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RATE OF FLOW OF DIGESTA AND ELECTRICAL ACTIVITY OF THE SMALL INTESTINE IN DOGS AND SHEEP

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SUMMARY

1. Spiking activity of the small intestine in the conscious dog and sheep was recorded continuously from electrodes chronically implanted on the jejunum and summed at intervals of 20 sec. The activity was related to the transit time and flow rate of intestinal contents as estimated by phenol red and by dilution of continuous marker infusions respectively. Also in some sheep the flow of digesta was measured directly from a cannula in the proximal part of the jejunum, and also by use of an electromagnetic flow meter.

2. In the fasted dog and in sheep on a normal diet the intestinal activity was characterized by a migrating myo-electric complex comprising an irregular phase followed by a regular phase. These migrating myo-electric complexes occurred regularly after a period of inactivity at a frequency of 15–20/24 hr. In dogs after feeding, a continuous spiking activity appeared and persisted for periods of 7–8 hr. This was associated with much higher rates of flow and shorter transit times than were observed during fasting. In sheep, continuous spiking activity could be induced by intravenous injection of 5-hydroxytryptophan and this, similarly, was accompanied by a more rapid flow and a shorter transit time than recorded during the control period.

3. In both species the longest transit time occurred when a phenol red bolus was injected during the period of electrical inactivity. Relatively short transit times were observed when the bolus was administered just before the period of regular spiking activity.

4. When relaxation of the bowel was induced by intraperitoneal injection of hypertonic saline there was no spiking activity and the transit time for the infused solution was greatly lengthened, especially in the sheep. A noticeable flow of digestive contents persisted in the dog.

5. In the sheep the intestinal contents flowed intermittently during

periods of 10–15 min and at the same frequency as the migrating myo-electric complex. Two thirds of this flow took place in the 4–6 min immediately preceding the periods of irregular spiking activity.

6. It is concluded that in the fasted dog and in the sheep the migrating myo-electric complex controls the pressure gradients on which the flow of intestinal contents depends. This is accomplished in the main by the prolonged phase of irregular spiking activity, and it is suggested that the regular spiking activity which follows it, though not in itself propulsive, serves as a barrier to prevent backflow of digesta into the quiescent part of the intestine. When continuous spiking activity is induced, by feeding in the dog and by injection of 5-hydroxytryptophan in the sheep, no part of the intestine is quiescent and the transit time is shortened by the incessant irregular spiking activity.

INTRODUCTION

Most information on the electrical activity of the small intestine has been derived from chronic preparations in the dog (Bass, 1968; Code & Schlegel, 1974). In this species the volume of intestinal contents is small and the flow irregular owing to the relatively small amount of food eaten and the scanty flow of digestive secretions (about 1000 ml./12 hr). Only a few studies have been made on the sheep (Ruckebusch, 1970) in which flow of digestive contents into the duodenum is rapid (mean value 4,300 ml./12 hr) and is almost continuous regardless of the feeding pattern (Hogan & Phillipson, 1960; Harrison & Hill, 1962).

The main patterns of electrical activity (slow waves and spike potentials) in both species were found to be similar. In fasted dogs Szurzewski (1969) identified a cyclic recurring sequence of the electrical events and described them as a migrating myo-electric complex (MMC). In further studies on other species, Grivel & Ruckebusch (1972) recorded a similar phenomenon in dogs, sheep and rabbits. The part of the migrating myo-electric complex during which regular bursts of spike potentials are superimposed on consecutive slow waves was termed segmental contractions because of its rhythmicity and its localization in successive segments of the small intestine; this part lasts from 3 to 9 min. The segmental contractions are preceded by a phase during which irregular spiking activity (peristalsis) is recorded. Integration of the amplitude and the duration of spike activity at 20 sec intervals (Latour, 1973) reveals that at any one site, the migrating myo-electric complex is (i) a prolonged period of irregular spiking followed by (ii) a shorter period of regular spiking.

These migrating myo-electric complexes were observed in sheep regardless of the feeding period. In addition they migrated downward at a mean

velocity for the whole intestine that was about five to ten times faster than that recorded in fasted dogs so that they recurred at about 90–120 min intervals. The fact that a similar pattern has also been recorded in other species, e.g. calves before and after weaning (Ruckebusch & Bueno, 1973) and rats when not feeding (Ruckebusch & Ferré, 1974), raised the question of its role in developing the intestinal pressure gradients that cause the flow of digestive contents.

From cinefluorographic, myo-electric and pressure recordings, Code & Schlegel (1974) suggest that in fasted dogs the migrating myo-electric complex can be regarded as the 'interdigestive housekeeper'. Such a role does not explain the function of the migrating myo-electric complex in sheep or calves in which intestinal digestion is continuous.

Another point of interest is the disappearance of the migrating myo-electric complex when the rate of flow of digesta is increased, e.g. in calves immediately after suckling. In this case, as in dogs, the increase of the flow (Stobo, Roy & Gaston, 1966) is accompanied by uniform, continuous propulsive patterns (Ruckebusch & Buéno, 1973).

The following experiments were undertaken on dogs and sheep (i) to investigate the relation between the migrating myo-electric complex and the rate of passage of digesta along the small intestine; (ii) to analyse the influence of the irregular spiking phase and of the regular spiking phase on the mean velocity of the intestinal contents; (iii) to emphasize the function of the migrating myo-electric complex as a permanent moving process which regulates the flow of intestinal contents.

