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THE ELECTRICAL ACTIVITY OF THE DIGESTIVE TRACT OF THE SHEEP AS AN INDICATION OF THE MECHANICAL EVENTS IN VARIOUS REGIONS

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SUMMARY

1. A method is described in the conscious sheep for recording oscillographically the electrical potentials led from enamelled stainless-steel wires implanted in the wall of the stomach and intestine.

2. Slow waves characterized by cyclically recurring and rhythmic fluctuation in voltage have been recorded, together with the superimposed fast activity or burst of spikes when the muscle is contracting. The whole activity comprised a distinguishable pattern of grouped discharge which is synchronous with mechanical events within different regions of the alimentary tract.

3. Grouped discharge occurs at a regular frequency of 7/min in the pyloric part of the abomasum and 18/min from the intestine, but 13/min from the middle duodenum and proximal ileum. Only the major grouped discharges of the fore-stomach is correlated with the orderly sequential movements of the reticulum and rumen.

4. The relationship between electrical and mechanical activity of the reticulo-rumenal movements was examined at rest, and during feeding and ruminating.

5. Electrical correlates of motor activity in the small bowel were investigated under different dietary regimens.

INTRODUCTION

Much of the present knowledge of the movement of the ruminant stomach has been obtained by balloons or open tipped catheters placed in the various compartments to record pressure changes. The development of methods for partial exteriorization of the reticulum helped investigation of the activity of the ruminant stomach a great deal. More recently the problem of transmitted pressure which occurs in voluminous organs such as the reticulo-rumen has been avoided by the implantation of small polyethylene balloons or strain gauges (Leek & Ullah, 1967; Ehrlein & Hill, 1966).

Omasal activity has been much more difficult to investigate in ruminants. Ohga, Ota & Nakasato (1965) have shown that omasal activity can be divided into contraction of the groove, which occurs regularly at each reticulo-ruminal cycle, and of the body, where contractions are irregular and may be absent for periods of 3–5 cycles.

The motility of the small bowel in sheep was first observed by the open-abdomen saline-bath method (Dukes & Sampson, 1937) and then with open-tipped catheters (Coombe, 1966). Manometric methods have also been used to show the strong peristaltic and anti-peristaltic waves of the caecum (Phaneuf, 1952; Berehoiu, 1966).

In 1922, Alvarez & Mahoney identified the electrical activity of the wall of the digestive tract in the dog and showed that recording the electrical activity of the isolated intestine could be used as an indication of the mechanical activity of the organ. An attempt was made in 1928 by Van der Heyde to apply this method to the rumen of a cow. The mechanical movements of the fore-stomach of goats have been investigated recently by recording the potential changes associated with muscular contraction of the reticulo-rumen (Matsumoto, 1961; Itabisashi & Matsumoto, 1966) or of the stomach (Ruckebusch & Laplace, 1967*a*).

When potential changes are recorded from the jejunal and ileal regions of the sheep intestine, peristalsis rather than segmentation is the main activity, in accordance with the fact that propulsive activity predominates (Ruckebusch & Laplace, 1967*b*).

This paper gives an extended account of an investigation in the conscious sheep to show how the electrical events can be correlated with the mechanical events of the digestive tract.

METHODS

Twenty-one sheep, aged 8–12 months, weighing 30–45 kg were used. Care was taken to select sheep that remained placid in the experimental situation. The individual sheep were retained in modified metabolism cages which allowed free movement but ensured sufficient restraint for the recording techniques. The sheep were fed at 9.00 a.m. each day, the normal feed being hay and water *ad lib*. When necessary (see below) this diet was changed to hay pellets or grain. The amount of food taken daily was measured and the times of eating and rumination were recorded from jaw movements.

Aseptic surgical procedures were always carried out with the animal under thiopentone anaesthesia with endotracheal intubation. The electrodes (120 μ diameter), made from the bared ends of insulated nichrome, were inserted in pairs, 2 mm apart, at the appropriate muscle site and anchored with ligatures to the serosa (Ruckebusch, Grivel & Santini, 1968). Where strain-gauges were used, they were constructed on a frame 2 cm in length and fixed immediately above the corresponding electrode pair. Strain-gauges were connected through a Wheatstone bridge to a direct-writing galvanometer, and muscular electrical activity was recorded by a pen oscillograph (R.C. coupling, T.C. 0·1 sec).

Ruminal movements were measured with air- or water-filled balloons (30 ml.) introduced via rumen cannulae and recorded by a water manometer on a kymograph or by a strain-gauge manometer on a pen recorder.

In three sheep, polyethylene cannulae were placed at appropriate places in the small intestine. Electrodes were established in the muscle 10 cm apart at each end of the T-shaped cannulae, so that the volume of ingesta moved could be correlated with the intestinal muscular activity. By placing a balloon (10 ml.) in the limb of the cannula, pressure events related to the movement of intestinal contents during a peristaltic wave could be recorded continuously with undisturbed flow. Three other sheep were fitted with Thirty-Vella loops (20 cm) of the duodenum and ileum. Electrodes were implanted in pairs 2 mm. apart on the antimesenteric side of the intestine, each pair being separated by 10 cm. Two pairs of electrodes were fixed to the loop and two pairs to the intestine, one pair being placed on each side of the anastomosis.

Observations were made at appropriate times of resting, feeding and rumination, and where necessary for 24 hr periods. All electrode positions were checked post mortem.

RESULTS

The nature of potential changes

Among the changes recorded from electrodes implanted in the muscle wall of the alimentary tract, two types of electrical activity—slow waves and spikes—can be recognized, sometimes with difficulty. The composite group of potential changes is called here 'the group discharge'. This includes slow waves, bursts of spikes and mechanical artifacts due to electrode movement as the muscle coats move. The discharges have been recorded from all sites investigated along the alimentary tract. The greater activity of group discharges is associated with the greatest muscle masses; for example, records from the reticulum and the rumenal pillars are more extensive than from the rumen muscle.

The pattern of the discharges in the sheep is probably similar to the electroenterogram described in the dog (Bass, Code & Lambert, 1961; Daniel & Chapman, 1963) and probably shows the same two components (Ambache, 1947). One component which is rhythmic, cyclically recurring, not associated with muscular contraction and propagated down the alimentary tract, varies in rate of propagation in different parts of the tract. The second component consists of a burst of spikes which occur immediately after the slow wave and vary in number with the strength of contraction of the muscle coats. It is probable that the spikes result from contraction of circular muscle. In the case of the rumen, reticulum and omasum, the complexity of the group discharge may be due to the variable architecture of the muscle layers.

The relation of group discharge to pressure change

The reticulum and rumen

The group discharge of the rumen pillars and the reticulum is not well defined for the 2 or 3 days after implantation of electrodes. Abnormal discharges from these sites occur for 48 hr and these may be due to the irritant effect of the electrodes on the very excitable muscle. The less excitable rumen does not show these 'noise-like' artifact potentials. Abnormal discharges from the reticulum which are at first continuous become periodic, to form small and major group potentials (Fig. 1).

