A RADIOLOGICAL STUDY OF THE PATTERNS OF CONTRACTION AND DIGESTA MOVEMENT IN THE ALIMENTARY TRACT OF THE SHEEP.

A thesis presented in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Veterinary Science at Massey University.

Robert Sharp Wyburn
B.V.M.S. D.V.R. M.R.C.V.S. M.A.C.V.Sc.

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THE OMASUM AND ABOMASUM

4:1 LITERATURE REVIEW

The omasum is a difficult organ to investigate because of its anatomical position. Wester (1926) was the first to present the results of a systematic investigation of the movements of the omasum in the cow. He palpated the omasum, made recordings of pressure changes by inserting balloons, and he made observations on some acute preparations. The conclusions Wester (1926) came to were that during reticular contraction the reticular groove formed a funnel round the reticulo-omasal orifice which dilated at the same time. Reticular contents then rushed through into the omasum and the reticulo-omasal orifice closed. Following this a wave of contraction passed over the omasum towards the abomasum and then a weaker wave which Wester called an "antiperistaltic wave of contraction" moved in the reverse direction. He also reported that a balloon placed in the abomasal end of the omasum recorded a sudden drop in pressure during the second wave of each reticular contraction. Schalk and Amadon (1928) to a large extent confirmed these findings, whereas Czepa and Stigler (1926, 1929), who studied sheep radiographically, said they could see only peristaltic contractions occurring. However, Magee (1932), who also used radiography reported that he could see no contractions of the omasum in sheep although trickles of barium could be seen passing from the reticulum through the omasum into the abomasum at the stage of the second reticular contraction. Phillipson (1939) confirmed this latter finding but added that "blobs" of barium could be seen entering the abomasum at other times than those related to reticular contractions. Still using radiography, Benzie and Phillipson (1957) reported in sheep some movement of the omasum apart from those associated with contractions of the reticulo-rumen. This movement was an elongation which occurred during the latter stages of the reticulo-ruminal cycle. Balch et al. (1951) used balloons to record pressure changes in the reticulo-omasal orifice in cows and noted that the orifice was open 60 - 70% of the time and that it had a biphasic contraction, the first associated with the first reticular contraction, and the second with

contraction of the cranial pillar. They also recorded in the omasal body a slow pressure wave which dropped suddenly in association with the second reticular contraction. These findings were confirmed by Stevens et al. (1960) and were added to. The pressures in the bovine omasal canal changed with the reticulo-ruminal cycle and followed the changes in the reticulo-omasal orifice. However, pressure changes in the body of the omasum did not follow the reticulo-rumen cycle except that there was a pressure drop at the time of the cranial pillar contraction. Sellars and Stevens (1966) reported that back flow of material from the bovine omasum to the reticulum can occur from time to time and suggested that the passage of food through the omasum is controlled by conditions within both the reticulo-rumen and the abomasum. Two types of contractions of the omasum of sheep have been described by Ogha et al. (1965) one of which was related to the reticulo-ruminal cycle and the other of which involved mainly the caudal part of the organ and lasted for two or more cycles.

In a review of omasal physiology Bost (1970) admitted that not much information concerning the movements of the omasum had been forthcoming in the previous few years. Ehrlein and Hill (1969) in studies on goats reported detecting contractions of the omasum with balloons and strain gauges but could see no changes radiographically. Not until the publications of Bueno et al. (1972), Bueno and Ruckebusch (1974) and Bueno (1975), were any significant new observations made on the motility of the sheep's omasum. Using recording electrodes, strain gauges and balloons, a comprehensive study of omasal movements was conducted which confirmed and added to much of the previous work. A brief summary of the collected findings follows. The movements of the orad two thirds of the omasum are linked to the reticulo-ruminal cycle. Between the two phases of the reticular contraction, a wave of contraction starts on the parietal surface of the omasum and extends over the greater curvature. With the second reticular contraction all activity of the omasum stops. The motility of the aborad third of the omasum is entirely independent of reticulo-ruminal activity and is characterised by sustained periods of contraction. Contraction of the omasal leaves occur independently from the wall and take place every 2 to 3 minutes, passing from the free edge of the leaves to their base. The reticulo-omasal orifice always dilates

during the second reticular contraction and this is followed by a series of opening and closing movements at a rate of 5 to 7 per minute. The flow of material through the orifice is also cyclic, and linked to reticular motility. Bueno (1975), in a summary of omasal function, says "The function of the omasum seems to be complimentary to that of the reticulo-rumen. It regulates by means of the reticulo-omasal orifice the rate of flow into the abomasum. It facilitates, due to its enormous surface area, the resorption of metabolites resulting from microbial fermentation. It controls the mineral exchanges related to saliva production. It represents a remarkable anatomical and functional adaption with regard to the nature of the food of ruminants under natural conditions".

The motility of the abomasum has been less well studied than that of the other compartments of the ruminant stomach. Schalk and Amadon (1928) inserted their hands, and balloons, through the reticulo-omasal orifice into the fundic part of the abomasum and reported little activity except that associated with reticular contractions. Czepa and Stigler (1926) using radiography reported that in sheep there were strong peristaltic contractions in the pyloric part of the abomasum but that in the body and fundic part there was little activity except, again, that associated with reticular contractions. These findings were confirmed by Magee (1932) and by Benzie and Phillipson (1957) in radiographic studies.

Ehrlein (1970) studied the motility of the abomasum in goats using strain gauges, induction coils and radiography. He detected no movement of the fundic part of the abomasum except that imposed by contractions of the reticulo-rumen. However, in the pyloric part there were continuous peristaltic movements which were intermittently interrupted for a period of a few minutes. The frequencies of these abomasal peristaltic waves were more or less constant at approximately 5.6 per minute and they were propagated at about 1 cm per second. He went on to state that contractions of the pylorus are a continuation of the peristaltic contractions of the pyloric antrum so that the contents at the end of a peristaltic contraction are forced back into the pyloric antrum with only a small amount passing out into the duodenum. No simultaneous contractions of the pyloric antrum, as occurs

in monogastric mammals, has been seen in the abomasum of sheep (Ehrlein, 1976).

The electrical activity of the abomasum has been studied by Ruckebusch and his collaborators (Ruckebusch, 1970; Ruckebusch and Kay, 1971; Ruckebusch and Bueno, 1977).

The pattern of electrical activity over the abomasum has been described as having a slow wave which migrates towards the pylorus (Ruckebusch, 1970; Bolton et al., 1976). This slow wave occurs about 6 times per minute and its velocity increases as it approaches the pylorus. The action potentials of muscle contraction are superimposed on the slow wave. Electromyographical investigation of the pyloric part of the abomasum and the pylorus demonstrated strong peristaltic activity moving towards the pylorus, with the relaxation of the pylorus coinciding with the arrival of a peristaltic wave (Ruckebusch and Kay, 1971). Ruckebusch (1970) reported finding a coordination between contractions of the abomasum and duodenum but this was subsequently disproved (Ruckebusch and Bueno, 1977).

Apart from these studies on the motility of the abomasum there have been a number of investigations into flow of material into and out of the abomasum, some of which have already been mentioned under the control of the reticulo-omasal orifice. The flow into the abomasum is influenced by the degree of filling of the abomasum, the volume of fluid in the rumen, and whether the animal is feeding or ruminating (Phillipson, 1939, 1952, 1963; Weiss, 1953; Titchen, 1958, 1960; Briggs, 1961; Ash, 1962, 1962a). The flow of digesta from the abomasum is influenced by the degree of distension of the abomasum and by the degree of distension of the duodenum with distension of the duodenum inhibiting flow through the pylorus (Phillipson, 1952; Hogan and Phillipson, 1960; Ash and Kay, 1963). The chemical composition of the abomasal contents (Bolton et al., 1976) and the pH and chemical composition of the duodenal contents (Bell and Watson, 1975; Bell and McLeay, 1978) also affect abomasal emptying. While the normal flow of contents through the abomasum is aborad, reports of orad movements have been made. Phillipson (1939) reported that gas from the abomasal

gas cap passed back through the omasum to the reticulum and that food material could flow from the duodenum back through the pylorus into the abomasum (Phillipson, 1952). The passage of milk through the abomasum in suckling animals is much slower than adult ruminant digesta. Hill et al. (1969) found that when a calf drinks milk, passing it directly to the abomasum it immediately forms a clot which then takes 12 - 18 hours to pass into the duodenum.

In the work reported here, radiological observations were made of the motility of the omasum and abomasum, and the passage of contents through these organs.