METHODS

Animal preparation. Measurements of the propagation of the migrating myo-electric complex were obtained from four dogs and five sheep. The dogs weighed from 19 to 28 kg and the sheep from 38 to 43 kg. Intestinal electrodes were implanted under thiopentone anaesthesia. The electrodes were made of insulated nichrome wire, 120 μm in diameter and 50–100 cm in length. The wire was inserted through the serous and muscular layers using a curved needle as a trocar and the free end was tied off close to the intestinal wall (Ruckebusch, 1970). Eight pairs of electrodes, 2 mm apart within each pair, were positioned beyond the ligament of Treitz at intervals of about 20 cm in dogs and 100 cm in sheep. The tip of an open catheter was inserted into the lumen of the intestine beneath the second electrode site, i.e. 40 cm beyond the pylorus in the dog and 200 cm beyond the pylorus in the sheep (Fig. 1). The animals were fitted with a T-shaped cannula in the intestine at the level of the seventh electrode site in dogs, and at the fourth electrode site in sheep, i.e. 100 and 200 cm respectively, aboral to the catheter. The observations were made on animals placed in modified metabolism cages which allowed free movement but assured sufficient restraint for long-term recordings.

Record analysis. Recordings of the electrical activity began one week after surgery and continued periodically for 8–12 weeks. The electrodes were connected to an e.e.g. machine (Reega VIII, Alvar, Paris) and a paper speed of 2·5 mm/sec was used.

Slow waves were eliminated by a high-pass filter and the level of remaining activity was automatically plotted by means of a four-line integrator connected to a potentiometric recorder. The percentage of spike activity during the recording time was determined by direct inspection of the integrated record as well as by the ratio of the length of irregular to the length of the regular phases of the spike complexes (Fig. 1).

Electrical activity and the flow of digesta. The catheter beneath the second electrode site was used for continuous infusion of a test solution: NaCl, 140 mM; D-mannitol, 16·7 mM and a 1 % solution (concentration C) polyethylene glycol (PEG), mol. wt. 4000. The infusion was given during 8 to 24 hr at a rate (F) of 3 ml./min. The total flow of intestinal contents at the site of the cannula (f_t) was determined from the concentration of PEG (c) in samples taken from the cannula. The following relation, f_t (ml./min) = $(F \times C)/c$ was used and flow rate of digestive contents (f) determined as $f = F\ (C-c)/c$. Two hours after beginning the perfusion samples were obtained from the cannula at 15 min intervals. PEG concentration was determined by the method of Hyden (1955). The test solution was also infused at rates of 6 and 9 ml./min to see what influence the infusion had on the electrical activity and on subsequent changes in flow of digestive contents. The rate of flow was at times directly measured by opening the T-shaped cannula and partially occluding its distal limb with a small balloon. The outflowing contents were collected at intervals of 2 min for periods of 2–4 hr. These contents were not returned to the intestine.

A phenol red bolus (1 ml. containing 20 mg phenolsulphonphthalein (PSP) in dogs and 100 mg in sheep) was rapidly injected through the catheter during the PEG infusion. The transit time was calculated from the PSP concentration profile in samples obtained from the cannula at 2 min intervals. The concentration of PSP was determined according to Smith (1964). The transit time of the bolus was calculated from the times at which the peak PSP concentrations were recorded (Barreiro, McKenna & Beck, 1968).

The flow rate of digestive contents and the transit time were measured three times a week in dogs fasted for 18 hr or fed 10 min before the beginning of the experiments and in sheep receiving hay twice daily at 8.00 and 18.00 hrs. Water was available *ad libitum*. In fed dogs, the injections of PSP were performed at hourly intervals. In fasted dogs and in sheep the bolus was injected before, during or after development of the activity corresponding to the regular phases of the migrating myo-electric complex (see Fig. 2).

Observations were made as well of the transit of PSP injected during a regular phase of the migrating myo-electric complex and during the continuous electrical activity induced by 5-hydroxytryptophan (2 mg/kg body weight) administered into the jugular vein or by NaCl solution 30 % (w/v) injected intraperitoneally.

Electrical activity, intraluminal pressure and the passage of digesta. Four additional sheep weighing 40 kg and receiving hay *ad libitum* were used solely for measurement of intraluminal pressure changes and passage of digesta related to the patterns of electrical activity. Two sheep were fitted with a simple cannula (7 mm in diameter) 5 cm below one electrode site on the proximal jejunum. A water-filled balloon, connected to a pressure transducer, was placed in the lumen of the cannula. The two other sheep were equipped with an electromagnetic flow transducer (12 mm in diameter) 10 cm below one electrode site on the proximal jejunum. The transducer was connected to an electromagnetic flow meter (model 375, Nycotron Drammen, Norway). The electrical activity was recorded directly and/or integrated at 20 sec intervals, while pressure changes and passage of digesta were simultaneously registered on a polygraph with a time constant of approximately 2·5 sec.

RESULTS

Electrical activity. Relatively long periods of inactivity (Phase 1) were followed by recurrent patterns (fifteen to twenty times per day) of spiking activity, the migrating myo-electric complex, in fasted dogs and in sheep fed normally. These complexes showed two phases: irregular bursts of spike potentials often propagating rapidly between two sets of electrodes (Phase 2) and regular bursts occurring at the rate of the slow waves and lasting for 3–9 min at any one site (Phase 3). Quantification of this activity from three electrode sites in the two species revealed a similar pattern which migrated slowly downward (Fig. 1). The end of each Phase 3 was abrupt so that measurements were easily made of the intervals between successive migrating myo-electric complex. The phase of irregular spike bursts occupied about 50% of each cycle (the latter being about 85 min) in both fasted dogs and sheep. The ratio of the duration of the period of irregular to the period of regular spiking activity was 4·6:1 in the dog and 6·5:1 in sheep (Table 1).

TABLE 1. Characteristics of the jejunal migrating myo-electric complex in dogs fasted for 18 hours and in normally fed sheep (mean value ± S.D. for three periods of observation)

	Dog (4)*	Sheep (5)*
Recurring intervals (min)	83·0 ± 24·2	88·4 ± 16·2
Mean velocity of propagation (cm/min)	4·0 ± 1·5	17·8 ± 5·7
Duration of inactivity (Phase 1) (min)	40·2 ± 16·2 (48·4%)†	42·0 ± 15·1 (47·5%)
Duration of activity (min)		
irregular (Phase 2)	35·3 ± 4·2 (42·5%)	40·1 ± 4·8 (45·4%)
regular (Phase 3)	7·7 ± 1·2 (9·1%)	6·2 ± 1·2 (7·1%)

* Number of animals.