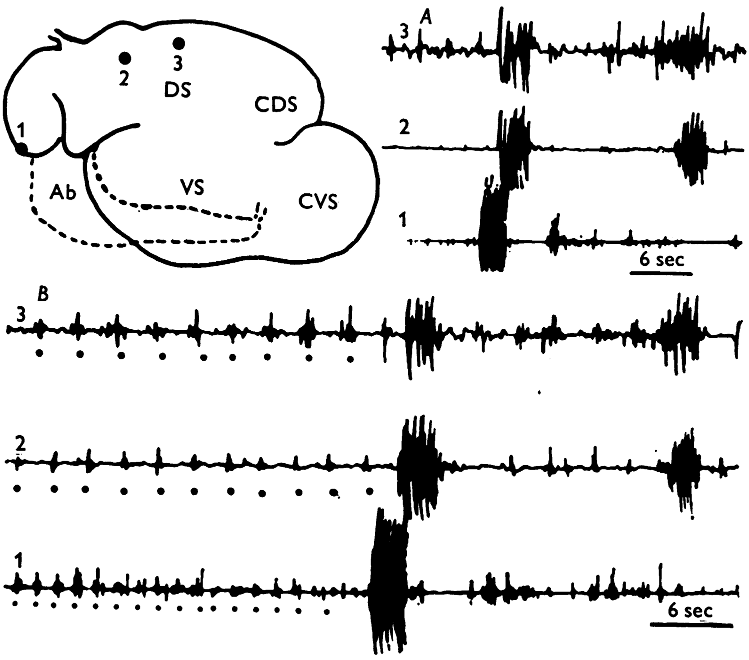

Fig. 1. Grouped discharge from three different points of the stomach. The points of electrode placement are shown in the diagram of the stomach and examples of the appropriate records are illustrated. In *A*, the records were made 3 weeks after electrodes were placed and, in *B*, only 1 week later. Small grouped discharges are indicated by dots. DS and VS, dorsal and ventral sac of rumen: CDS and CVS, caudo-dorsal and caudo-ventral sac of rumen; Ab, abomasum. Time scale: 6 sec.

The periodicity of small group discharges varies in different localities of the reticulo-rumen. The rate is highest in the reticulum (about 40/min), less in the ruminal pillars (25–30/min) and less still in the dorsal sac (18–28/min) and the main ventral sac of the rumen (15/min). This rate of activity was seen in both the full and the empty rumen. In addition to these small group discharges, a second one of much greater magnitude can be recorded at about 60 sec intervals from the reticulum and rumen. In the rumen, including the pillars, this major discharge may occur at about 30 sec intervals.

The group discharge associated with the contraction of the reticulum is biphasic like the pressure changes. On rumination, an extra contraction

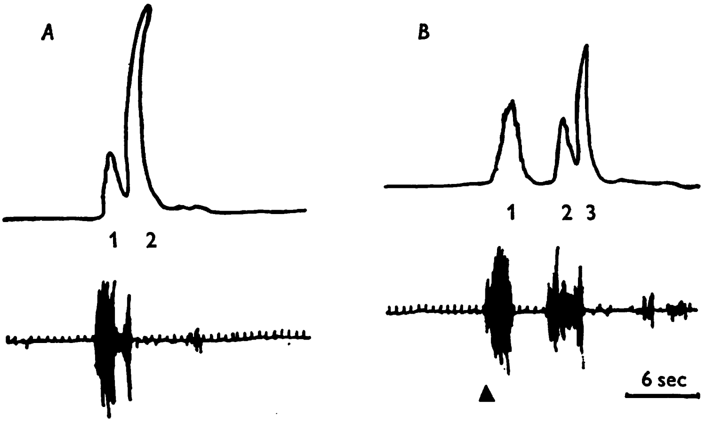

Fig. 2. Shows the correlation of electrical activity of the reticulum with pressure records. In *A*, the upper trace shows the double contraction of the reticulum with an associated group discharge. In *B*, the extrareticular contraction which occurs with rumination has its own group discharge (▲). Time scale: 6 sec.

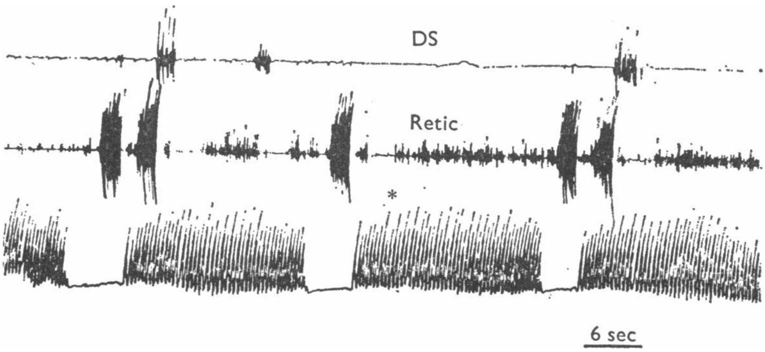

Fig. 3 Shows the events of rumination. The group discharge of the dorsal sac is recorded on the upper trace (DS) and that of the reticulum on the second trace (Retic). The lower trace is that of jaw movements. The discharge of the first reticular contraction occurs with the regurgitation phase of rumination while that of the second contraction occurs only after remastication has commenced. * Shows that the reticular contraction associated with regurgitation can occur alone. Time scale: 6 sec.

of the reticulum usually occurs and is accompanied by an extra single phase of group discharge (Fig. 2). Occasionally, the reticular contraction is single and then the discharge is also single. In this event, the rumen contraction following is weak and its group discharge is small or missing (Fig. 3).

The major group discharge was directly related to pressure changes recorded from the reticulo-rumen. The number of spikes and the time course of such a discharge gives a good index of the strength of the contraction. The relationship between rumino-reticular group discharge and the pressure in the dorsal sac of the rumen during primary and secondary movements is illustrated in Fig. 4. The number of spikes and the duration of the discharge for a secondary movement of the rumen are about 30–50 % less than for the primary contraction associated with the reticulum contraction.

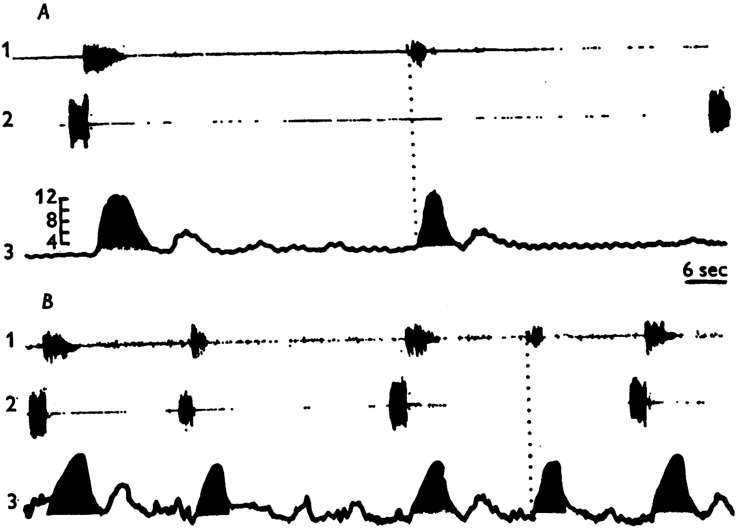

Fig. 4. Relationship between pressure changes and group discharge in the dorsal sac of the rumen. Traces from top to bottom: group discharge from rumen (1) and from reticulum (2); 3, pressure recorded by a water-filled balloon in dorsal sac of rumen. In *A*, the sheep is standing at rest and, in *B*, it is feeding. The duration of rumen pressure changes does not exceed 6 sec and the time course of the group discharge of rumen is about 2–3 sec. The discharge of the reticulum delimits a reticulo-ruminal cycle which can be seen to be much shorter during feeding. The secondary contraction of rumen with its related discharge is seen in both *A* and *B* (dotted line). Time scale; 6 sec; pressure scale in cm H_2O.

It appears from the correlation of pressure effect and the group discharge that its slow wave component triggers the spikes and the spikes are associated with contraction of the muscle. To test the electrical correlates of motor activity, it was shown that the sustained contraction of the wall of the reticulum evoked by acetyl-β-methylcholine (3 μg/kg; I.V.), is accompanied by a prolonged discharge of spikes.