4:2 MATERIALS AND METHODS

4:2:1 The Omasum

The objective of this series of observations was to determine whether any radiographic evidence of omasal contractions could be obtained. The omasums of each of 5 sheep were viewed for 30 minutes in the fasted and replete state. Video-tape recordings, cine-film and spot-films were taken and later scrutinized for any evidence of omasal contractions.

The five animals used were sheep 6, 7, 8, 9 and 12, all New Zealand Romneys between 13 and 16 months old and female. They were housed in individual crates at Massey University and fed a diet of chaffed lucerne ad libitum with water freely available. Sheep 6, 7 and 8 had no surgical modification; sheep 9 and 12 had a rumen fistula inserted four months previously (See 3:2).

Radiographic observations: The sheep in their crates were positioned between the x-ray tube and the image intensifier as described in Chapter II. They were drenched with 50 ml of barium sulphate and, using the magnification facility on the image intensifier, the omasum was observed continuously for 30 minutes; a video-tape recording was made during the entire period. Cine-film was taken at 12 frames per second during one reticulo-ruminal contraction sequence and during the

quiescent period between contractions. Serial spot-films at 2 per second were taken at two similar periods. The video-tape was reviewed and the cine-film analysed by projecting it at fast and slow speeds and by tracing the outline of the projected image onto paper to determine any small changes in outline. The spot-films were examined and compared with the others from the same sheep by overlaying them.

For the first recording session, which was with the animals in the replete state, food was available up to and during the period of observation. The animals were fasted for 18 hours prior to the second session which was separated from the first by 7 days.

4:2:2 Abomasum

The object of the first series of observations was to establish the characteristics of abomasal motility in unweaned, partially weaned and weaned sheep. The objectives of the second series of observations were to examine the relationship between abomasal motility patterns and small intestinal motility and how these were affected by distension of the abomasum to various degrees and with different substances.

Animals and their preparation: Ten animals were used for this series of investigations (Table IX).

These sheep were all housed in individual pens at the Rowett Research Institute and the weaned animals were fed dried grass ad libitum with a small amount of concentrate ration occasionally added. Water was freely available.

Abomasal cannulae were inserted in Sheep 1 and 5, and an abomasal catheter was inserted in Sheep 4 two weeks prior to the first investigations. Abomasal cannulae were inserted in Sheep 2 and 3 after the first investigation and 2 weeks prior to the second investigation. The surgical techniques used have been previously described (Dougherty, 1955; Hecker, 1974) and were as follows:

Following a thorough antiseptic preparation of the site, a low right

TABLE IX

SHEEP USED TO INVESTIGATE ABOMASAL FUNCTION

Sheep No.	Breed	Age	Sex	Feeding Management
1	Soay	7 mths	F	Weaned
2	Soay	7 mths	F	Weaned/bottle-trained
3	Soay	7 mths	F	Weaned/bottle-trained
4	Dorset/Suffolk	9 mths	F	Weaned
5	Dorset/Suffolk	9 mths	F	Weaned
21	Dorset/Finnish	12 mths	M	Bottle-fed 800 ml cow's milk 3 times/ day
22	Dorset/Finnish	3 wks	F	Bottle-fed 150 ml cow's milk 8 times/ day
23	Dorset/Finnish	3 wks	F	Bottle-fed 150 ml cow's milk 8 times/ day
Lamb I	Dorset/Finnish	1 wk	M	Feeding from mother
Lamb II	Dorset/Finnish	1 wk	F	Feeding from mother

flank paracostal incision was made into the abdominal cavity. Great care was taken to stem all haemorrhage before opening the peritoneal cavity. Once the peritoneal cavity was opened, the abomasum was identified and the site for the insertion of the catheter or cannula exteriorised, emptied of contents, and isolated from the rest of the abomasum by a pair of rubber-shod bowel clamps. The site selected for catheterisation or cannulation was in the body of the abomasum on its right side approximately half way between the greater and lesser curvatures.

Catheterisation: The catheters used were made up from polyvinyl-chloride tubing (Portex Plastics Ltd.) of 9 mm external diameter and 7 mm internal diameter and were 30 cm long. Two 20 mm diameter alkathene discs were welded to one end of this tubing, one set 3 mm, the other 8 mm behind it, back from the lip (Plate 50). Into the other end of the catheter was welded the plastic boss from the end of an 18 gauge Luer hypodermic needle. Using 2/0 chromic gut with a swaged-on curved atraumatic needle, a purse-string suture was placed in the abomasal wall large enough to accommodate the alkathene disc. An incision was then made in the centre of the purse-string suture into the lumen of the abomasum. The disc closest to the tip of the catheter was inserted through into the lumen and the purse-string tightened, pulling the abomasal wall up against the tubing between the two discs. Care was taken to ensure the abomasal wall was inverted as it was pulled inwards. A second purse-string suture was then placed as close to the catheter as was feasible and again care was taken to ensure inversion as this suture was pulled up tight. The bowel clamps were removed and the abomasum returned to the peritoneal cavity. A small loop of catheter was left close to the abomasum to allow for any movement which might take place. The free end of the catheter was then passed up in the peritoneal cavity and brought out through a stab wound high in the right flank. The laparotomy was closed layer by layer, using 1 chromic gut and a continuous suture. The skin was closed using 2/0 nylon in vertical mattress sutures.

The exposed part of the catheter was buried in the wool on the sheep's back and held in place by tying it to the wool. It was then filled with normal saline and closed off with a small rubber bung. The

catheter was flushed out daily with 10 ml of normal saline.

Examinations were carried out postmortem at the completion of the experiments 3 to 9 months after the surgery. The findings were as follows. The intraperitoneal part of the catheter had become completely encased in a layer of fibrous tissue 1 - 2 mm thick and to this parts of the omentum had become adherent. In no animal were there any adhesions to other intra-abdominal organs. At the site where the catheter entered the abomasum, the outer disc was completely encased in fibrous tissue, and the abomasal wall for approximately 10 mm diameter round this was thickened. There were no adhesions to the abdominal wall but in some animals the omasum had become adherent. When the abomasum was opened, there was very little change to be seen on its mucous membrane lining. In one animal there was some slight thickening and hyperaemia where the edge of the intra-luminal disc had been in contact.

Cannulation: The cannula used was flanged and made of ebonite. The total length of the cannula was 40 mm and it had an external diameter of 10 mm and an internal diameter of 7 mm. The diameter of the flanges was 35 mm and the external flange was held in position with a lock nut.

The internal flange was introduced into the lumen of the abomasum using a double purse-string technique as for the catheter. The cannula was then brought out through the abdominal wall as high as possible without pulling the abomasum out of position, and the external flange screwed on firmly and held in place with the lock nut. The cannula was closed with a rubber bung.

Examination of these animals postmortem showed that there was a marked adhesion between the abomasum and abdominal wall where the cannula passed through. Where the abomasum was adherent to the abdominal wall there was a marked fibrous thickening of the visceral and parietal peritoneum. The abomasal mucous membrane under the internal flange was thickened, hyperaemic, and in one case ulcerated.

Radiographic observation: For radiographic viewing, the sheep were restrained between the x-ray tube and the image intensifier in the holding crush as described in Chapter II. A video-tape recording was made throughout each session and a number of radiographs were taken to illustrate the various features observed. The video-tapes were reviewed and compared to establish patterns of abomasal activity. The analysis of the various events seen was carried out using a stop watch and the "stop frame" on the video-tape recorder. At the beginning of each session a short video-recording of a stop watch was made, using a television camera, and at each review this was compared with the actual stop watch to check that the play back speed matched the recording speed. No timing of events was taken from the video-tapes of the first series of observations. From the video-tapes of the second series the following measurements were made:

(a) the time elapsing between successive contractions of the duodenal bulb,

(b) the time elapsing between successive phases of rhythmic spiking activity (RSA) seen in the jejunum,

(c) the time of abomasal activity in relationship to (a) and (b), and

(d) the frequency of peristaltic contraction of the pyloric antrum during periods of abomasal activity.

Sheep 2 and 3 were bottle-trained so that radio-opaque marker given from a bottle by mouth would pass directly into the abomasum (See 3:2).

For the first series of observations the weaned animals had food available up to but not during the period of observation. The bottle-fed animals were fed 90 minutes before the period of observation and the bottle-trained animals were not given their bottle until during the session. The bottle-fed and bottle-trained animals were given 25 ml of barium sulphate in 25 ml of cow's milk by mouth. The others were given 25 ml of barium sulphate in 25 ml of water through their abomasal cannula or catheter. The activities of the abomasum,

duodenum and jejunum were then viewed and recorded continuously for 120 minutes.