† Mean percentage of each phase on total duration of migrating myo-electric complex.

These migrating myo-electric complexes occurred continuously regardless of feeding periods in sheep but disappeared immediately during and for a period of about 8 hr following a meal in the dog (Fig. 1). In these 8 hr, continuous irregular activity occurred during the first 5 hr; later, this was interspersed with short quiescent phases and then again with the regular phases. In sheep the intravenous injection of 5-hydroxytryptophan (2 mg/kg) induced a similar activity lasting for about 4 hr.

Transit time and total flow rate of contents. When the pattern of electrical activity was continuously irregular as during the period of 5 hr following

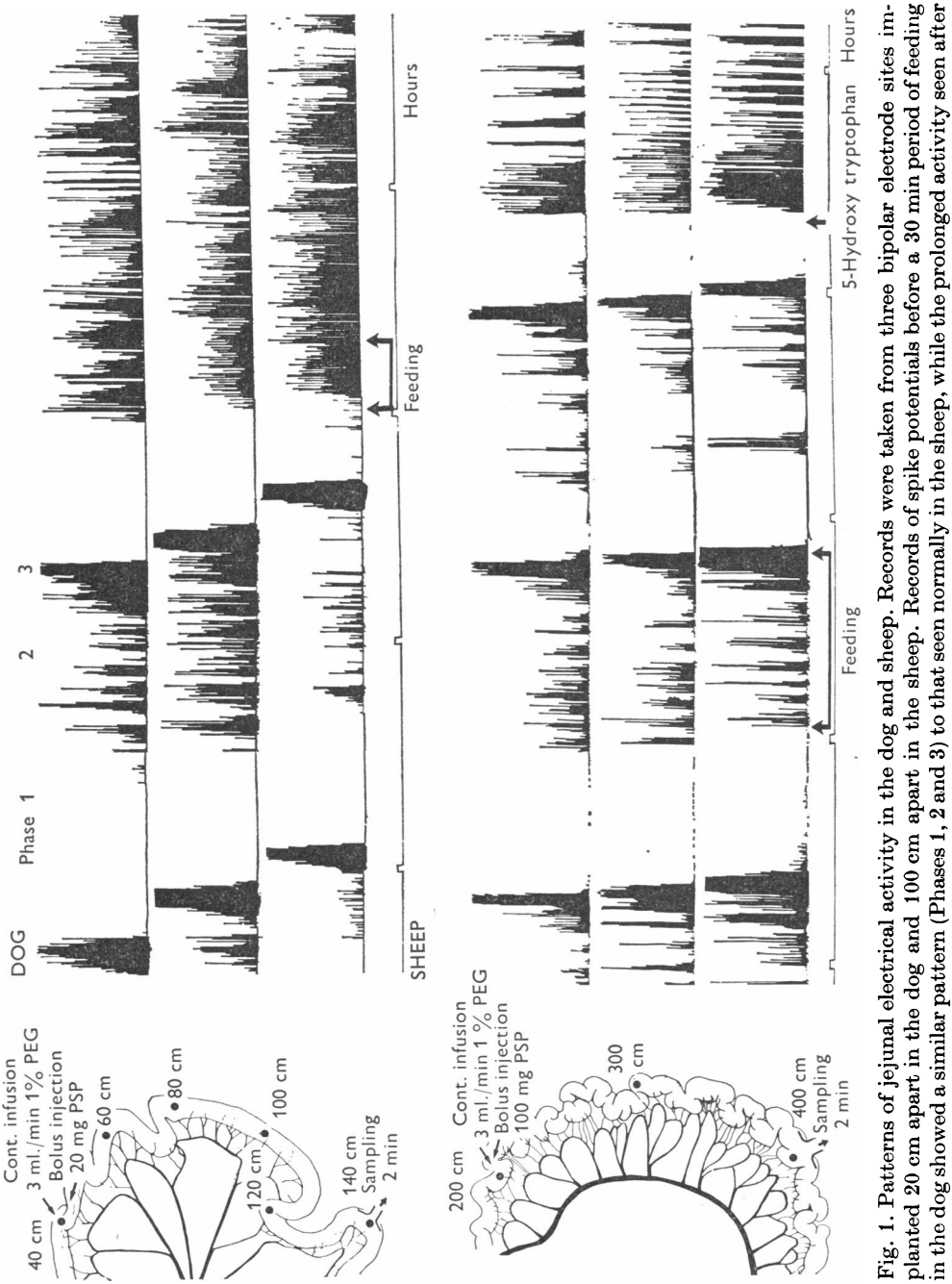

Fig. 1. Patterns of jejunal electrical activity in the dog and sheep. Records were taken from three bipolar electrode sites implanted 20 cm apart in the dog and 100 cm apart in the sheep. Records of spike potentials before a 30 min period of feeding in the dog showed a similar pattern (Phases 1, 2 and 3) to that seen normally in the sheep, while the prolonged activity seen after feeding in the dog resembled that observed after intravenous injection of 5-hydroxytryptophan (5HTP), 2 mg/kg, in the sheep.