The minor group discharge (see Fig. 1) does not persist for longer than about a week and this is probably due to encasement of the electrodes in fibrin which prevents the adjacent muscle fibres from contracting. To test this hypothesis a preparation was devised in which three pairs of electrodes

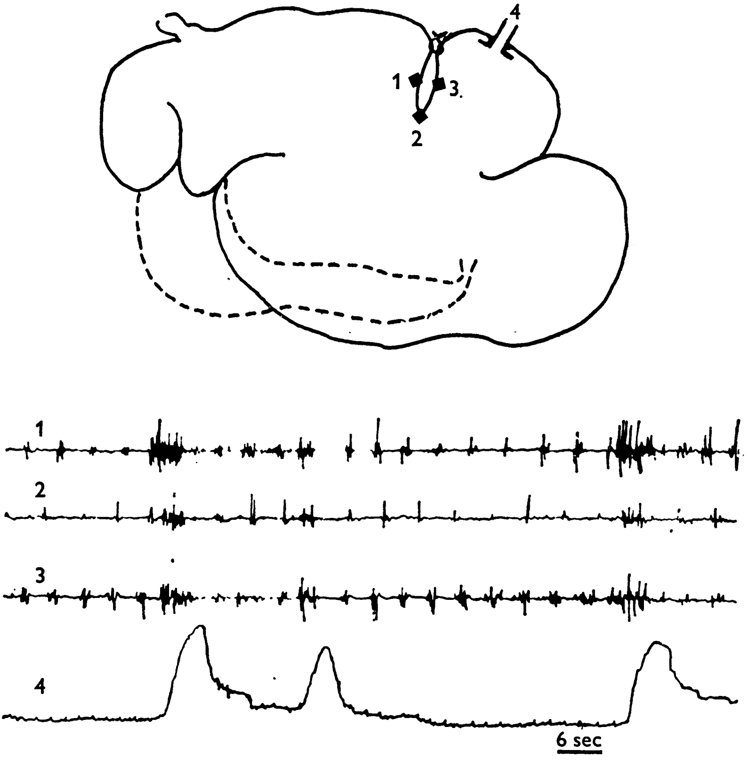

Fig. 5. Recording from an invaginated fold of rumen made to prevent movement of electrodes (see text). The upper three records show group discharge from electrodes placed as in diagram. The lower trace shows pressure change in the dorsal sac of the rumen. Time scale: 6 sec.

were placed on the rumen wall with these electrodes infolded and fixed with sutures to prevent movement occurring with rumen distension. Under these circumstances the small group discharge persisted for many weeks which suggests that loss of electrode reactivity is due to stimulation of pathological reaction from movement of the implanted wire (Fig. 5).

Recordings of the major group discharge persisted for many weeks without change although eventually the spikes were lost. The sequential pattern of pressure changes within the reticulum and rumen is well correlated with the recordings (see Figs. 2 and 4). The secondary cycle is apparently generated from an area adjacent to the longitudinal pillar which contracts before the dorsal sac. During the primary cycle, the sustained contraction of the reticulo-ruminal fold after the contraction of reticulum is illustrated in Fig. 6. Contractions of the caudo-ventral sac are usually, but not always, associated with the primary or secondary cycle of contraction.

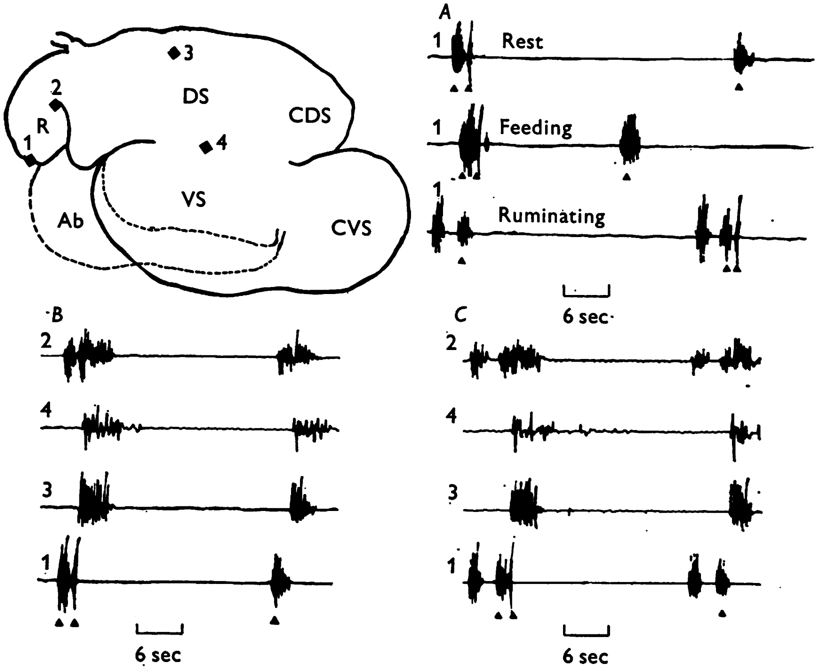

Fig. 6. Group discharge recorded from reticulum and rumen. The diagram shows the electrode positions. In *A*, the record illustrates from top to bottom typical group discharge from biphasic (▲▲) and single (▲) contractions of the reticulum only, when the sheep was at rest, during food intake or ruminating. The extra-contraction of the reticulum is well illustrated when the animal is ruminating. In *B*, the sequential pattern of muscular contraction of the reticulum, the reticulo-ruminal fold, the dorsal sac and the longitudinal pillar of the rumen (1 to 4) is illustrated with the animal at rest. In *C*, the pattern of rumination is illustrated. Time scale: 6 sec. Abbreviations as in Fig. 1.

The speed of conduction is more rapid in the primary cycle of contraction than in the secondary cycle, the rate of spread in the former being

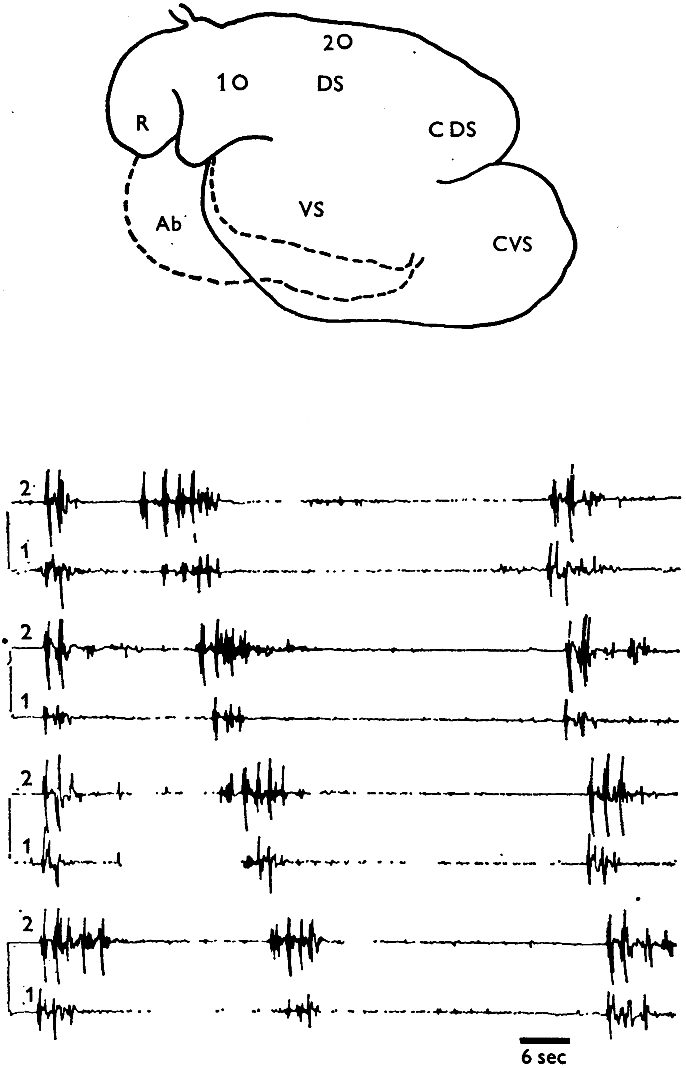

Fig. 7. Group discharge recorded from two pairs of electrodes implanted on the dorsal sac of rumen. A series of four selected records shows that the rate of contractions varies. The primary waves passing to the posterior, associated with and following contractions of the reticulum, are relatively faster than the retrograde secondary waves. From top to bottom for a ruminal cycle of about 60 sec, the retrograde wave occurs at increasing intervals. This variation may be in relation with the amount of food in the rumen and with the state of sleep and wakefulness. Time scale: 6 sec. Abbreviations as in Fig. 1.

