
these areas (Fig. 2).

In the third procedure, in which a set of five experiments
was performed on each of five animals, after a 10-min
period of control recordings, 500 ml of water (approximately
37 C) was placed in the stomach via an oral-gastric tube.
The tube was then removed and the recordings were con-
tinued for 1 hr.

In the fourth procedure, in which a set of five experiments
was performed on each of five animals, the same procedure
was followed except that 100 ml of polyunsaturated cotton-
seed oil (Wesson Oil, Hunt-Wesson Foods, Fullerton, Calif.)
was given. The oil was generally administered on days when
the fasting animals showed some evidence of action poten-
tials because inhibiting effects could not be identified in
their absence.

The tracings from the three series of tests in which stimuli
were given were analyzed in the same way as the tracings
from the first series, in which no stimulus was administered.

The same five dogs were not used in all of the four groups
of tests. Therefore, when comparisons were made between
unstimulated and stimulated groups, the results were
-treated as unpaired data.

RESULTS

Fasting Pattern

A characteristic, regularly recurring change in potential,
the pacesetter potential (PP) or slow wave, was consistently
recorded from the antrum and caudad two-thirds of the
corpus of the stomach (Fig. 3 and Table 1). Each cycle of
the pacesetter potential was composed of two parts. The initial
portion of the cycle was usually triphasic, consisting of a
small positive, a large negative, and then a small positive
deflection. The large negative deflection was most consistent
and its amplitude was greater in the antrum than in the
corpus (Table 2). The general configuration of the initial
portion was similar, however, at each of the sites from which
the cycle was recorded.

In the second portion of the cycle the potential changed
little under resting conditions, being represented by a
nearly straight horizontal line which continued until the
beginning of the next triphasic deflection (Fig. 3).

Pacesetter potentials were never recorded from electrode 1
in the fundus, and only infrequently from electrode 2 (Table
1). They were recorded regularly from electrodes 3 through
8 in two of the eight dogs and from electrodes 4 through 8 in
the remaining six (Table 1). Thus, the site of origin of the
PP was almost always between electrodes 3 and 4 or 4 and
3, which positions the site of origin close to the junction be-
tween the oral one-third and the caudad two-thirds of the
stomach (Table 1 and Fig. 3). The site of origin was the
same from day to day in each dog.

The PP in each dog was detected at the same frequency
and at the same regular rhythm by all of the gastric elec-
trodes distal to the midcorporal area. The frequency was
exceedingly consistent in individual animals from day to
day. The standard error of the mean of 10 daily frequencies
at electrodes 4 through 8 was 0.10 within dogs and 0.54 be-
tween dogs.
these electrodes was approximately 5 times as much between dogs as within dogs (Table 1).

The PP was propagated from the orad corpus to the pylorus. This was identified by two means. Sometimes a pause occurred in the regular rhythm of the PP in the orad corpus owing to failure or disappearance of one cycle (Fig. 4). This produced a pause in the pattern which was detected sequentially in caudad electrodes (Fig. 4). Second, when the recording technique was changed from monopolar to bipolar and differential recordings were made between adjacent gastric electrodes, a diphasic pattern was recorded which is consistent with caudad propagation of the PP (Fig. 5).

The time required for propagation of the PP between adjacent electrodes was consistent from cycle to cycle in each animal. It diminished as the PP passed over the corpus and antrum. Thus, the velocity of propagation increased as the PP approached the pylorus (Fig. 6)

Variation in interelectrode conduction within individual dogs was very small compared with that between dogs (Table 2).

The wavelength of the PP, determined by its velocity of conduction and its frequency (wavelength = velocity/frequency), was longer in the antrum than in the corpus. The antral wavelength was 15.4 cm and the corporal wavelength 4.0 cm (calculated from grand means in Tables 1 and 2).

Bursts of action potentials (fast activity, spikes) were sometimes superimposed on the PP (Fig. 4). They always occurred during the second portion of the PP cycle, just after the triphasic complex, and were usually accompanied by a monophasic, negative deflection (Figs 4 and 7). They were detected more clearly and more frequently in the antrum than in the corpus (Fig. 4 and Table 2) and were not found in the fundus. In the group of eight fasting dogs, action potentials were superimposed on approximately one-fourth of the antral PPs. Variation in the incidence of antral action potentials between dogs was 2–4 times as large as within dogs (Table 2).