TABLE 2. Influence of total flow rate (digesta plus PEG solution) on transit time of a PSP bolus after feeding in three dogs and during activity enhanced by 5-hydroxytryptophan injection in three sheep (mean ± S.D. for three rates of infusion of the test solution)

	3 ml./min		6 ml./min		9 ml./min	
PEG infusion rate	Total flow rate (ml./hr)	Transit time (min/m)	Total flow rate (ml./hr)	Transit time (min/m)	Total flow rate (ml./hr)	Transit time (min/m)
Dog						
0–60 min	640 ± 21	4·1 ± 0·3	746 ± 32	2·2 ± 0·5*		
120–180 min	426 ± 16	4·4 ± 0·1	645 ± 21	3·9 ± 0·2†	791 ± 32	2·1 ± 0·6*
240–300 min	387 ± 18	4·3 ± 0·2	667 ± 34	4·5 ± 0·3†	755 ± 36	2·5 ± 1·2*
Sheep						
0–60 min	455 ± 97	2·2 ± 0·2	620 ± 10	2·3 ± 0·1†	822 ± 20	1·4 ± 0·3*
60–120 min	460 ± 17	2·6 ± 0·1	617 ± 20	2·6 ± 0·2†	841 ± 30	1·2 ± 0·4*

* With changes in the electrical activity patterns relative to 3 ml./min infusion rate.

† Without any change in the electrical activity patterns relative to 3 ml./min infusion rate.

feeding in dogs or after 5-hydroxytryptophan in sheep, the transit time of the PSP bolus when the infusion rate was 3 ml./min was twice as long in dogs (4·1) as in sheep (2·2 min/m). By doubling the infusion rates (6 ml./min), the electrical activity and the transit time were usually unchanged in both species although there was presumably an increase in the volume of luminal contents. A shortening of the transit time was observed when the infusion rate was set at 9 ml./min. These values were significantly different from those seen at lower rates of infusion (Table 2) and corresponded to a transient increase in electrical activity.

The flow rate of digestive contents in the dog decreased from 640 to 387 ml./hr in the period of 5 hr following feeding without major changes in the pattern of electrical activity. The total flow rate at the third and fifth hour after feeding was increased when the infusion rate was 6 ml./min but the transit time changed little. It is therefore unlikely that an infusion rate of 3 ml./min disturbed the intestinal flow rate.

TABLE 3. Relations between the progression parameters, the electrical patterns, feeding and intraperitoneal injection of saline 30 % (w/v), or intravenous injection of 5-hydroxytryptophan, in the small intestine of the dog and sheep

	Transit time (min/m)	Mean velocity of the bolus (cm/min)	Mean flow rate of digesta (ml./hr)
Dog (fasted for 18 hr) (18)*			
inactivity (Phase 1)	23·3 ± 4·1	4·3 ± 2·6	104 ± 26
irregular activity (Phase 2)	6·2 ± 1·3	16·1 ± 3·4	
regular activity (Phase 3)	8·0 ± 2·0	12·5 ± 3·1	
Dog (after feeding) (18)*	4·3 ± 1·6	23·2 ± 8·6	333 ± 78
Dog (after saline) (5)*	46·1 ± 16·2	2·2 ± 0·5	52 ± 21
Sheep (normal regimen) (30)*			
inactivity (Phase 1)	18·0 ± 5·8	5·3 ± 1·6	380 ± 72
irregular activity (Phase 2)	5·7 ± 1·6	17·5 ± 4·1	
regular activity (Phase 3)	8·2 ± 2·3	12·2 ± 3·4	
Sheep (after 5-hydroxytryptophan) (7)*	2·4 ± 0·2	83·3 ± 7·1	277 ± 14
Sheep (after saline) (5)*	72·5 ± 15·2	1·3 ± 0·3	20 ± 22

* Number of observations.
The test solution was infused at 3 ml./min.
Values shown are mean ± S.D. of the observations.

Transit time and patterns of electrical activity. Major differences in the transit time were observed according to the phase of the migrating myoelectric complex at which the PSP bolus was given. When the bolus was given to the fasted dog at the end of the irregular spiking phase (Phase 2), just before the regular spiking phase began, the transit time was only

6·2 min/m. However, when it was administered during the inactive phase (Phase 1) that immediately followed the regular spiking phase, the transit time was lengthened to 23·3 min/m, a 73 % reduction in velocity (Table 3). A similar phenomenon was observed in sheep with a similar reduction, 69 %, in the velocity.

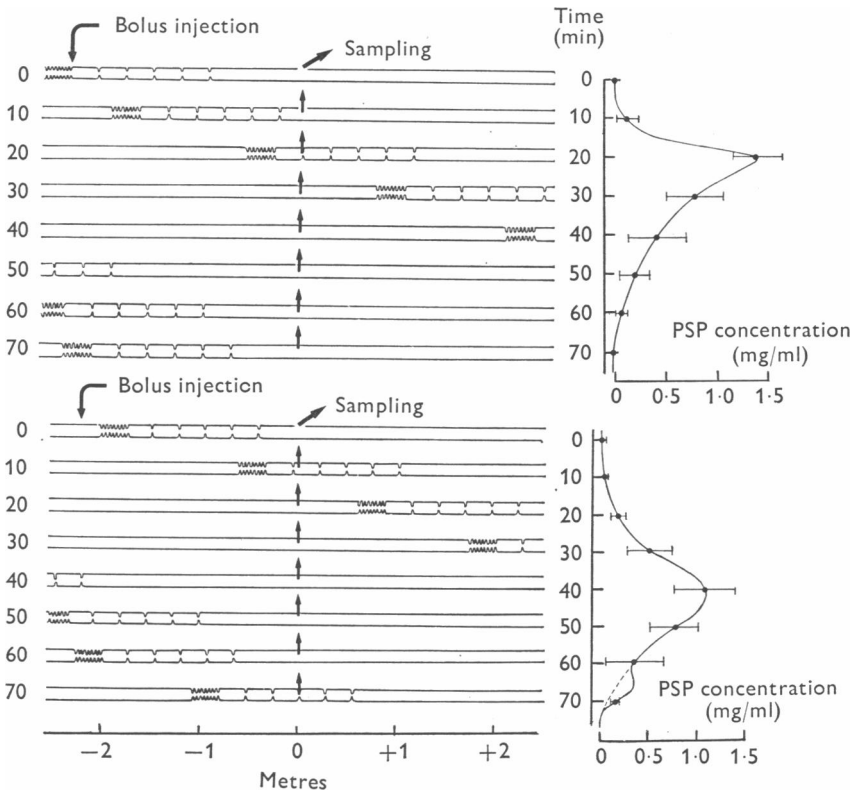

Fig. 2. Phenolsulphonphthalein, PSP, concentration profile (mean ± S.D.) from twenty-five experimental dye dilution curves in one sheep. Diagrammatic representation of the migrating myo-electric complex to illustrate its different phases in the jejunum. The bolus was injected before (top tracing) or after (bottom tracing) the passage of phase 3 of the migrating myo-electric complex indicated by frequent corrugation. The sampling was performed at 2 min intervals, 2 m downstream, but for clarity only the 10 min samples are shown.