The two suckling lambs were removed from their mothers for 3 hours by placing them in an adjoining pen. They were given 20 ml of barium sulphate by mouth and their abomasal activity was viewed for 15 minutes. They were then returned to their mothers and allowed to suckle before viewing the abomasal activity for a further 30 minutes.

For the second series of observations the route of administration and amounts of barium sulphate used are given in Table X. The weaned sheep had food available up to but not during the sessions. Bottle-fed and bottle-trained animals were not fed prior to the sessions, which meant that the period of fasting for the bottle-fed animals ranged from 18 hours with sheep 21 fed 3 times per day, to 3 hours with sheep 22 and 23 fed every 3 hours. The abomasums in some of these sheep were then distended by giving various volumes of milk, whey or saline, or by inflating a balloon in the abomasum. The details of these treatments are given in Table X. Abomasal activity was viewed and recorded continuously for 100 minutes at each session.

4:3 RESULTS

4:3:1 The Omasum

Barium sulphate was seen to pass into the omasum at the height of the second phase of the first reticular contraction that occurred. This gave a complete outline of the omasum and omasal leaves but made it impossible to detect the arrival of any further material during subsequent reticulo-ruminal contraction sequences. The contrast material could be seen trickling through into the abomasum at various times which could not be related to the reticulo-ruminal cycle. However, there was consistently an increase in this flow shortly after the second reticular contraction.

As the reticulum contracted the omasum was rotated and displaced ventrally and bent in its middle with the concave aspect of the bend

TABLE X

TREATMENTS OF SHEEP TO AFFECT ABOMASAL MOTILITY

Session No.	Sheep No.	Treatment
I	1	$BaSO_4$ infused through abomasal catheter at 0.8 ml/min.
	2	Bottle-fed 50 ml $BaSO_4$.
	3	Bottle-fed 50 ml $BaSO_4$.
	4	$BaSO_4$ infused through abomasal catheter at 0.8 ml/min.
	5	$BaSO_4$ infused through abomasal catheter at 0.8 ml/min.
	21	Bottle-fed 50 ml $BaSO_4$.
	22	No treatment.
	23	No treatment.
II	1	$BaSO_4$ infused through abomasal catheter at 0.8 ml/min. Abomasum distended by infusion of 500 ml isotonic saline at 100 ml/min.
	2	Bottle-fed 50 ml $BaSO_4$ plus 500 ml whey.
	3	Bottle-fed 50 ml $BaSO_4$ plus 500 ml whey.
	4	$BaSO_4$ infused through abomasal catheter at 0.8 ml/min and balloon in abomasum inflated with 500 ml of air.
	5	$BaSO_4$ infused through abomasal catheter at 0.8 ml/min and balloon in abomasum inflated with 100 ml of air.
	21	Bottle-fed 50 ml $BaSO_4$ plus 500 ml milk.
	22	Bottle fed 50 ml $BaSO_4$ plus 120 ml milk.
	23	Bottle-fed 50 ml $BaSO_4$ plus 120 ml milk.
III	2	Bottle-fed 50 ml $BaSO_4$ balloon in abomasum inflated with 500 ml air.
	3	$BaSO_4$ infused through catheter at 0.8 ml/min. balloon in abomasum inflated with 500 ml air.
IV	3	Bottle-fed 50 ml $BaSO_4$ plus 50 ml of whey.

facing cranially (Fig. 7). It appeared that this action along with the associated displacement of the abomasum either pushed, sucked or washed some of the contrast material out of the omasum into the abomasum. There was a further slight rotational movement of the omasum associated with the more vigorous contractions of the cranial part of the ventral sac of the rumen. No other movement of the omasum was detected radiographically.

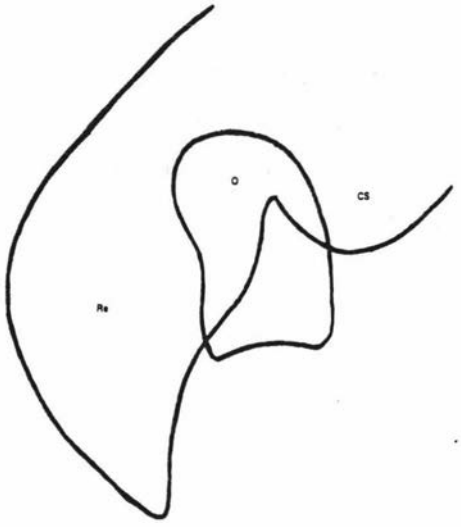
4:3:2 The Abomasum

The approximate position of the abomasum could be identified on the lateral radiograph without the use of a contrast agent (Plate 41). An almost constant feature was a small gas cap outlining the dorsal fundic region which was superimposed on the shadow of the cranial sac of the rumen and lay between the shadows of the caudal wall of the reticulum and the cranial wall of the ventral sac of the rumen. Ventral to this gas cap, the remainder of the fundic region and the body of the abomasum could be distinguished from the reticulum and rumen because its contents were more homogeneous and more dense. This part occupied a triangular space between the caudal wall of the reticulum, cranial wall of the ventral sac of the rumen and the ventral abdominal wall; the ventral edge could be seen extending caudally ventral to the ventral sac of the rumen.

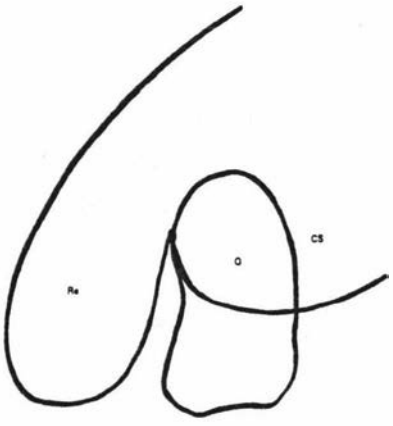
When the contents of the abomasum were made radio-opaque by the introduction of barium sulphate suspension, the outline of the abomasum was clearly demonstrated (Plate 42). The fundic region was orientated vertically, extending ventrally to the abdominal floor where the body region curved caudally. After a short distance it turned dorsocaudally toward the pyloric region which was also orientated vertically with the pylorus directed dorsally and completely superimposed on the shadow of the ventral rumen.

The following general description of abomasal activity was derived from interpretation of all the screening sessions and is illustrated as far as possible with selected spot-films that were taken during each of these sessions.

1



2



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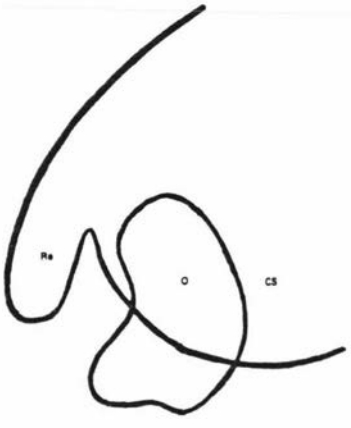
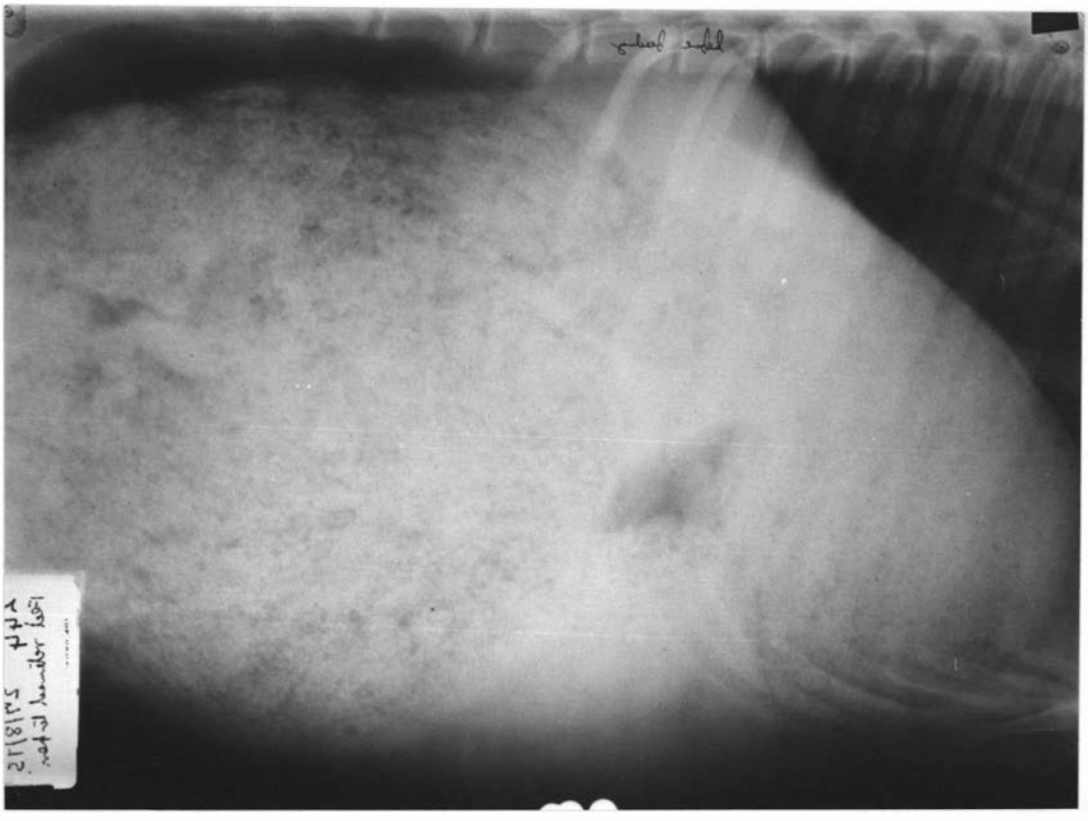