Correlation Between Electrical and Mechanical Activity

Simultaneous recordings of the electrical events, the changes in intragastric balloon pressure, and motility as seen cinerhinoscopically showed that contractions occurred only when action potentials were recorded (Fig. 7). The onset of the contractions occurred at or just after the onset of action potentials (Fig. 7). The relationship of the amplitude of the contractions to the amplitude of the action potentials and the duration of the burst appeared to be linear in four of the five dogs, while in the one dog in which the pressure increased to more than 200 cm H2O, the linearity failed at the high values (Fig. 8). In all cases the fit is questionable.
near the origin and the residual variation is relatively large (Table 3).

Patterns During 1-Hr Control Period

An analysis of the initial 6 min \(t = 0\) of the 1-hr control recordings from the group of five dogs that received no stimulus was made to determine if the electrical patterns and variations during fasting in these dogs during these experiments were similar to the patterns and variations in the larger, more extensively tested group of fasting dogs described in the previous section. The frequency of the PP and the time required for its propagation in the corpus and antrum in the initial 6 min of the control period in this group of five dogs were quite consistent from day to day and varied more between than within dogs (Table 1). The variations in the incidence of antral action potentials within dogs were large and were of the same order of magnitude as those between dogs (Table 4). The electrical parameters in this group of dogs were quite similar to those described in previous section, and the preparations were therefore considered suitable for providing control data for the test procedures described below (compare Tables 1 and 2 with Table 4).

Analysis of the 1-hr control recordings was then made at \(t = 0\), 10, 20, 30, and 60 min to establish the pattern of electrical activity over the 60 min in the unstimulated stomach. Little change occurred in the frequency of the PP, the time required for conduction of the corporal and antral PPs, the corporal and antral wavelengths, or the incidence of antral action potentials during the 60 min (Figs. 9 through 13).

Patterns During Stimulation

Balloon distention. Distention of the stomach with a balloon decreased the frequency of the PP and prolonged the time required for PP propagation between adjacent corporal electrodes in 15 of 15 tests (Fig. 9 and 10). The average decrease in frequency 30 min after the onset of distention was 30 %, and the range in average decrease for the five dogs was 23-36 %. The average increase in corporal conduction time 30 min after the onset of distention was 20 %, and

![Figure 6](http://ajplegacy.physiology.org/)

**FIG. 6.** Recording of canine gastric and duodenal electrical activity illustrating velocity of caudad conduction of gastric PP. Velocity, indicated by slope of lines connecting a cycle as it was detected in sequence by electrodes placed at equal intervals on surface of stomach, increases as the PP approaches pylorus.

**TABLE 2.** Characteristics of gastric PP in fasting dogs

<table>
<thead>
<tr>
<th>Dog</th>
<th>Electrodes</th>
<th>Electrode</th>
<th>Electrodes</th>
<th>Electrode</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4 6 8</td>
<td>4-5 5-6</td>
<td>6-7 7-8</td>
<td>4 6 8</td>
</tr>
<tr>
<td>2</td>
<td>0.6 0.4 1.9</td>
<td>9.8 9.2 7.5</td>
<td>1.1 1.3 3.5</td>
<td>6.8 6.9 2.3</td>
</tr>
<tr>
<td>3</td>
<td>1.2 1.0 3.1</td>
<td>8.4 8.6 6.0</td>
<td>2.0 2.5 1.5</td>
<td>6.7 6.5 3.1</td>
</tr>
<tr>
<td>4</td>
<td>0.5 1.0 4.8</td>
<td>8.9 8.3 4.5</td>
<td>3.2 3.0 1.5</td>
<td>6.7 6.5 3.1</td>
</tr>
<tr>
<td>5</td>
<td>0.4 1.2 2.0</td>
<td>9.6 9.4 4.0</td>
<td>1.5 1.5 1.5</td>
<td>6.7 6.5 3.1</td>
</tr>
<tr>
<td>6</td>
<td>1.3 1.3 3.5</td>
<td>7.6 7.4 2.3</td>
<td>1.3 1.5 1.5</td>
<td>6.7 6.5 3.1</td>
</tr>
<tr>
<td>7</td>
<td>1.0 0.7 2.7</td>
<td>6.7 6.5 4.5</td>
<td>1.5 1.5 1.5</td>
<td>6.7 6.5 3.1</td>
</tr>
<tr>
<td>8</td>
<td>0.9 1.0 2.4</td>
<td>9.3 9.1 3.0</td>
<td>2.2 2.2 1.5</td>
<td>6.7 6.5 3.1</td>
</tr>
<tr>
<td></td>
<td>Grand mean</td>
<td>0.8 0.9 2.8</td>
<td>8.4 8.6 4.9</td>
<td>2.2 2.2 1.5</td>
</tr>
<tr>
<td></td>
<td>Mean square (s²)</td>
<td>0.05 0.11 0.21</td>
<td>0.65 0.30 0.11</td>
<td>0.09 0.07 0.06</td>
</tr>
</tbody>
</table>