Fig. 2 is a diagrammatic representation of the mechanism of PSP propulsion when the dye was injected before and after the regular spiking phase. When transition from irregular to regular activity was imminent, the PSP concentration curve was almost normal for a constant rate of flow with its sudden upswing and exponential decrease (top tracing). When

the injection was made after the regular spiking phase, i.e. during the quiescent phase, the dye appeared later and was less concentrated. The shape of the curve indicated a longer transit time. In some cases a small peak on the tail-end of the bolus curves corresponded (bottom tracing) to the approach of the following migrating myo-electric complex.

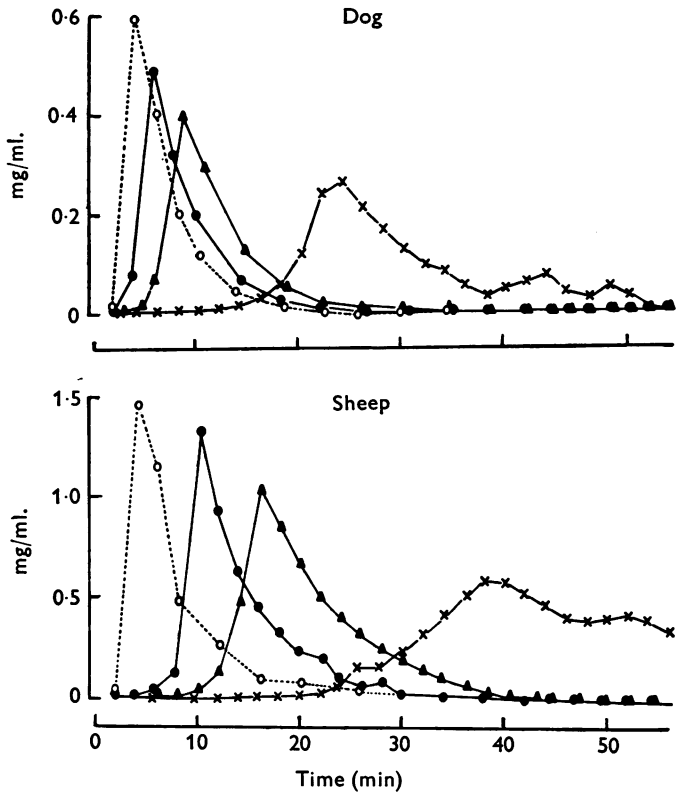

Fig. 3. Comparative PSP dilution curves with sampling done at 1 m downstream from the point of injection in dogs and 2 m downstream in sheep. Injections were made before (filled circles), during (triangles) and after (crosses) the phase of regular spiking activity (Phase 3) in fasted dogs and in sheep. A greater velocity was induced by feeding in dogs or by injection of 5-hydroxytryptophan in sheep (dashed line).

An injection of the PSP bolus during the regular spiking phase gave intermediary values for the mean transit time and PSP peak concentration. In all cases the transit time was shorter after feeding in dogs or after the injection of 5-hydroxytryptophan in sheep (Fig. 3).

Correlation between the mean velocity of the PSP bolus and that of the propagation of the migrating myo-electric complex was almost linear in

sheep (r = 0·91) when the injection was made before the regular spiking phase. In dogs there was no significant correlation (r = 0·06). The PSP bolus transit time (16·1 ± 3·1 cm/min) was about four times greater than the velocity of propagation of the migrating myo-electric complex (4·0 ± 1·5 cm/min) (Fig. 4).

Flow rate of digesta and patterns of electrical activity. For a similar pattern of electrical activity the flow rate of digestive contents was about four times faster in sheep than in fasted dogs (Table 3). Feeding changed the flow rate in dogs by establishing a new pattern of continuous, irregular

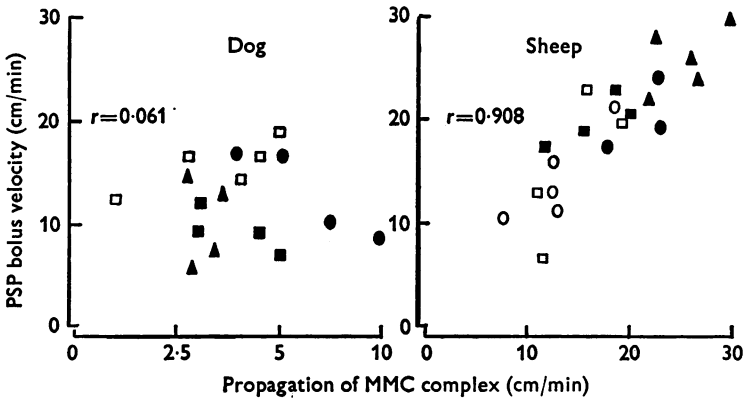

Fig. 4. Relation of the velocities of the migrating myo-electric complex, *MMC*, to the propagation of the PSP bolus in dogs (four) and sheep (five). Note that the abscissa is expanded for the dog values.