PLATE 41

Plain lateral radiograph of the abdomen. The gas cap in the fundus of the abomasum is visible and part of the abomasum is outlined by the more homogeneous region between the cranial wall of the ventral rumen and the caudal wall of the reticulum.

Ab abomasum, B ball-bearings in abomasum, D diaphragm, DRu dorsal rumen, G gas caps, Re reticulum, S spleen, VRu ventral rumen.



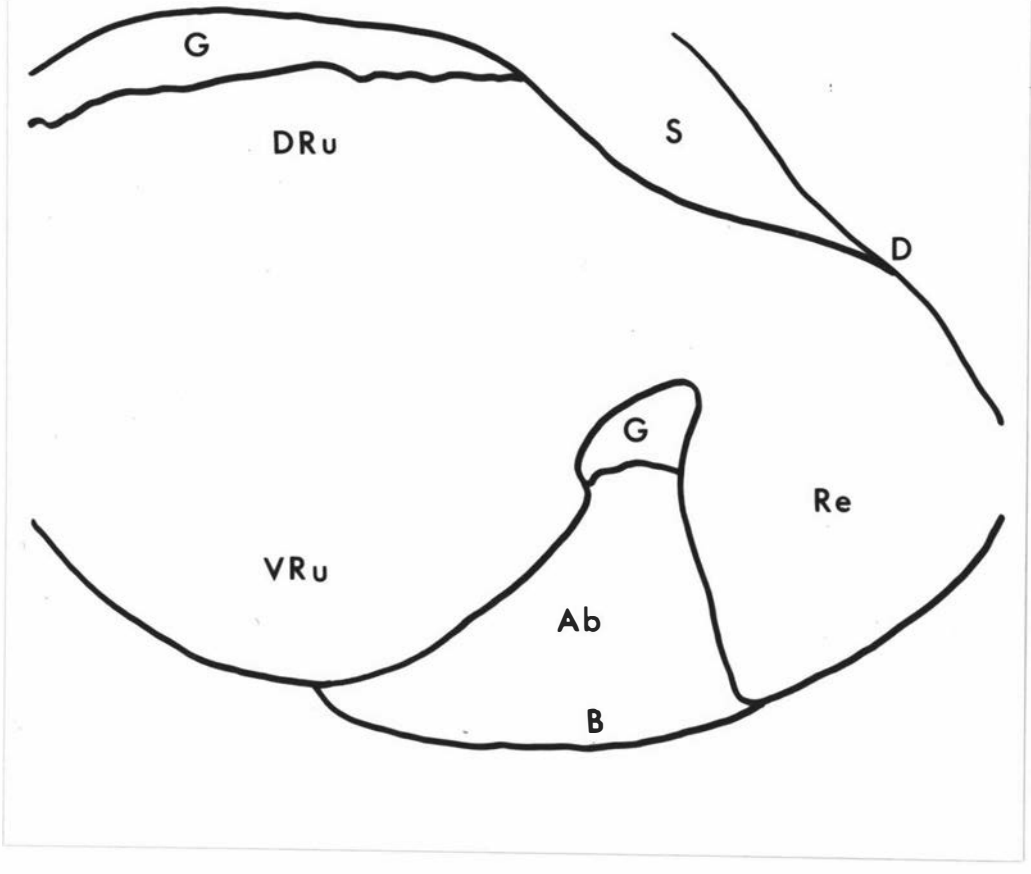
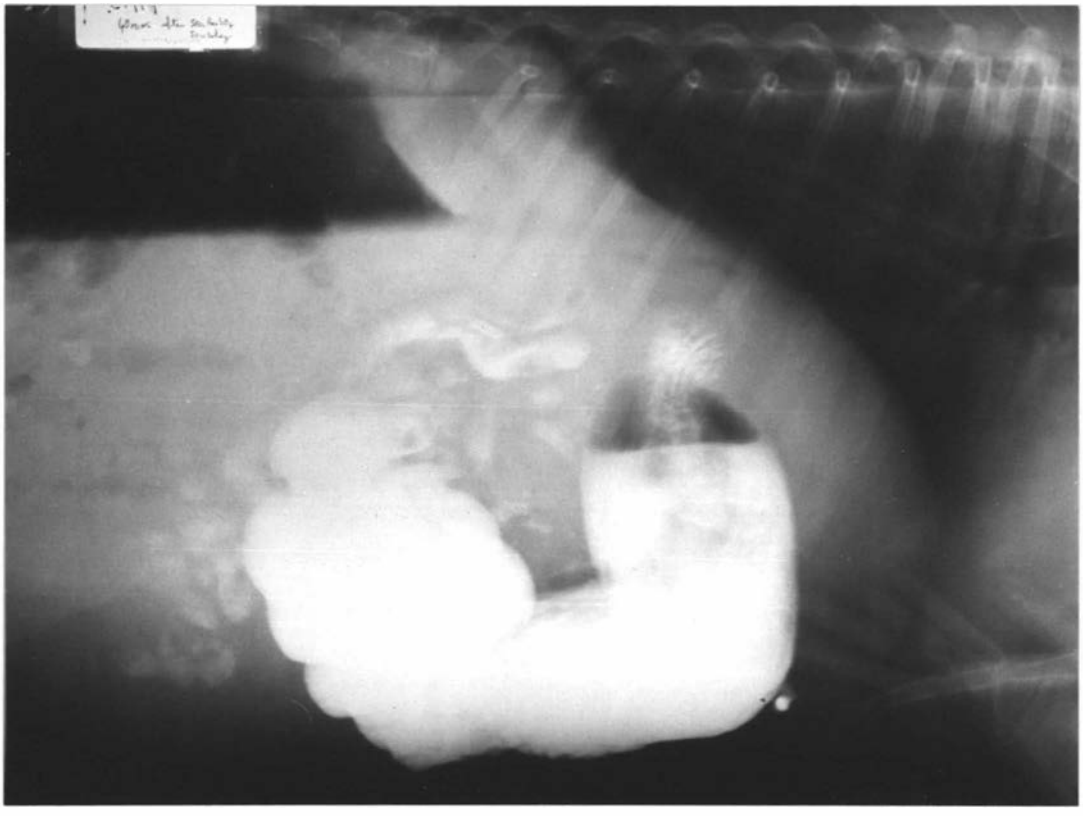
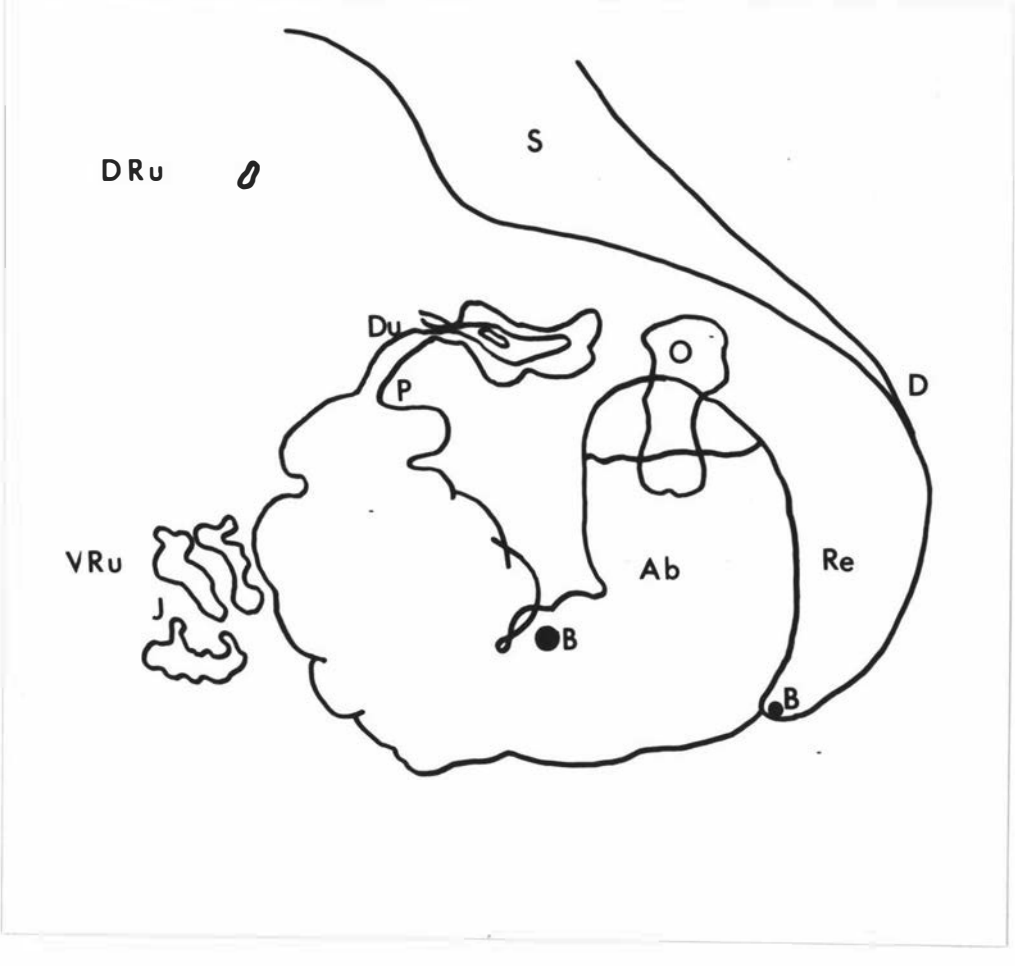