2–6 cm/sec while, in the latter, the rate is only 0·9–1·3 cm/sec. The variable rate of the spread of contraction is seen in Fig. 7 which also illustrates that the secondary cycle can occur from 12 to 49 sec after the primary one.

The influence of the adjacent area on the group discharge was examined by making a horizontal incision of 10 cm along the rumen wall (serosa and muscle coats) at the level of the longitudinal pillar on the left side. In such a situation, only small group discharges occurred distal to the section. Above it, the major discharge of the primary cycle is associated normally with the reticulum contraction (Fig. 8).

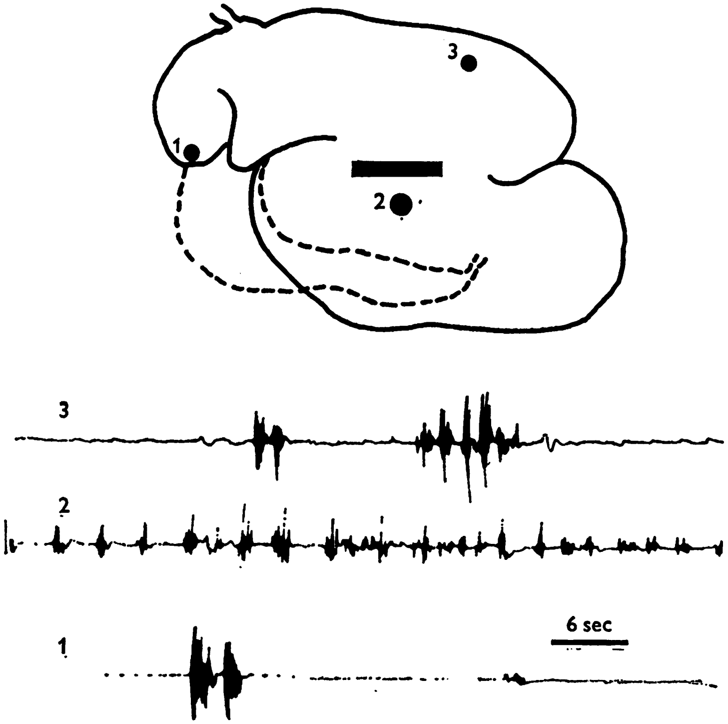

Fig. 8. Group discharge from the reticulo-rumen after a section of the muscular coat. Diagram shows the electrode positions and the size of the section. The group discharge of the primary contraction of the dorsal sac of the rumen (3) following the biphasic discharge of reticular contraction (1) and that recorded before the section are shown. No major group discharge is seen from electrode (2) but only small periodic fluctuation of potentials. Time scale: 6 sec.

The fact that section of the nerves which are distributed along with the left ruminal artery produces a similar effect, suggests that the major group discharge is a complex of small ones co-ordinated by periodic nerve impulses carried by extrinsic nerves.

The omasum

The group discharge of the omasum was difficult to record because the movement of this organ tended to displace the electrodes. A series of slow waves with few spikes were recorded. This type of discharge was recorded from many areas of the omasum including the right and left sides of the greater curvature as well as from the omasal groove near to the reticulo-omasal orifice. The omasal group discharge was of about 12 sec duration. If the assumption is made that such an occurrence is indicative of the contractions of the organ then contraction occurs first at the omasal groove, from which it extends to the body. The omasal contraction occurs before the contraction of the reticulum (Fig. 9).

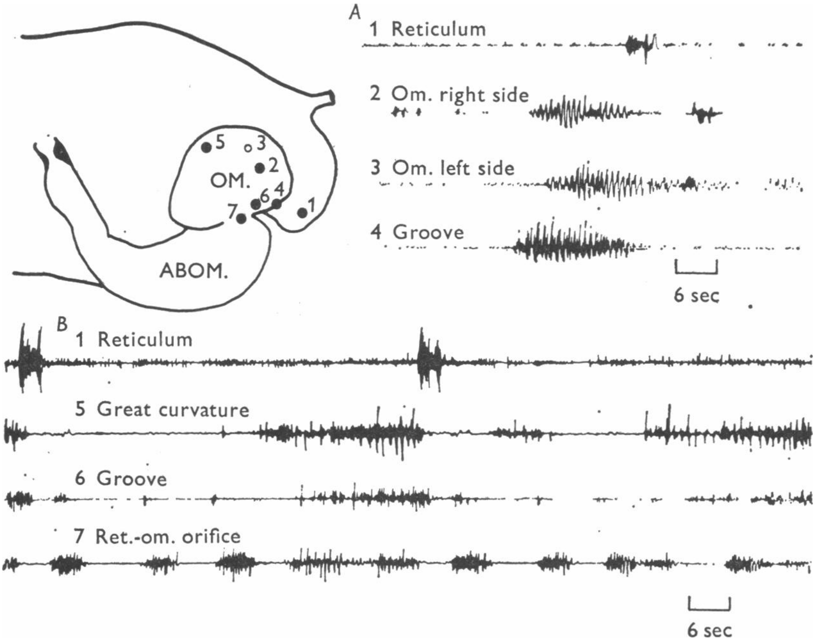

Fig. 9. Group discharge recorded from reticulum and omasum. In *A*, all electrodes on the omasum show activity preceding that of the reticulum. In *B*, the electrical activity near the reticulo-omasal orifice shows contraction at 6–8 sec intervals probably indicating opening and closing (see text). Time scale: 6 sec.

The group discharge recorded from the omasum shows a train of slow waves, about twenty in number, at 0·8–1·2 sec intervals with spike potentials occurring throughout. With feeding the omasum shows greater activity and this is reflected in the group discharge recorded. It may persist over a whole reticulo-ruminal cycle or only part of it but no organization was apparent from the records. When food is withheld the omasal discharge is very much shortened or may not occur. During rumination the omasal activity is similar to or slightly greater than that of an animal at rest. Immediately before the cessation of rumination it is different. It is prolonged and is associated with a long contraction of the omasum, which probably discharges most of the fluid contents of the organ to the abomasum.

Records of group discharge from the omasal groove and the reticulo-omasal orifice are shown in Fig. 9. A periodic group discharge occurs at about 6–8 sec and the muscle is always relaxed during the contraction of the reticulum. The discharge of the omasal orifice, however, may be misleading with regard to the mechanical events, for endoscopic examination when the reticulum is contracted shows the orifice to be closed. This closure may be due to the distortion of the musculature of the oesophageal groove, which surrounds this orifice, during contraction of the reticulum.

The abomasum

Group potentials were recorded regularly from the pyloric antrum of the abomasum (Fig. 10). These group discharges occurred two or three times with each reticulo-ruminal cycle. Normally none was recorded from the fundic part of the abomasum, including the greater curvature. The antral discharge consisted of a slow wave with a burst of spikes at a frequency of approximately 7/min. Feeding or the sight of food increases the electrical activity, indicating increased muscular activity and irregular activity of the fundus. The injection of adrenaline causes relaxation of the abomasal antrum and this affects the group discharge: the spikes are abolished but the slow waves persist and are reduced in amplitude. The interval between the discharges is prolonged (Fig. 10).

The velocity of propagation of the wave of contraction in the abomasal antrum is about 5 cm/sec. When a group discharge is recorded simultaneously from the duodenal bulb, there is no regular transmission of the abomasal wave of contraction to the duodenum (Fig. 11). Some correlation of pyloric and duodenal contractions does occur, however, as can be seen in Fig. 11. It is possible that these records may have an element of artifact in the group discharge but more probably they indicate propulsive activity throughout the gastro-duodenal junction. It is not possible to be emphatic on this point as records have been made from only two sheep.