Values are means of 10 daily measurements. * Obtained from measurements of 6 consecutive electrical complexes on each day. † Obtained from measurements of 6 consecutive intervals between electrodes on each day. ‡ Obtained from 6 consecutive minutes of tracing on each day. § Data from alternate electrodes recording PP are presented. See Fig. 1 for electrode positions on stomach.
the range in average increase for the five dogs was 2–44%. However, propagation between antral electrodes was slightly faster in 14 of 15 tests (Fig. 11). The average decrease in antral conduction time 30 min after the onset of distention was 12%, and the range in average decrease for the five dogs was 8–19%. The wavelength of the corporal PP was

Table 4. Variation in gastric PP parameters within and between dogs during fasting

<table>
<thead>
<tr>
<th>Dog</th>
<th>Frequency of PP, cycles/min</th>
<th>Corporal Conduction Time, sec</th>
<th>Antral Conduction Time, sec</th>
<th>% of Antral PPs with Action Potentials</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x} \pm s$</td>
<td>$CV_{1/2} %$</td>
<td>$\bar{x} \pm s$</td>
<td>$CV_{1/2} %$</td>
</tr>
<tr>
<td>A. Means and SD and coeff. of variation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>5.0</td>
<td>.15</td>
<td>3.0</td>
<td>7.0</td>
</tr>
<tr>
<td>8</td>
<td>5.2</td>
<td>.19</td>
<td>3.7</td>
<td>9.0</td>
</tr>
<tr>
<td>9</td>
<td>4.7</td>
<td>.11</td>
<td>2.3</td>
<td>7.8</td>
</tr>
<tr>
<td>10</td>
<td>5.2</td>
<td>14.2</td>
<td>2.7</td>
<td>8.5</td>
</tr>
<tr>
<td>11</td>
<td>5.0</td>
<td>.37</td>
<td>6.6</td>
<td>8.7</td>
</tr>
</tbody>
</table>

B. Mean squares ($s^2$) $

<table>
<thead>
<tr>
<th></th>
<th>Within dogs</th>
<th>Between dogs</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.05</td>
<td>0.29</td>
<td>0.01</td>
</tr>
</tbody>
</table>

* $\bar{x}$ Values are means of 5 daily values obtained from 6 consecutive minutes of tracing. |
† Values are means of 5 daily values obtained from measurements of 6 consecutive intervals between electrodes.

Table 3. Regression of amplitude of antral contractions on antral action potentials

<table>
<thead>
<tr>
<th>Dog</th>
<th>N</th>
<th>Least Squares</th>
<th>$s_{y,x}$</th>
<th>$s_{x,y}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>48</td>
<td>$y = 21.0 + 37.7x$</td>
<td>28.1</td>
<td>2.32</td>
</tr>
<tr>
<td>2</td>
<td>50</td>
<td>$y = 20.6 + 27.0x$</td>
<td>15.8</td>
<td>3.31</td>
</tr>
<tr>
<td>3</td>
<td>50</td>
<td>$y = 15.8 + 42.0x$</td>
<td>15.4</td>
<td>4.21</td>
</tr>
<tr>
<td>4</td>
<td>50</td>
<td>$y = 54.1 + 50.7x$</td>
<td>24.3</td>
<td>6.93</td>
</tr>
<tr>
<td>5</td>
<td>48</td>
<td>$y = 7.5 + 18.8x$</td>
<td>12.8</td>
<td>1.32</td>
</tr>
</tbody>
</table>

* $y =$ antral balloon pressure in centimeters of water; $x =$ amplitude (mv) multiplied by duration (sec)/2; amplitude and duration are those of action potentials at electrode adjacent to antral balloon. Equations derived from consecutive observations made on the same day on each dog. † $P < 0.01$ for each dog. ‡ See Fig. 8.