G
DRu
S
D
G
Re
VRu
Ab
B

PLATE 42

Lateral radiograph of the abdomen with abomasum outlined with barium sulphate.

Ab abomasum, B ball-bearing in reticulum and abomasum, D diaphragm, DRu dorsal rumen, Du duodenum, J jejunum, O omasum, P pylorus, Re reticulum, S spleen, VRu ventral rumen.




DRu
S
Du
P
O
D
VRu
J
Ab
Re
B
B

Bottle-trained or bottle-fed sheep became obviously excited when they first saw the bottle. Radiographic screening of these sheep showed that at the time the bottle was first sighted, the omasum moved sharply towards the cardia and the pole of the reticulum jerked a short distance dorsally. They then started to swallow some air, which passed directly into the abomasum and caused an increase in size of the abomasal gas cap. When they first started sucking from the bottle, a small amount of the ingested fluid would leak into the reticulum from the first bolus through the cardia but thereafter all the liquid passed directly into the abomasum. Along with the liquid from the bottle, a large amount of air was swallowed which on a number of occasions was estimated (Appendix 2) to be almost equal in volume to the liquid. By contrast the two lambs suckling from their mother showed only a very small increase in the size of the abomasal gas cap. Four distinct types of movement of the abomasum were identified.

1. Passive Movements. These movements appeared to be imposed by contractions of contiguous parts of the reticulo-rumen: there was no obvious contribution by contraction of the abomasal wall. It was the only abomasal movement that could be related to the contraction sequence of the reticulo-rumen. The most pronounced of this group of movements was associated with contractions of the reticulum. As the reticulum contracted and the cranial sac of the rumen dilated, the cranial wall of the fundic region of the abomasum was pulled cranially and dorsally while the dorsal wall was pushed ventrally, displacing the gas cap. The gas cap returned to its normal resting position as the reticulum relaxed. Contractions of the cranial ventral region of the ventral sac of the rumen were reflected by displacement of the adjacent wall of the abomasum.

2. Peristaltic contractions. The most common and persistent type of contractions of the abomasal wall were peristaltic waves migrating towards the pylorus (Plate 43). These waves were chracteristic of the aborad regions of the compartment: they were infrequent in the fundic region. The region of the abomasal wall where they were first seen appeared to depend on the degree of distension of the pyloric antrum. When the pyloric antrum was distended peristaltic waves were seen only close to the pylorus; but as the pyloric antrum emptied, the zone where peristalsis first appeared migrated orad. The effect

PLATE 43

Radiograph showing rings of peristaltic contractions on the pyloric antrum as they move towards the pylorus.

Ab abomasum, E electrode, M loops of small intestine, P pylorus.


M
M
E
P
Ab

of this orad migration was to push digesta into the antral region. As the pyloric antrum filled the zone of peristalsis migrated aborad again and the cycle was repeated. When the abomasum was relatively empty peristalsis was seen as far orad as the fundic region. This peristaltic activity was not continuous - there were frequent short periods and some more widely spaced longer periods when there was no visible contractions of the abomasal wall. Irrespective of the point of origin of these peristaltic waves, once initiated, they always travelled to the pylorus. As the rings of contraction approached the pylorus they became closer together. This combined with the narrowing diameter of the abomasal lumen, reduced the volume of digesta that could be contained between two consecutive waves of contraction (Plate 43, Figure 8). The excess digesta was expelled orad through the following contraction ring, causing efficient mixing of abomasal contents. The pylorus functioned as an integral part of the abomasum, contracting as each ring of contraction arrived.

3. Stationary contractions. These contractions were seen as small, sharply-defined indentations along the greater curvature in the body region (Plate 44). They formed, disappeared and reformed, but did not migrate either orad or aborad and did not appear to cause any significant movement of abomasal contents. This type of activity was superimposed on peristaltic contractions and lasted for periods of 2 - 4 minutes. It was not commonly seen and could not be related to any other activity.

4. Fundic contractions. These contractions were observed only in sheep which had the fundic region grossly distended with gas after suckling from a bottle. Waves of contraction started up in the fundic region and migrated aborad round the lesser curvature, with no corresponding contraction being visible on the greater curvature as occurred in peristaltic contractions (Plate 45). Also the frequency of these was much greater than peristaltic contractions in the same region. The main effect of these contractions was to displace the gas around to the pyloric region from where it was rapidly eliminated through the pylorus.

The mean time taken for 7 peristaltic contractions of the abomasal

FIGURE 8

Diagramatic representation of rings of contractions approaching the pylorus. Dotted lines connect the same contraction as it migrates towards the pylorus; arrows indicate movement of digesta.

Ab abomasum, P pylorus, Du duodenum.