The small intestine

The correlated activity of the anterior duodenum is seen in Fig. 11 where discharges recorded from three points indicate different types of activity. They may occur only in a restricted length of the duodenum or

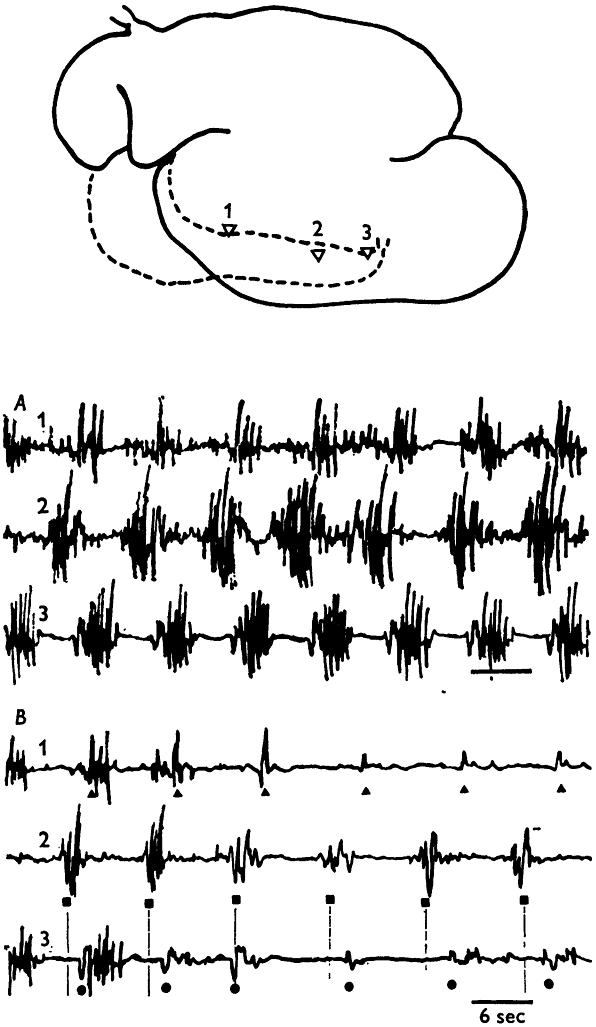

Fig. 10. Group discharge from the abomasum during eating. Position of electrodes on diagram shows: (1) lesser curvature, (2) 10 cm anterior to pylorus, (3) 2 cm anterior to pylorus. In *A*, rhythmic group discharges are seen in the abomasal antrum. In *B*, the inhibition of the spikes of the discharge and an increase in the interval between those at 1 (▲) and at 2–3 (■ ●) is illustrated following the i.v. injection of adrenaline (7 μg/kg) at the beginning of the record.

may be recorded over greater lengths and be associated with propulsive movement of chyme. They may also show antiperistaltic waves (Fig. 11).

The activity of the middle duodenum has been examined by electrical recording and balloons placed near the recording electrodes via a duodenal

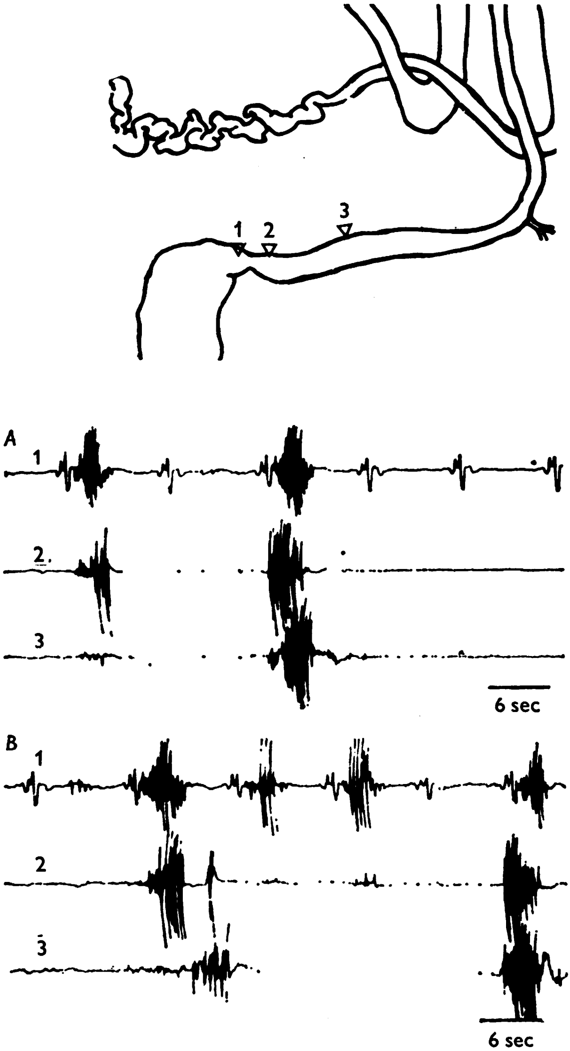

Fig. 11. Group discharge recorded from the pylorus and anterior duodenum. The electrodes are (1) on pylorus, (2) 2 cm distal to the pylorus and (3) 10 cm from the pylorus. In trace 1, the group discharge rhythm is similar to that of the abomasal antrum. The record *A* shows that the group discharge from electrode 2 is correlated with that of the pylorus and occurs both after and then before it. The record *B* shows a typical pattern of peristaltic and anti-peristaltic propagation of the propulsive activity.

cannula. The results are illustrated in Figs. 12 and 13. Usually, a group discharge is correlated with constriction of the duodenum, presumably due to contraction of the circular muscle of the duodenum (Fig. 12). There appears to be a direct correlation of the magnitude of the mechanical event with the electrical activity.

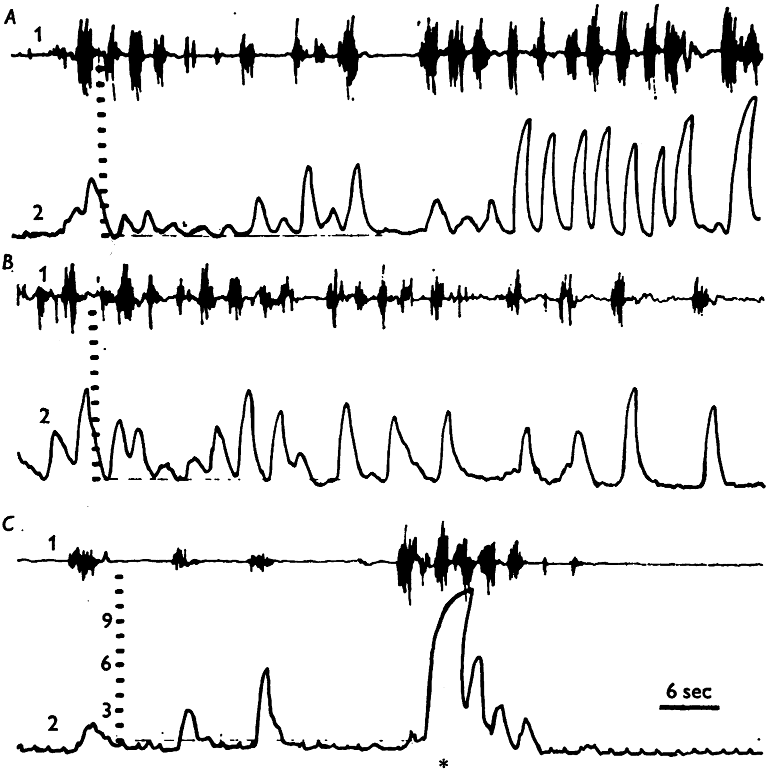

Fig. 12. Electrical and mechanical activity of the middle duodenum. In trace 1, the group discharge is recorded from a pair of electrodes near to the balloon. In trace 2, the intraluminal pressure, measured by a water manometer, is given by the scale (cm.); * indicates a strong wave, presumably propulsive. The pressure changes are related to segmenting activity in *A* and *B*. Time scale: 6 sec.