The parabola $y = 7.637 + 3.175x + 6.0371x^2$ fits better, the residual variation ($s_{x,y}$) decreasing to 23.1.

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The parabola $y = 7.637 + 3.175x + 6.0371x^2$ fits better, the residual variation ($s_{x,y}$) decreasing to 23.1.
lengthened slightly by balloon distention, whereas that of the antral PP was markedly lengthened (Fig. 12). In addition, the incidence of antral action potentials was increased in 15 of 15 tests (Fig. 13), the incidence on the average increasing from 20 to 85%.

Although each dog showed variation in the magnitude of responses from day to day (as illustrated for a single dog in Figs. 9 through 13), the sequence of the changes as indicated by the shape of the response curves did not change greatly. In the balloon test the response curves based on means may be taken as typical of each experiment for that dog.

The changes in frequency, propagation, and incidence of antral action potentials with distention lasted until the distention was released. All characteristics had returned almost to control values by 30 min after deflation (Figs. 9 through 13).

**Water instillation.** The frequency of the PP decreased within 10 min after the instillation of 500 ml of water in 23 of 25 tests and decreased in all tests by 20 min (Fig. 9). The
average decrease 10 min after instillation was 11 %, and the range in average decrease for the five dogs was 4–22 %. A longer time was required for propagation of the PP between adjacent corporal electrodes at 10 min after instillation in 25 of 25 tests (Fig. 10). The average increase for the five dogs was 25 % (range 16–43 %). However, conduction time between adjacent antral electrodes was increased in three dogs and decreased in two (Fig. 11). In repeated tests on the same dog the results were quite consistent. The only example of reversal of sign of the response in all 25 tests is given in Fig. 11. The two dogs in which more rapid antral conduction was noted after the instillation of water had shorter mean antral PP conduction times in the fasting state (1.6 and 2.3 sec). The wavelengths of the corporal and antral PPs varied markedly and inconsistently during the 5 days, and again a dog’s mean response curve may be taken as typical for that dog.

**DISCUSSION**

These experiments confirm the existence of an omnipresent, cyclically recurring change in electrical potential in the gastric wall described by others in vitro (14) and in anesthetized animals (1, 4, 7, 11, 12). We have called this phenomenon the “pacesetter potential,” while one of us (CFC) with others has used the term “basic electrical rhythm” (BER) (3), and still others have identified it as the “slow wave” (6) or “initial potential” (8). We recognized that all of these terms have merit and prefer to continue their use. The term basic electrical rhythm, the BER, has appeal when describing the overall pattern of visceral electrical activity, but we have found its use cumbersome when specifying changes in individual cycles of the rhythm. Slow wave and initial potential are very useful descriptive terms which, however, give no indication of function. Strong evidence supports the conclusion that these cyclic changes in potential synchronize the contractions of the smooth muscle cells through which they pass and determine the maximal frequency at which they contract. The term pacesetter potential thus has a justified functional connotation which we have found helpful when describing gastrointestinal electrical activity to others. We continue use of the other terms when they seem more appropriate and to avoid monotony. In this report, too, we have used the term action potentials to describe the electrical changes associated with contraction, preferring this, because of its indication of function, to the purely descriptive terms spike or fast potentials. We do not intend
or propose to abandon the use of the latter terms, for they have historical significance and may, with further knowledge, prove most suitable.

Our findings are particularly relevant to those of three prior studies (7, 11, 12) in which electrodes were also sewn onto the surface of the canine stomach and the electrical activity was then recorded for weeks or months while the animals were conscious and in good health. All recorded, as did we, a pacesetter potential (PP) consisting of two portions, an initial triphasic deflection, followed by a second portion which lasts until the next triphasic deflection. We found the second portion of the cycle to be nearly a straight, horizontal line in the record when no contractions were present. Nevertheless, it is possible that slow variations in potential might have been occurring during the second portion which we would have missed because we used a time constant of 1 sec in our recording system.