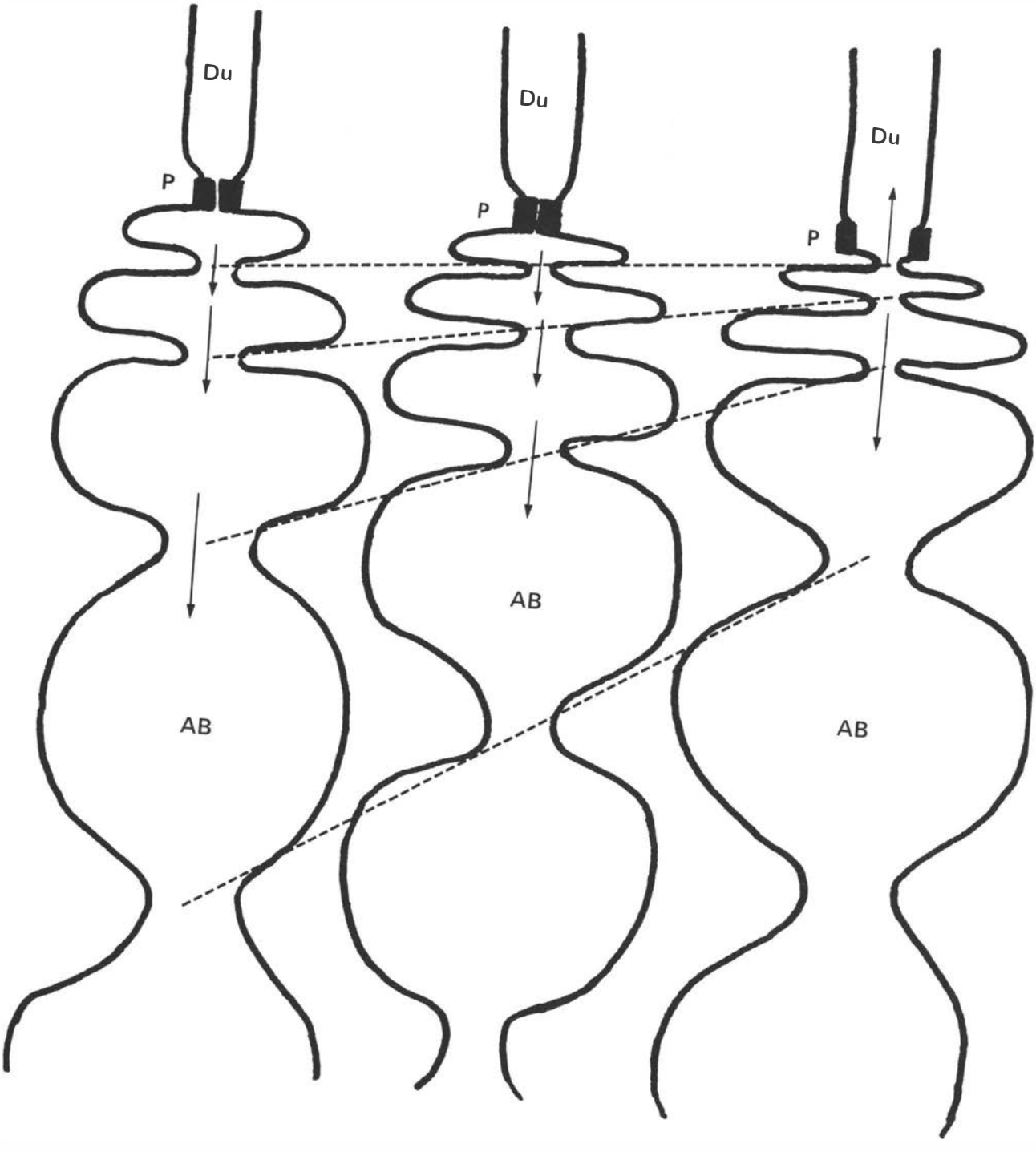
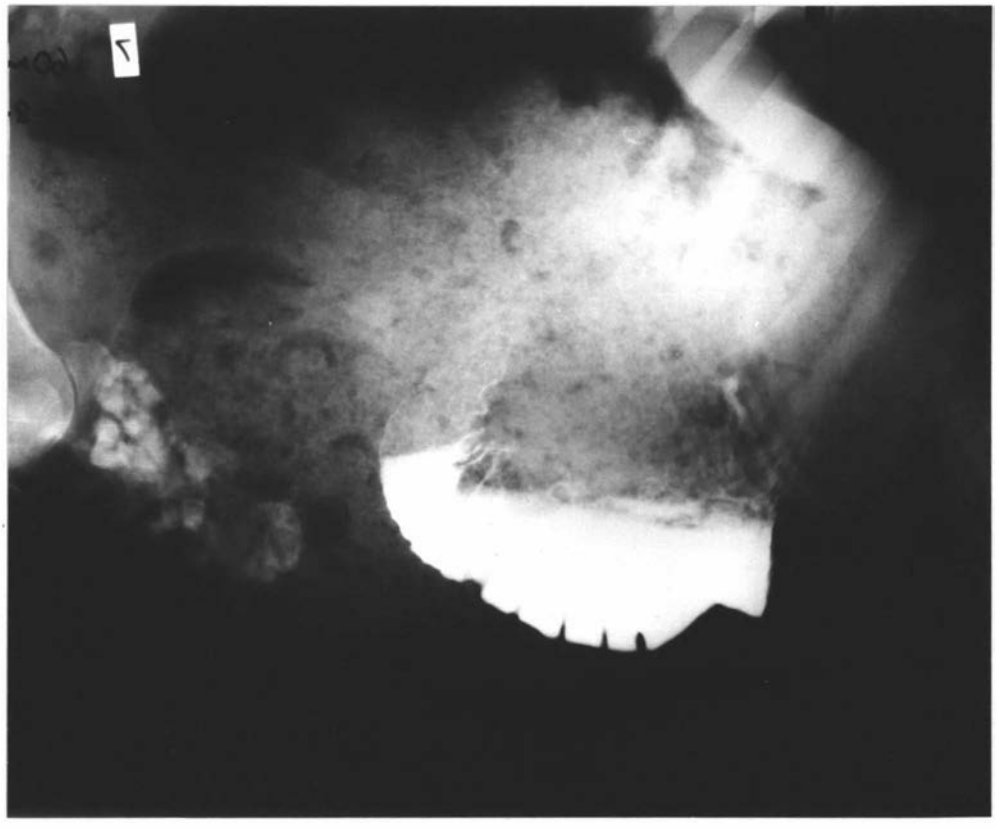

Du
P
Du
P
Du
P
AB
AB
AB

PLATE 44

Lateral radiograph of abdomen with abomasum outlined with barium sulphate. Stationary contractions on the greater curvature of the body of the abomasum are outlined.

Ab abomasum, Ce caecum, CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, G gas caps, P pylorus, Re reticulum, VRu ventral rumen.