In the middle duodenum the pattern of electrical activity is complex, with isolated bursts occurring at uncorrelated points. When the electrical events were correlated with the physiological event, a peristaltic wave with propulsion of chyme, they occurred continuously for 2–5 min. When the electrical records indicated non-propagated activity of the gut, there is only a tonal pressure change. This was verified by examining whether or

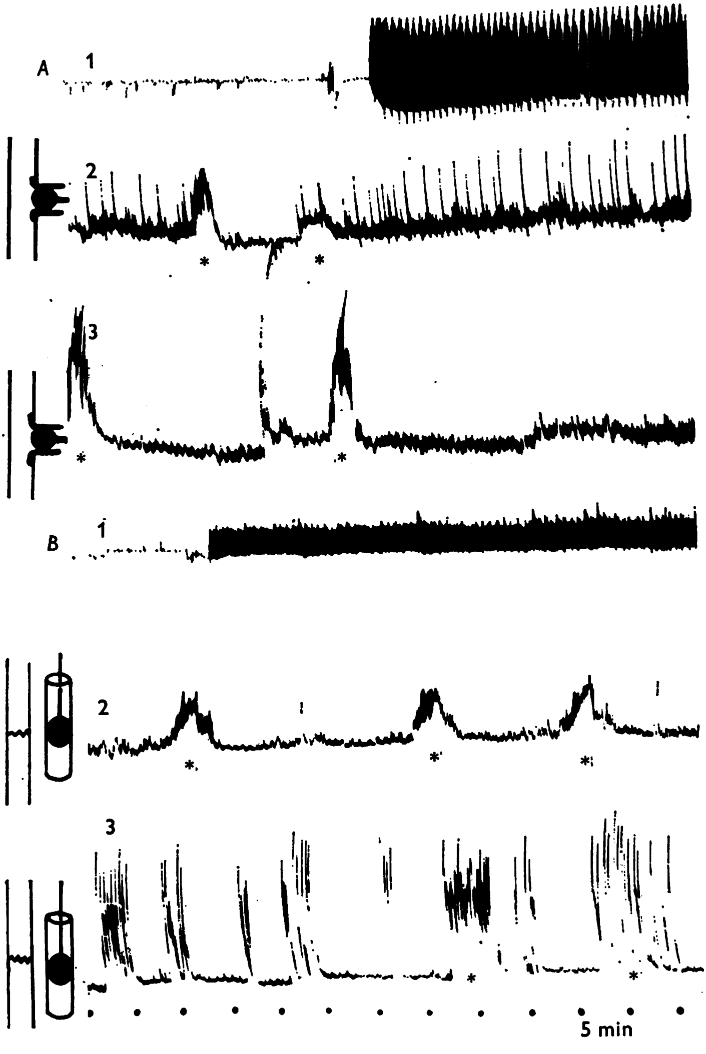

Fig. 13. Pressure recorded from a T-cannula and isolated loops of the intestine in conscious sheep. In *A*, the jaw movements are recorded on the upper trace (1), the pressure from the T-cannulae in the duodenum 50 cm beyond the pyloric sphincter (2), and T-cannulae in the ileum 30 cm anterior to the ilo-caecal junction (3). Tonic contractions in the duodenum and in the ileum are seen at *. Many short contractions are also recorded which may be associated with movements of gut contents. The activity is less in the ileum than in the duodenum. In *B*, recordings from isolated loops of the duodenum (20 cm length) and ileum (40 cm length) of another sheep are shown. In the duodenum (2) the tonic changes are apparent but short propulsive contractions are absent. In the ileum (3) the motility is quite different and tonic changes appear to occur with the propulsive contractions. Time scale: 5 min.

not flow occurs from the T-shaped duodenal cannula (Fig. 13). This type of electrical activity indicates mixing of the duodenal contents without propulsion.

Distal to the bile duct there is reduction in the frequency of the group discharge with a gradient from 19 to 22/min near to the bile duct to 13/min in the ileum. It is interesting to note that electrical activity is markedly different where the bowel anastomosis was made for the Thiry-Vella loop. When the loop is made at the middle duodenum, the anterior segment of the loop shows activity at a rate of 19/min and the distal segment 16/min but at the jejunum the ratio is 16/15 while at the ileum it is 13/12. The two portions of the middle duodenal anastomosis show a marked variation in activity; the proximal side shows bursts at 19/min and the distal side 14/min, while the ileal anastomosis shows a ratio of 13/10. The decline in the activity as shown by group discharge is not the same throughout the intestine but is greatest in the duodenum and least in the jejunum.

The large intestine

The potential changes in the caecum and the sigmoid colon are complex and the rhythm of the group discharge was about 17–18/min near the ileocaecal junction and only 7–8/min for the spiral colon (third turn) or the blind end of the caecum. The group discharge associated with a propagated activity persists for 60–90 sec at each pair of electrodes 10 cm apart. Small ones occur continuously in the caecum and for about 6 hr in the colon, indicating continuous segmenting activity.

The electrical activity of the gut and the movement of ingesta

Small intestine

Movement of the ingesta can be recorded by placing an air-filled balloon so as to occlude the limb of an implanted cannula. Care was taken, by observation of movement of fluid without the balloon, that the recorded pressure change is in fact a record of fluid flow (Fig. 13). Movement of the gut can also be correlated by using Thiry-Vella loops and recording muscular activity after introducing a water-filled balloon (Fig. 13). Tonic contractions occur for a period of 5 min about 15–20 times each 24 hr. Propulsive waves are twice as frequent in the duodenum as in the ileum.

The electrical activity recorded from the gut wall near to the T-cannulae shows a group discharge coincidental with the tonic contraction. When two sets of electrodes are placed 10 cm apart, a variety of effects are recorded (Fig. 14). The group discharge may occur only at one pair of electrodes, the other pair remaining silent, or it may be seen at both, sometimes first at one site and then first at the other. Sequences of discharges may continue for as long as 5 min, indicating segmental contractions which mix the chyme.

The propulsive activity of the intestine is shown in Fig. 15 where electrical activity is recorded from four pairs of electrodes placed on the wall of the middle duodenum. The wave of contraction may be recorded sequentially by all electrodes in turn or by only one or two pairs if the peristaltic wave is short. When the wave is very short, the group discharge may be recorded from one pair of electrodes only.

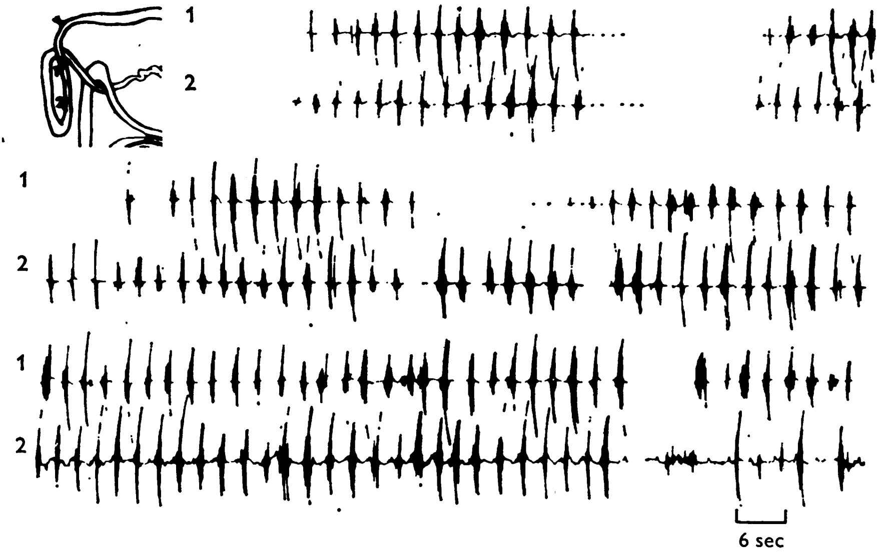

Fig. 14. Group discharge from duodenum during tonic contraction. Diagram of duodenum shows the arrangement of paired electrodes at 1 (oral) and 2 (aboral) positions set 10 cm apart. The discharge becomes continuous but the activity from the electrodes is not synchronous. A coincidental burst from the two pairs of electrodes may be initiated from either site. Time scale: 6 sec.