The frequency of the PP as reported by the three groups (7, 11, 12) and by us ranged from 4.5 to 5.7 cycles/min. McCoy and Bass (11) found the velocity of conduction of the antral PP to be 2.7 cm/sec and Carlson and co-workers (7) found it to be 2.0 cm/sec, while Nelsen and colleagues (12) estimated the antral velocity at 4.0 cm/sec. We cannot be certain of the distance between antral electrodes during our tests, but using that between them at the time of placement (3 cm) we calculated the mean velocity in the antrum as 1.4 cm/sec. The slower velocity is probably due to the fact that our electrodes were more orad on the stomach. All who have tested it agree that the velocity of conduction increases as the PP sweeps aborally through the gastric wall (7, 12).

Action potentials were readily seen in our tracings and in those of McCoy and Bass (11) and Carlson and colleagues (7). However, Nelsen and colleagues (12) did not identify action potentials, for there is no mention of them in their report and little or no indication of them in their published recordings. Nelsen and colleagues (12) correlated contractions with the "electrical wave," which in their records is clearly the PP. We and others have correlated contractions with action potentials. Past workers (3) in our laboratory have found that during fasting conditions many cycles of the duodenal PP are devoid of action potentials and with these cycles no contractions are recorded. We found the same correlation between action potentials and contractions in the stomach.

The mean incidence of antral PP with action potentials at electrode 8 in fasting dogs in this study was 26% (Table 2). In tests by Allen and colleagues (1) on the same region of the stomach, the incidence was only 13%, but the range was wide in both investigations, being 11-10% in theirs and 2-47% in ours, and the difference cannot be regarded as significant.

In none of the past studies on conscious animals were electrodes positioned sufficiently orad on the stomach to determine the site of origin of the PP. By placing electrodes sequentially from the oral extremity of the stomach to the pylorus we found the PP absent in the fundus, but we regularly detected it in the orad corpus. It was propagated aborally from that site. Furthermore, its frequency was the same in the distal part of the stomach as in the orad corpus. Our results thus support the hypothesis of Alvarez and Mahoney (2) and Sato (16) that the gastric PP originates in the orad corpus.

The overall pattern of fasting electrical activity in our trained, conscious dogs was very stable from day to day. Aberrant pacemakers and changing myoelectric patterns in the distal part of the stomach, as described by others in acute experiments (2), were almost never encountered. In addition, the frequency of the PP in these observations was faster than that recorded by previous workers in short-term experiments on anesthetized animals (5, 8, 12, 15, 17, 18), or in experiments in which a portion of the stomach was displaced from its usual location (4). Also, action potentials were more clearly seen in our tracings.

The technique we used allowed simultaneous comparison of the characteristics of the PP in different regions of the stomach. The PP in the antrum had greater amplitude, velocity, and incidence of action potentials than in other regions. It is difficult to draw inferences regarding underlying cellular electrical changes from the magnitude of the antral deflection. Amplitude as detected by extracellular electrodes is influenced by many variables, one of which is certainly the nature of the contact between the electrode and the surrounding muscle. The rapid passage of the PP over the distal part of the stomach, however, represents a valid measurement and accounts for the nearly simultaneous onset of contraction found in this region which results in the characteristic terminal antral contraction (7). The increased incidence of antral action potentials correlates with the greater incidence of contractions in the antrum compared to the corpus (7).

The ever-present cycles of the PP appear to provide an electrical framework through which stimuli can act to modify gastric motility. The stimuli we used changed the frequency and velocity of propagation of the PP as well as the incidence of antral action potentials associated with it. These changes in electrical parameters prescribe the adjustments in gastric motility to the stimuli. The mechanisms of their production are unknown, but clearly effects were produced both at the site of origin of the PP, since the PP frequency changed uniformly over the entire stomach, and in the smooth muscle cells of the corpus and antrum, since the velocities of PP conduction in these regions were sometimes altered independently.

Thanks are expressed to Dr. J. H. Szuszewski and Messrs. J. F. Schlegel and C. C. Berkis for their help during the experiment.

This investigation was supported, in part, by National Institutes of Health Research Grant AM-2015.

Received for publication 4 October 1968.

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