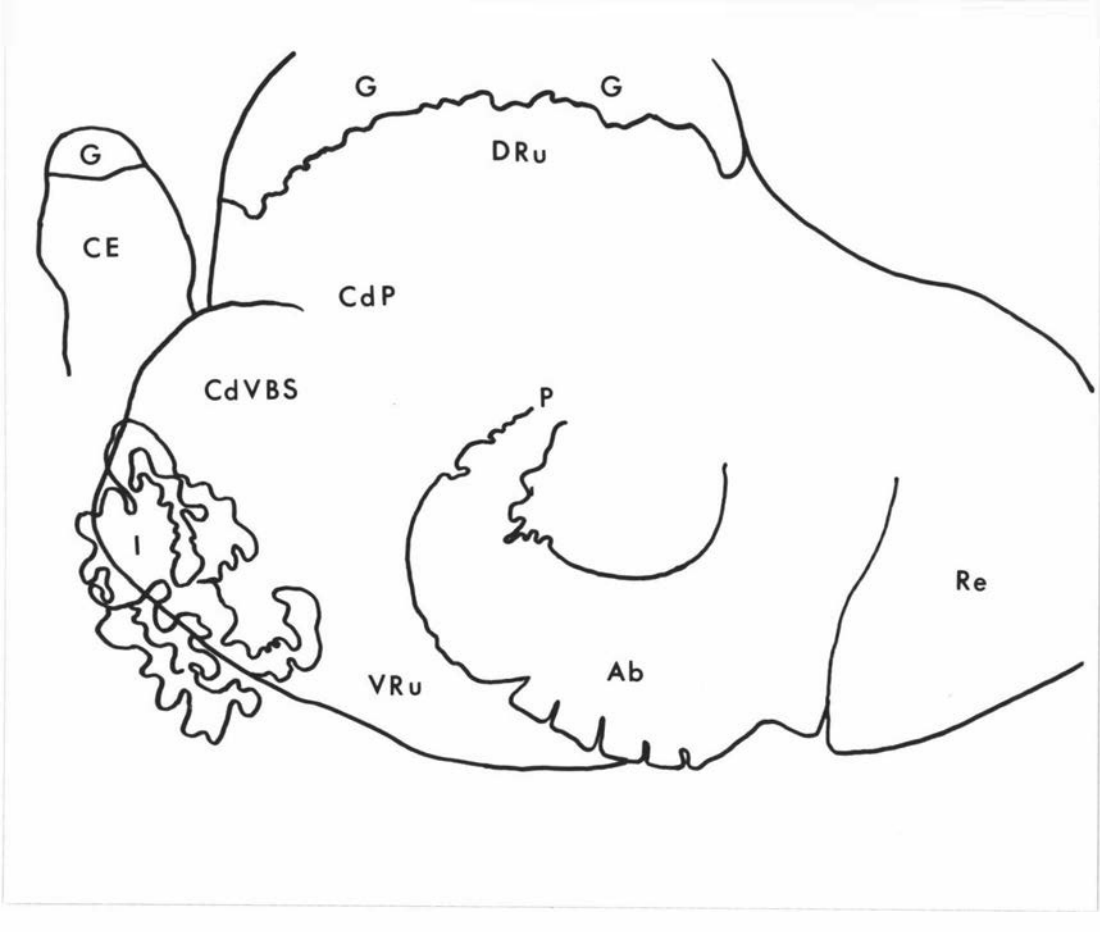
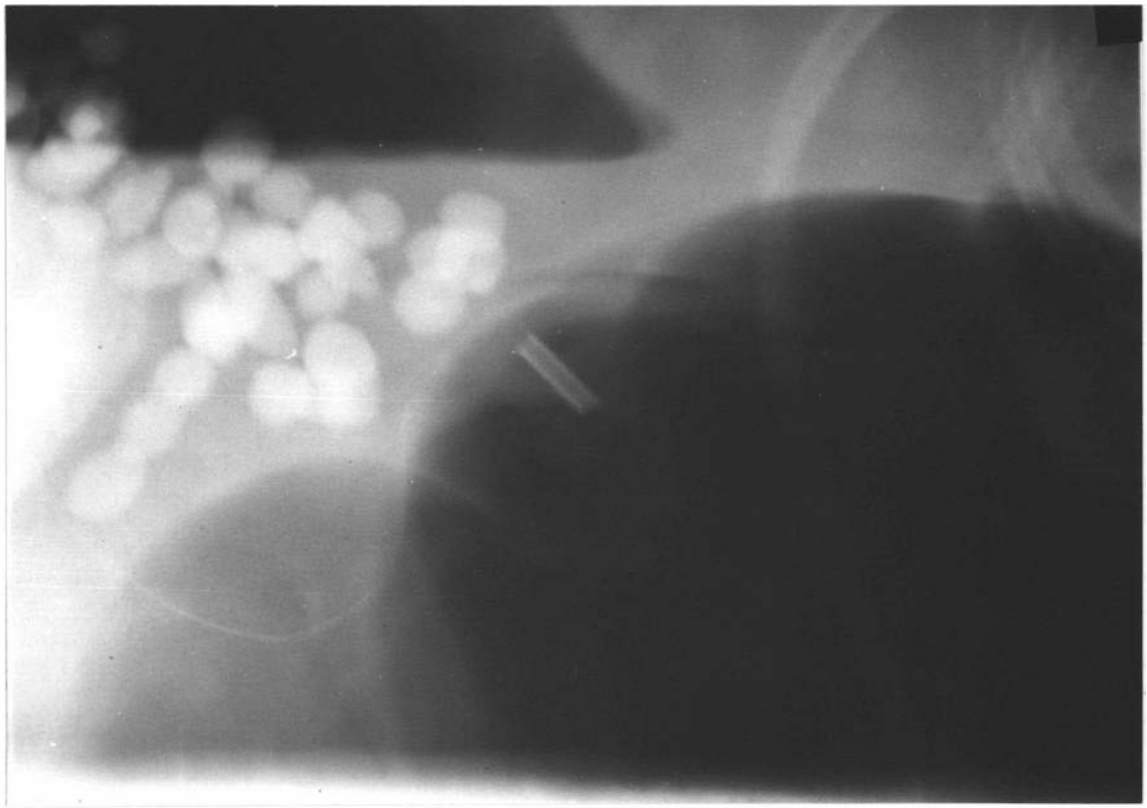
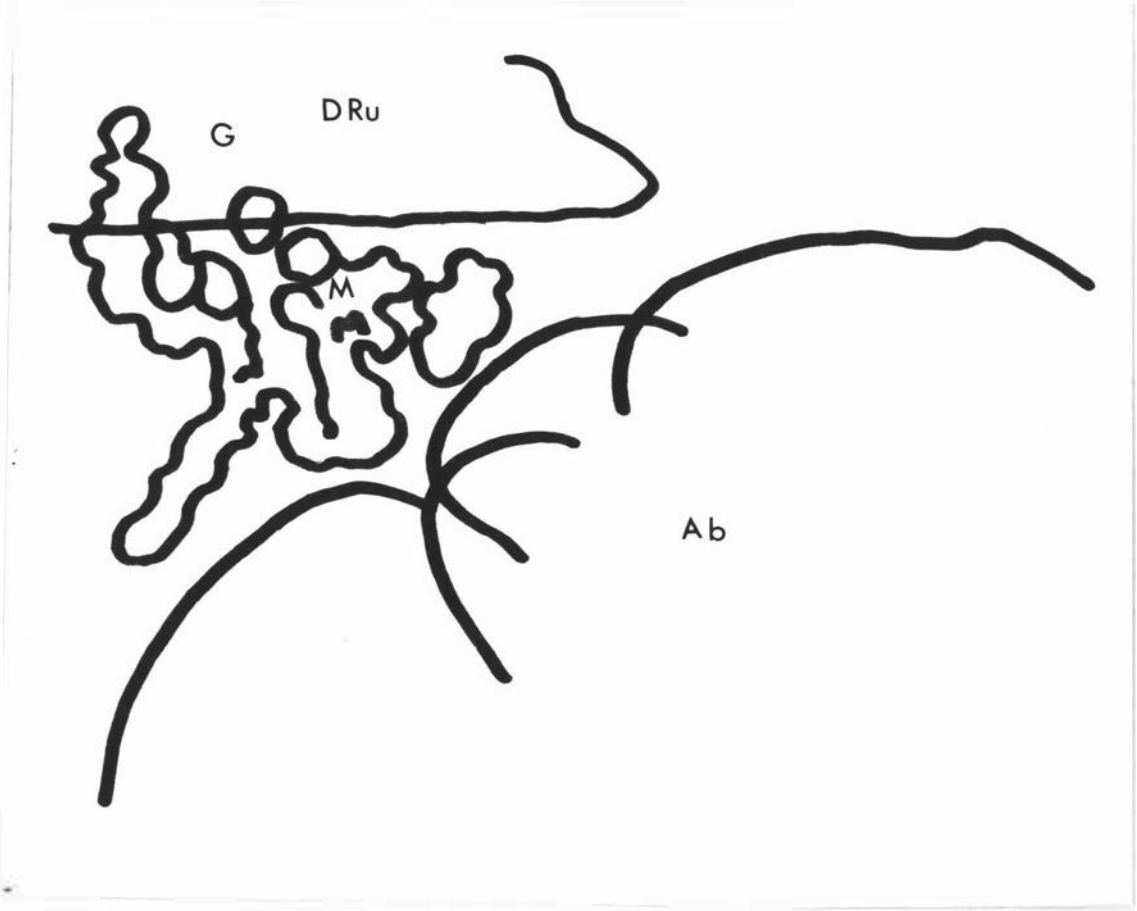

G
G
G
DRu
CE
CdP
CdVBS
P
I
Re
VRu
Ab

PLATE 45

Enlarged area of a lateral radiograph of the abdomen showing the fundic region of the abomasum distended with gas. A number of fundic contractions are visible on the lesser curvature. The thin white line curving across the lower left of the gas in the abomasum is an electrode lead.

Ab abomasum, DRu dorsal rumen, G gas in dorsal rumen, M loops of small intestine.




G
DRu
M
Ab

wall to reach the pylorus in each sheep at each of the observation sessions is given in Table XI. Analysis of variance (Table XII) shows that this time was remarkably consistent within individuals and within breeds, and that it was not affected by distension of the abomasum. However, there was a highly significant difference between the Soay sheep and the others ($P < 0.01$). Only on one occasion was the gas cap in the abomasum seen to pass up into the reticulo-rumen.

Figures 9, 10 and 11 depict the time relationships between pyloric antral activity, the passage of a bolus through the duodenum and the rhythmic segmental activity of the orad jejunum and the effects of abomasal distension. When the abomasum was in its normal undistended state, digesta was propelled down the duodenum at randomly spaced intervals of 1 to 5 minutes, followed by a brief period of approximately 30 seconds when all abomasal activity ceased. A phase of rhythmic segmental activity started every 30 - 65 minutes, and for a period of 10 - 15 minutes following this there was no abomasal activity except that imposed by movements of the reticulo-rumen.

Distending the abomasum, by whatever means, altered this pattern. The frequency with which digesta was propelled down the duodenum increased and the periods of abomasal inactivity were abolished. The occurrence of a phase of rhythmic segmental activity was delayed until the abomasal distension was eliminated to the extent where the frequency of boluses of digesta moving through the duodenum had returned to a level approximating that seen in the undistended state.

The activity of the normal abomasum followed a consistent and predictable pattern related to the occurrence of a phase of rhythmic segmental activity in the jejunum. During periods of complete abomasal inactivity associated with these, digesta in the pyloric antral region moved back towards the body of the abomasum. When activity recommenced, peristalsis started up in the body of the abomasum, pushing digesta up into the pyloric antrum. Once the pyloric antrum was filled, the point where peristalsis appeared migrated aborad. Each peristaltic contraction pushed digesta up to the pylorus and a variable volume passed through into the duodenal bulb. The frequency

TABLE XI

THE TIME TAKEN FOR 7 PERISTALTIC WAVES TO REACH THE PYLORUS IN SOAY (A) AND OTHER BREEDS OF SHEEP (B) UNDER A VARIETY OF CONDITIONS.