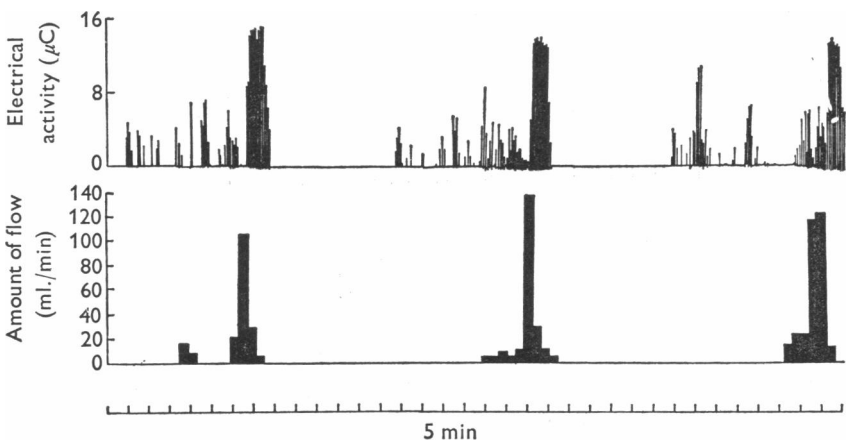

Fig. 5. Volume of digesta collected and jejunal electrical activity recorded at the same level in one sheep. About 75 % of the outflow occurred just before and at the transition to regular spiking activity.

spiking activity. After feeding, the flow rate reached a level almost as high as in sheep (333 *v.s.* 380 ml./hr) even when the spiking activity pattern was markedly different.

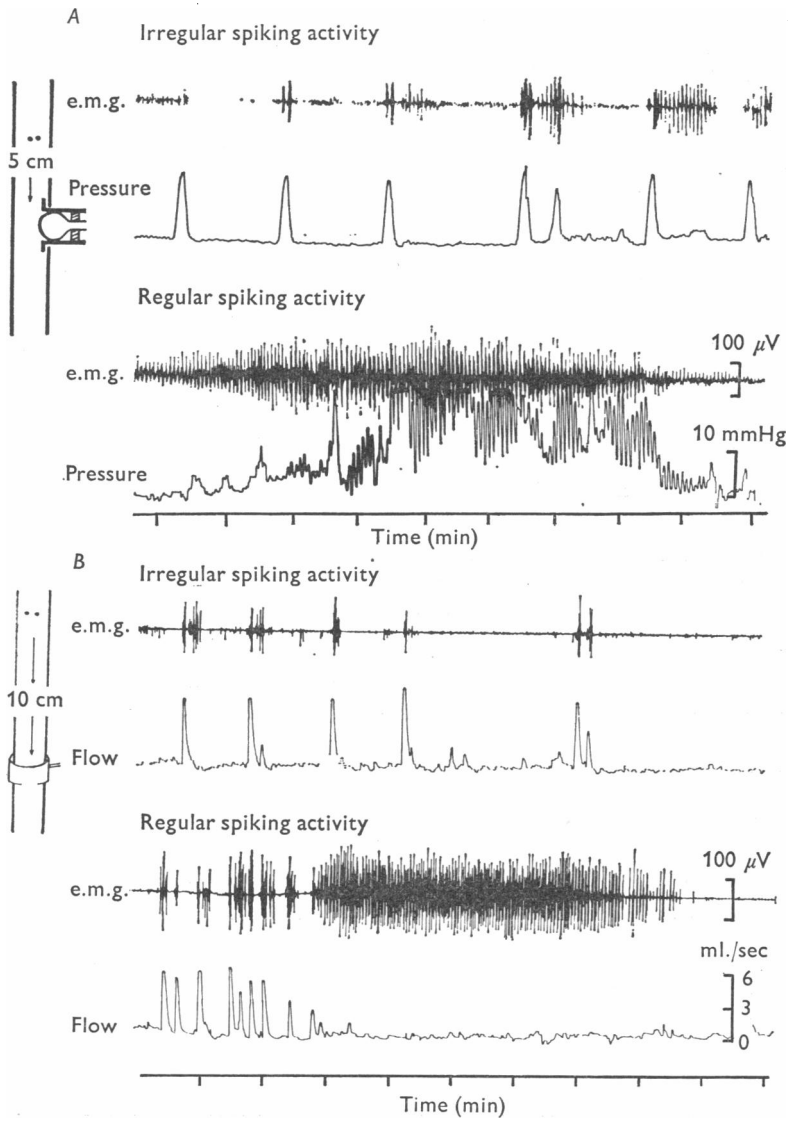

Fig. 6. Pressure changes and passage of digesta during irregular and regular spiking phases. (*A*) Each group of spike bursts was followed by an increase in pressure. During regular spiking activity the pressure changes were superimposed on an elevated base line. (*B*) Passage of digesta occurred at each group of spike bursts during irregular spiking activity but no flow was registered during regular spiking activity.

Opening of the cannula in the sheep showed that the greatest flow of contents occurred during the second half of the irregular phase of spiking activity recorded at the level of the cannula (Fig. 5). The flow progressively increased to a peak and suddenly diminished at the transition to the regular spiking activity (Fig. 5). The flow occurred as an intermittent stream lasting for 10 min and briefly interrupted from time to time by periods of shorter and shorter duration (from 20–40 to 8–10 sec).

When hypomotility was induced by intraperitoneal injection of saline the velocity of the PSP bolus remained twice as fast in dogs as in sheep and the flow rate of digesta was reduced to 52 ml./hr in dogs and 20 ml./hr in sheep (Table 3).

Intraluminal pressure and the passage of digesta. During irregular spiking activity, the pressure changes (obtained from a point 5 cm below one electrode site) related to groups of spike bursts were characterized by peaks of 5–10 sec duration and of 10–15 mmHg amplitude. During the regular spiking phase, pressure variations occurred on an elevated base line (Fig. 6*A*).