Large intestine

Movement of the caecum was recorded from three water-filled balloons situated at 10 cm intervals in the body of the organ introduced through a cannula placed in the blind end of the caecum. Slight tonal changes could be recorded from an individual balloon at a frequency of 7–8 min, and the activity might then move to another balloon, indicating a periodicity of tonal activity within different regions of the caecum. When the activity of the caecum is recorded for 24 hr periods, about 7–10 periods can be recorded when total contraction of the organ occurs.

The group discharge pattern recorded from the caecum shows groups of minor electrical activity occurring at intervals of 10 min from individual electrodes. Occasionally marked electrical activity continuing for periods of 60–90 sec occurs synchronously from all recording electrodes. It is likely that the first discharges reflect tonal change and the latter caecal contraction with emptying of its contents.

The sigmoid colon shows electrical and mechanical activity similar to that in the caecum, contractions occurring at about 10 min intervals in bunches of three or four, with strong tonal changes. The events of the spiral colon are irregular with group discharge bursts lasting from 4 to 35 min.

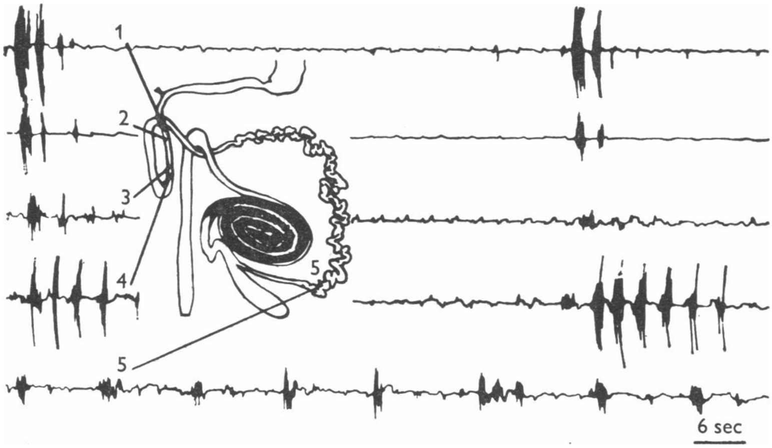

Fig. 15. Electrical activity of the duodenum during propulsive activity. The diagram shows arrangements of paired electrodes 1 and 2, 4 cm apart, and paired electrodes 3 and 4, 4 cm apart also but 10 cm from the anterior two. The paired electrodes at 5 are located 60 cm before the ileo-caecal junction. The group discharge is propagated at a velocity of 20 cm/sec. Time scale: 6 sec.

The effect of diet on movements of the gut

When paired electrodes are placed at intervals along the intestine, records of the mechanical events can be made for 25 hr periods. By this type of recording it is possible to compare the effects of different diets on motility in a single sheep.

The diets investigated are shown in Table 1 together with behavioural activity such as the time spent in feeding and ruminating. The duration of electrical activity has been compiled from the records and expressed as a percentage of activity for both peristaltic and segmenting movements (Fig. 16). It can be seen that activity varies at different levels of the gut, and that peristaltic activity is greater than segmental activity in the duodenum, ileum and caecum. The reverse is true for the jejunum and spiral colon.

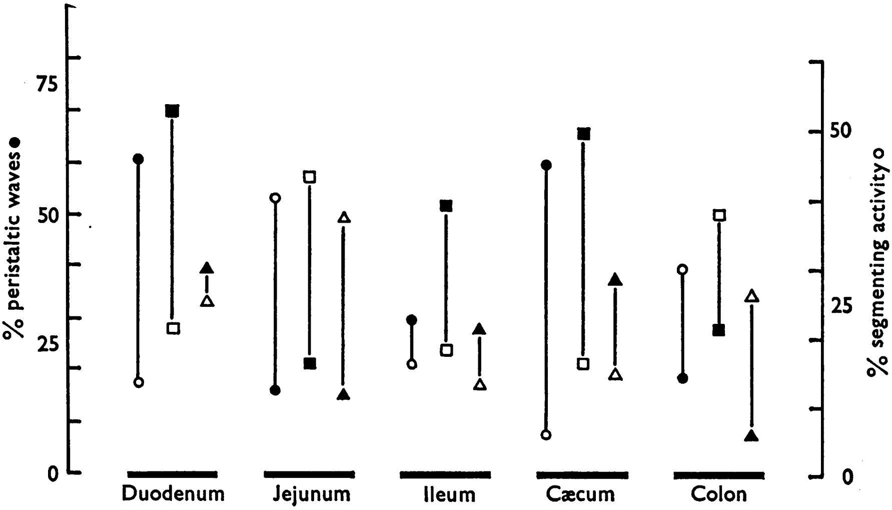

Fig. 16. The electrical activity at different levels of the digestive tract on different diets in the same sheep. The diagram shows the duration of segmenting activity and peristaltic waves from paired electrodes placed along the intestine at 10 cm intervals (for five recordings of 3 hr from 2 to 5 p.m.). The percentage peristaltic waves is shown as ● for hay, ▲ for grain, and ■ for pelleted grass, the segmenting activity as ○ for hay, △ for grain, and □ for pelleted grass.

TABLE 1. Behavioural data of sheep during 24 hr

Diet	Hay	Grain	Pelleted grass
Dry matter (g)	900	780	900
Water (ml.)	1369	800	2500
Time spent (hr)			
Feeding	6	2	2
Rumination	8	2	2
Faecal output (g): Wet	333	250	775
Dry	159	155	255
Number of defaecations	7	4	20
Duodenal flow (ml./hr)	490	240	800
Mean retention time (hr) of stained straw particles in the intestinal tract	29·36	41·26	16·24

The relationship between total activity as well as the ratio between peristaltic wave and segmental activity is altered by the diet (Fig. 16). Grain feeding reduces the total gut activity especially the peristaltic component but the segmenting activity may be increased. That the peristaltic activity is decreased is confirmed when retention time is measured by the movement of small coloured disks (2 mm diameter) introduced in the duodenal cannulae. Further confirmation was obtained by measuring duodenal flow for an hour when a marked *decrease* in flow occurred with the grain diet and a marked *increase* with the pelleted grass (see Table 1).

It should be noted, however, that when short records of electrical activity for 1 hr are correlated with duodenal flow, some periods of continuous electrical activity associated with tonic contractions can reduce or even stop the flow. This effect is greatest when the sheep is fed pelleted grass and least when hay is fed.

DISCUSSION

Electrical discharge from the muscle layers of the stomach and intestine has been recorded. Alvarez & Mahoney (1922) have applied the term electroenterogram to the group of potentials obtained from the intestine wall. For the purpose of the discussion, the term group discharge is used for the complex group of potential changes that can be recorded at any level of the digestive tract. It is important to note that the discharge varies with the electrical recording system and that artifacts due to mechanical movement can easily be introduced. When nichrome electrodes are used to obtain records over long periods of time, the group discharges are derived from many cells and are affected by a synchrony between them. The pathological reaction caused by the movement of electrodes can also affect the nature of the discharge, especially for the stomach (Fig. 5). An analysis of the complex group of potentials that can be recorded when the various visceral smooth muscle layers contract has been made by Bozler (1938), Ambache (1947), Daniel, Carlow, Watcher, Sutherland & Bogogh (1959), Bortoff (1961), and was recently reviewed by Daniel (1968). Bass *et al.* (1961) studied the electrical activity of muscular contraction in the duodenum and showed that the group discharge was made up of two types of potential. One potential has a slower time course and a regular rhythmicity, and Bass *et al.* (1961) designated this the slow wave or basic electrical rhythm. In the dog, the basic electrical rhythm occurs at 4–5 c/min near the pylorus and about 18/min in the middle duodenum. The rhythms are transmitted at about 13 cm/sec in the antrum and 10 cm/sec in the duodenum regardless of the state of muscle activity. The second component consists of a burst of spike potentials which occupies a specific segment of the slow wave and is conducted only a few centimetres. Since only one burst of spikes occur with each slow wave then the frequency of the basic electrical rhythm indicates the frequency of contractions of a segment of the bowel. The group discharge recorded from various sites along the alimentary tract of the sheep is similar to that described by Bass *et al.* (1961) and Daniel & Chapman (1963). The slow component frequency of the discharge recorded from the abomasal antrum is, however, more rapid (5–7/min) than that from the pyloric antrum of the dog (4–5/min).