The passage of digesta was detected, using a flow transducer 10 cm below the electrode site, as a series of interrupted movements related to groups of spike bursts during the irregular spiking activity. Flow rate varied from 2 to 6 ml./sec (Fig. 6*B*). Both the amount of flow and the frequency of occurrence increased during the transition to the phase of regular spiking activity during which no flow occurred. Back flow was only exceptionally recorded, no more than one to three times per day and usually at the end of a period of regular spiking activity. More detailed analysis showed that occasionally some groups of spike bursts intermingled with the regular spiking activity. In this case, some flow was detected.

Each migrating myo-electric complex had its own configuration with its individual effect on propulsion. Slow speed records in which electrical activity was integrated at 20 sec intervals (Fig. 7) showed the variations between consecutive migrating myo-electric complexes clearly. The number of passages of digesta during the irregular spiking phase was directly related to the length of this phase. A progressive increase in flow occurred during this period due to increases in both the volume and the frequency of passage. At the transition to the regular spiking phase the record of flow became continuous. In the course of a normal regular spiking phase, and for the first 10 min of the quiescent phase which followed, no flow could be detected.

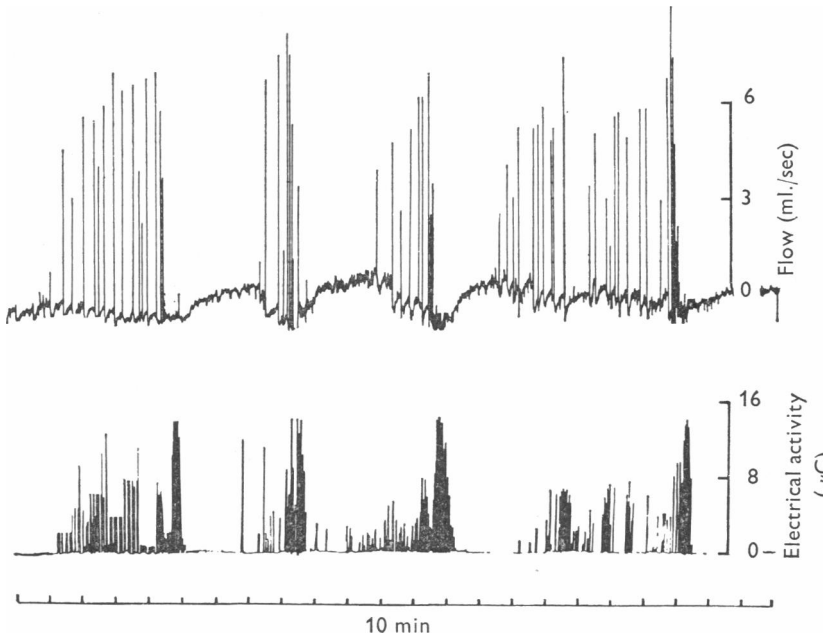

Fig. 7. Patterns of flow associated with migrating myo-electric complexes recurring at different intervals. The passage of digesta was registered by an electromagnetic transducer. An increase in the volume and frequency of digesta flow during the course of the irregular spiking phase can be seen.

DISCUSSION

With the use of integration of spike bursts at 20 sec intervals, it is relatively easy to follow the alternation of quiescent and spiking phases of the small intestine. The duration of the migrating myo-electric complex is almost identical in fasted dogs and in sheep on a normal diet. Under these conditions their aboral propagation past specific electrode sites can be predicted.

The use of a multitube device for injection and sequential sampling of intestinal perfusion fluids as practised in man by Dillard, Eastman & Fordtran (1965) necessarily limits the study to a short (20 cm) length of intestine. Our experiments, using PSP to measure transit time and PEG dilution for flow rate, examined greater lengths of intestine, the distance between injection and sampling sites being 1 m in dogs and 2 m in sheep. In the dog 1 m represents about 50 % of the length of the small intestine and allows good mixing of both markers. In sheep 2 m, about 10 % of the small intestine, permits with frequent sampling an accurate determination of the peak of the PSP concentration curve.

By noting the electrical activity at the first electrode site a PSP bolus

may be injected by the catheter located at the second electrode site at a known phase of the migrating myo-electric complex. Although PSP is readily absorbed by the intestinal mucosa it can be used to measure transit time provided this is registered as the time to reach peak concentration rather than by calculation of mean transit time (Zierler, 1958). PEG is suitable as an indicator for flow measurement because it is poorly absorbed (Soergel & Hogan, 1967).

Direct measurement of the volume of contents via the cannula was limited to 2–4 hr periods to reduce major effects on the distal empty section. During this relatively short period no development of abnormal electrical activity was observed.

The rate of propulsion of a PSP bolus in sheep or fasted dogs is obviously dependent upon the phase of the migrating myo-electric complex. In both species, the velocity is about three times faster when the bolus is injected before the regular spiking phase than subsequently. Similar preliminary observations have been reported recently using an ileal Biebl loop and ^{51}Cr tracer in dogs (Summers & Helm, 1974). In sheep, the mean velocity of a PSP bolus injected before the regular phase parallels that of the propagation of the migrating myo-electric complex. This is not the case in the fasted dog where the velocity of a similar PSP bolus is four times faster than the propagation of the migrating myo-electric complex. Possibly the thickness of the dog's intestinal wall favours the development of a cylindrical shape thus lessening its resistance to the onward passage of a bolus of digesta. Another possibility is that the intestine contracts more powerfully. The sheep's intestine is relatively thin walled and dilated segments containing digesta are separated by variable lengths of collapsed intestine with almost no lumen. It may be that the effective propulsive part of the migrating myo-electric complex is located at the junction between collapsed and dilated intestine and impresses its velocity on the bolus. Direct measurements of the volume of digesta passing a cannula in sheep confirm that almost all the contents flowed in advance of the regular spiking phase of the migrating myo-electric complex. A similar pattern of flow probably persists as far as the terminal ileum since digesta are expelled from an open ileal cannula as a rapid series of discrete boli at intervals of 1–2 hr (Goodall & Kay, 1965).

Measurements from the flow transducer and pressure records suggest that the digesta cannot move backward due to the increased luminal pressure observed during the phase of regular spiking. Thus the contractions seen towards the end of the irregular spiking phase become more and more efficient for the propulsion of digesta. This may explain why a stream of contents is collected from an open cannula at this time. It is likely, however, that the resistance to flow of the T-shaped cannula and of the

20 cm tubing used for collection of the digesta may have caused a fusion of the many individual gushes.

Continuous regular spiking activity as produced in dogs after feeding or in sheep after injection of 5-hydroxytryptophan is associated with the most rapid propulsion of the bolus. On the other hand, absence of activity induced by intraperitoneal injection of hypertonic NaCl is accompanied by a very slow transit time. The flow of digesta then recorded represents movement of intestinal contents solely due to the pressure gradient developed in the absence of any spiking activity. During such hypomotility, the transit time is shorter and the flow rate more rapid in dogs than in sheep.

Such an artifact was not observed when the passage of digesta was recorded by means of a flow transducer that did not impede the flow.

The significance of each phase of the migrating myo-electric complex is not yet fully understood. For Code & Schlegel (1974) there are four phases in the migrating myo-electric complex of the fasting dog, with Phase 3, the 'interdigestive housekeeper', being the propulsive one. Our results indicate that this is equivalent to our Phase 3, the regular spiking activity. The presence of the migrating myo-electric complex in normally-fed sheep suggests that this concept should be reconsidered, at least for such herbivorous species in which there is no interdigestive period.

In the dog after feeding, irregular spiking activity becomes continuous, replacing the migrating myo-electric complex, and digesta are propelled more rapidly than in the sheep. However, equally rapid flow rates are recorded in the sheep when continuous irregular spiking is produced by injection of 5-hydroxytryptophan.

Finally, it seems that the sheep, unlike the fasted dog, cannot propel the digesta faster than the regular spiking phase of the migrating myo-electric complex which thus acts as a regulating factor. The transition from irregular to regular activity marks the effective point of propulsion. This does not exclude the possibility that individual boli may be propelled more rapidly than the migrating myo-electric complex over short lengths of the intestine by peristaltic contractions.

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REFERENCES

BARREIRO, M. A., MCKENNA, R. D. & BECK, I. I. (1968). Determination of transit time in the human jejunum in the simple injection indicator-dilution technique. *Am. J. dig. Dis.* **13**, 222–232.

BASS, P. (1968). In vivo electrical activity of the small bowel. In *Handbook of Physiology*, section 6, ed. CODE, C. F., pp. 2051–2071. Washington: American Physiological Society.

CODE, C. F. & SCHLEGEL, J. F. (1974). The gastrointestinal housekeeper. Motor correlates of the interdigestive myoelectric complex of the dog. In *Proc. Fourth Int. Symp. on Gastro-Intestinal Motility*, pp. 631–634. Vancouver, B.C.: Mitchell Press Ltd.

DILLARD, R. L., EASTMAN, H. & FORDTRAN, J. S. (1965). Volume-flow relationship during the transport of fluid through the human small intestine. *Gastroenterology* **49**, 58–66.

GOODALL, E. D. & KAY, R. N. B. (1965). Digestion and absorption in the large intestine of the sheep. *J. Physiol.* **176**, 12–23.

GRIVEL, M. L. & RUCKEBUSCH, Y. (1972). The propagation of segmental contractions along the small intestine. *J. Physiol.* **227**, 611–625.

HARRISON, F. A. & HILL, K. J. (1962). Digestive secretions and the flow of digesta along the duodenum of the sheep. *J. Physiol.* **162**, 225–243.

HOGAN, J. P. & PHILLIPSON, A. T. (1960). The rate of flow of digesta and their removal along the digestive tract of the sheep. *Br. J. Nutr.* **14**, 147–155.

HYDEN, S. (1955). A turbidimetric method for the determination of higher polyethylene glycols in biological materials. *K. LantbrHögsk. Annlr* **22**, 139–145.

LATOUR, A. (1973). Un dispositif simple d'analyse quantitative de l'electromyogramme intestinal chronique. *Ann. Rech. veter.* **4**, 347–353.

RUCKEBUSCH, M. & FERRÉ, J. P. (1974). Origine alimentaire des variations nycthemerales de l'activité electrique de l'intestin grêle chez le rat. *C. r. Séanc. Soc. Biol.* **167**, 2005–2009.

RUCKEBUSCH, Y. (1970). The electrical activity of the digestive tract of the sheep as an indication of the mechanical events in various regions. *J. Physiol.* **210**, 857–882.

RUCKEBUSCH, Y. & BUENO, L. (1973). The effect of weaning on the motility of the small intestine in the calf. *Br. J. Nutr.* **30**, 491–499.

SOERGEL, K. H. & HOGAN, W. J. (1967). On the suitability of poorly absorbed markers as dilution indicators in the gastrointestinal tract. *Gastroenterology* **52**, 1056–1057.

SMITH, R. H. (1964). Passage of digesta through the calf abomasum and small intestine. *J. Physiol.* **172**, 305–320.

STOBO, I. J. F., ROY, J. H. B. & GASTON, H. J. (1966). Rumen development in the calf. 1. The effect of diets containing different proportions of concentrates to hay on rumen development. *Br. J. Nutr.* **20**, 171–185.

SUMMERS, R. W. & HELM, J. (1974). The effects of feeding and the myoelectric complex on transit in the canine small intestine. *Gastroenterology* **66**, *A*-132/786.

SZURZEWSKI, J. H. (1969). Migrating electric complex of the canine small intestine. *Am. J. Physiol.* **217**, 1757–1763.

ZIERLER, K. L. A. (1958). A simplified explanation of the theory of indicator-dilution for measurement of fluid flow and volume and other distributive phenomena. *Bull. Johns Hopkins Hosp.* **103**, 199–205.