In the cat it has been shown that the group discharge may be transmitted over the pylorus from the stomach to the duodenal bulb (Bortoff & Weg, 1965). This was apparently not so in the dog (Daniel & Chapman, 1963). In the limited investigation of this problem in the sheep, definite but not invariable passage of the group discharge from the abomasum to the duodenum was recorded (Fig. 10).

The electrical activity recorded as group discharge in the sheep varies at different sites, being most complex in records from the ruminal pillars or reticulo-omasal orifice and least complex from the dorsal sac of the rumen or distal duodenum. Its complexity, particularly marked in records from the pillars which constitute the boundaries of the various anatomical subdivisions of the stomach, may be directly related to the nature and greater mass of muscle. Bortoff (1961) has shown that the slow electrical rhythm is associated with the well arranged longitudinal muscle layer. The records from the sheep support this suggestion for the slow component of the group discharge is best recorded from the pyloric antrum where the longitudinal muscle is thick and well defined. The discharge from the reticulum and rumen, where the muscle masses are complex, is complex. In the omasum, a thin outer longitudinal muscle layer runs parallel to the greater curvature and the thick inner circular layer is reinforced at the omasal groove by oblique fibres. The nature of the group discharge became more complex at this level.

The electrical activity of the circular muscle is recorded as spike potentials when the muscle contracts (Bortoff, 1961). This has been shown to be the same in sheep. The group discharge recorded from the reticulum has a large number of spike potentials and this area has a great deal of circular muscle which is well known to be highly contractile. The major movements of the reticulum and rumen are accompanied by synchronous electrical activity of the muscle demonstrable as major cyclic group discharge. As well as the latter, small groups of spike potentials can be recorded, which may indicate minor activity of the circular muscle (Fig. 1). These minor discharges may indicate intrinsic activity of the rumen, since they occur in areas of the rumen caudo-ventral sac remote from vagal influence. There is some verification of this hypothesis since section of the muscle layers of the rumen prevents transmission of the major group discharge but the minor ones can still be recorded distal to the line of section (Fig. 8).

This would corroborate the idea that the minor discharges are generated by local activity and accelerated, co-ordinated and recruited by the effect of extrinsic vagal stimuli of adjacent areas. The vagal efferent activity described by Iggo & Leek (1967) is mainly reflex and is depressed by emptying the reticulo-rumen. The frequency and the amplitude of the reticulo-rumen contractions then gradually decreased in a conscious sheep. The major group discharge becomes progressively weaker and the small one related to the intrinsic movements increases under these conditions. The loss of tone presumably reduces the reflexly induced recruiting-effect of the vagal efferent activity on the minor group discharge to give a major one.

The correlation of group discharges and the movements of the alimentary tract recorded by conventional means has shown that they can be used to confirm or reflect the physiological activity of the organ. The results described in this investigation confirm the well known movements of the ruminant stomach (Phillipson, 1939). Preceding and during the two phases of contraction of the reticulum, there is a major group discharge which occurs in two distinct groups, the spikes of the second group being shorter and of higher density (Fig. 2). Monophasic contraction of the reticulum, particularly when the animal is fed after a period of fasting, or isolated extra-biphasic reticular contraction associated with regurgitation in sheep during short cycles of rumination, are verified by the electrical recording (Fig. 3). The retrograde movement of the ruminal wave as its secondary contraction is well demonstrated by the electrical records of the dorsal sac (Fig. 7). The interval between primary and secondary contractions is correlated with the duration of the longitudinal and caudal pillar contraction. The intensity and speed of propagation of the secondary contraction differs according to whether an animal is being fed or fasted, ruminating or drowsy. These results are in accordance with the mechanical records of Reid (1963) during feeding and of Ruckebusch (1968) during sleep.

The reticulo-ruminal fold has been shown by Dougherty & Meredith (1955) to remain contracted after the completion of the second phase of the diphasic contraction of the reticulum. This finding is corroborated by its group discharge. Another fact is its correlation with the extra-reticular contraction (Fig. 6).

The electrical recording from the omasum has helped to elucidate the role of this organ, which is difficult to investigate by normal methods of gastroenterology. The group discharge of the omasum is difficult to record but it does show the slow component; spikes are relatively few as there is little muscle coat. As the largest omasal leaves contain a central band of muscle that is continuous with the inner layer of the wall, the contractile activity of leaves can be well seen by endoscopic examination and can also be recorded as discharges. The movements of the omasum have been shown by the electrical recordings to be correlated with the reticulo-ruminal cycle. The omasum shows contractions which precede those of the reticulum and thus confirm the finding for the cow by Balch, Kelly & Heim (1951).

When continuous records over long periods are made, the omasum may become quiescent for 2–5 rumen cycles, which confirms the results shown by Ohga *et al.* (1965) using manometric methods. The omasal groove has been found to be a very active region which shows contraction before the omasal body. The group discharges recorded from near the reticulo-omasal orifice shows discharges which probably indicate contractions of the circular muscle of the orifice. The relaxation of this muscle is not recorded but the 'silent' intervals between such activity suggest a continuous rhythmic opening and closing of the reticulo-omasal orifice.

The group discharges recorded from the abomasum shows that muscular contractions are restricted almost exclusively to the pyloric antrum which is very active. The lesser curvature of the fundus does, however, show some contractility. The abomasal activity is not correlated with the reticulo-ruminal cycle although two or three contractions may occur after the reticular contraction. A sustained tonic wave may occur in the abomasum lasting for 2–3 min associated with a prolonged record of group discharges.

Electrical recordings show that the mechanical movements of the small bowel of the sheep are similar to other species with peristalsis, anti-peristalsis and segmental movements being readily demonstrable (Ruckebusch, Grivel & Santini, 1969).

The electrical changes recorded from the caecum indicate continuous movement with occasional tonal contraction being superimposed. Two or three times a day, however, the organ shows great activity, discharging its contents by a peristaltic contraction and being recharged from the ileum and probably from the contents of the sigmoid colon which shows an intense muscular activity.

The correlation of electrical records made over 24 hr with feeding behaviour has produced interesting results. The motility of the abomasum increases not only after the ingestion of food but is also activated by the sight of food, as in man and dog. In the omasum, however, increased activity occurs only with the ingestion of food. The existence of a gastro-colic reflex with, as in man, an increased activity of the colon 1–10 min after eating a meal was also observed in sheep; the burst of spikes in the sigmoid colon almost double in frequency during the first 10 min after feeding.

When different types of food are given the change in activity of the gut can be readily demonstrated by recording the group discharge from electrodes placed at suitable points along the alimentary canal. When grain or grass pellets are substituted for hay, a marked change in activity can be recorded. An interval of some days must be allowed, however, between change in activity at many levels of the gut. The prolonged recording of alimentary activity with different diets serves to show different sections of the intestine in activity. The jejunum and spiral colon of the sheep show much greater segmental activity than peristaltic movement, but in the duodenum, ileum and caecum the reverse is true. Feeding grain reduces the peristaltic activity of the gut although segmental activity may be increased in the duodenum. This is associated with a reduction in duodenal flow and faecal output. With grass pellets on the other hand, peristaltic activity increased at many points along the intestine. The increase in intestinal activity recorded electrically when grass pellets are fed is paralleled by increased duodenal flow and faecal output.

As in the dog, it is possible to obtain, for a given diet, a predictable pattern of the number and duration of bursts of spikes recorded from paired electrodes (McCoy & Baker, 1968). It must be remembered, however, that the ileal flow varies considerably, changing by as much as 60 % from day to day (Goodall & Kay, 1965).

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