Breed	Sheep no.	Session no.	Treatment	No. of readings	Time (sec) mean ± standard deviation
A	1	1	$BaSO_4$ through cannula 0.8 ml/min.	22	49.50 ± 2.32+
A	1	2	500 ml saline through cannula	19	50.37 ± 2.09
A	2	1	50 ml $BaSO_4$ per os	18	51.67 ± 2.28
A	2	2	50 ml $BaSO_4$ + 500 ml whey per os	27	50.96 ± 1.79
A	2	3*	Balloon inflated with 500 ml air	23	51.09 ± 1.85
A	3	2*	50 ml $BaSO_4$ per os	25	51.48 ± 4.77
A	3	2*	50 ml $BaSO_4$ + 50 ml whey per os	18	50.28 ± 3.14
A	3	3	50 ml $BaSO_4$ + 500 ml whey per os	16	48.63 ± 1.93
A	3	4*	Balloon inflated 500 ml air	24	51.17 ± 3.76
B	4	1	$BaSO_4$ through cannula 0.8 ml/min.	17	58.88 ± 1.73
B	4	2	500 ml of air into abomasum	13	59.00 ± 3.27
B	5	1	$BaSO_4$ through cannula 0.8 ml/min.	8	56.57 ± 2.49
B	5	2	Balloon inflated with 500 ml air	10	60.20 ± 1.69
B	21	1	50 ml $BaSO_4$ per os	29	59.28 ± 2.85
B	21	2	50 ml $BaSO_4$ + 500 ml milk per os	24	59.71 ± 2.63
B	22	1	Before feeding	7	58.43 ± 3.73
B	22	2	After feeding	7	56.14 ± 3.02
B	23	1	Before feeding	7	57.71 ± 3.25
B	23	2	After feeding	12	58.17 ± 1.75

* To simplify further analysis and achieve a constant subsample size for the mean readings within sheep, these readings have not been included in the analysis of variance.

\+ Excluding quiescent periods.

TABLE XII

ANALYSIS OF VARIANCE

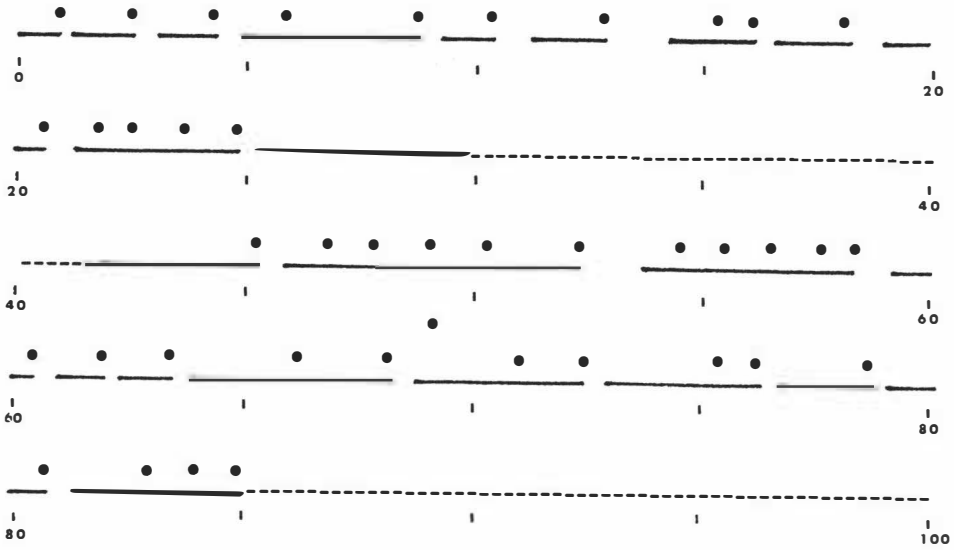
Variation	d.F	Sum of Squares	Mean Square	F Ratio
Between breeds	1	238.44	238.44	24.33 (P < 0.01)
Between sheep within breeds	6	8.23	1.37	0.14 NS
Between sessions within sheep	8	14.11	1.76	0.18 NS
Between readings within sessions	245	2400.2	9.80	--

FIGURE 9

Depiction of the relationship between abomasal pyloric antral activity (solid line), onward passage of a bolus from the duodenal bulb (dots) and rhythmic segmental activity in the jejunum (broken line). Time scale in minutes.

Graph A after bottle-feeding 50 ml $BaSO_4$: graph B after bottle-feeding 50 ml $BaSO_4$ mixed with 500 ml whey.

SHEEP No. 2 GRAPH A



SHEEP No. 2 GRAPH B

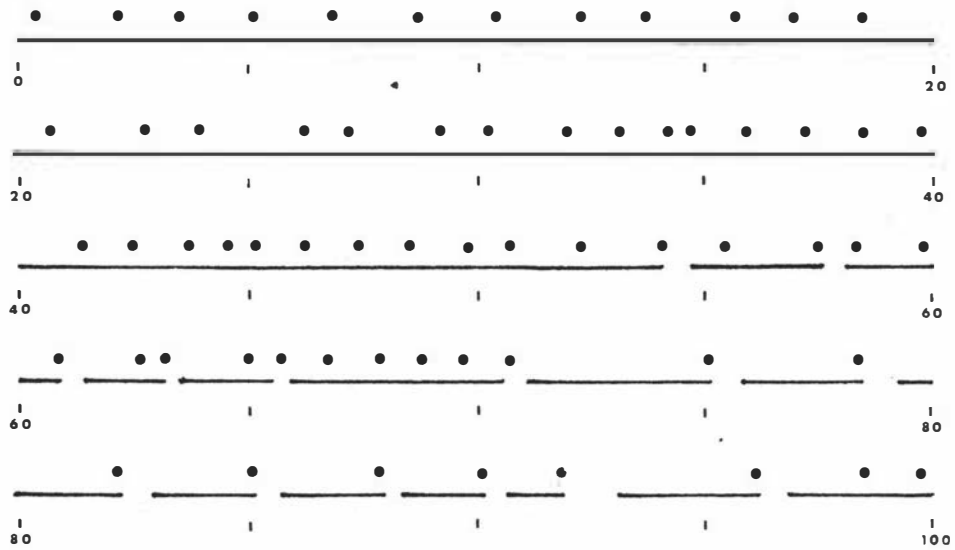
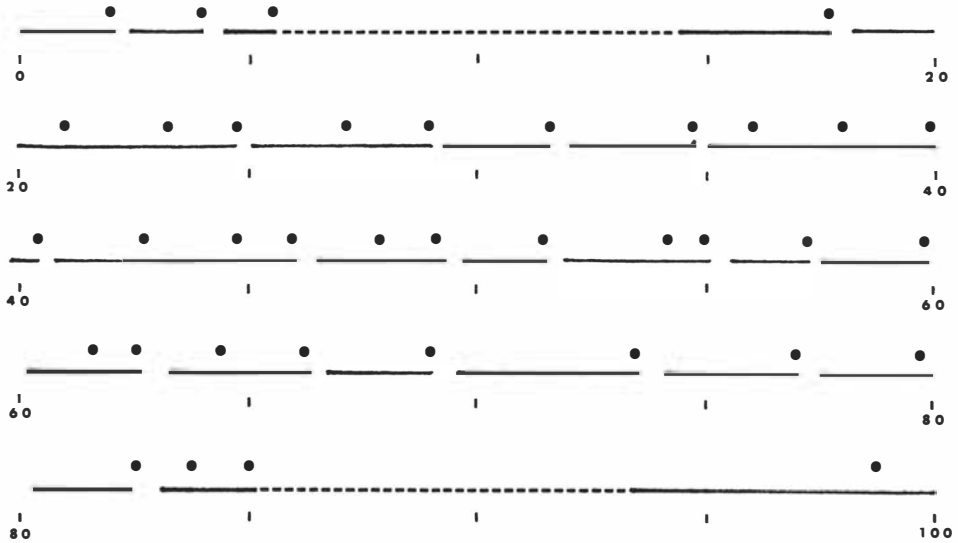


FIGURE 10

Depiction of the relationship between abomasal pyloric antral activity (solid line), onward passage of a bolus from the duodenal bulb (dots) and rhythmic segmental activity in the jejunum (broken line). Time scale in minutes.

Graph A $BaSO_4$ infused through an abomasal catheter at a rate of 0.8 ml/min : graph B $BaSO_4$ infused through an abomasal catheter at a rate of 0.8 ml/min and a balloon inserted in the abomasum inflated with 100 ml of air (downward pointing arrows) then deflated (upward pointing arrows).

SHEEP No. 5 GRAPH A



SHEEP No. 5 GRAPH B

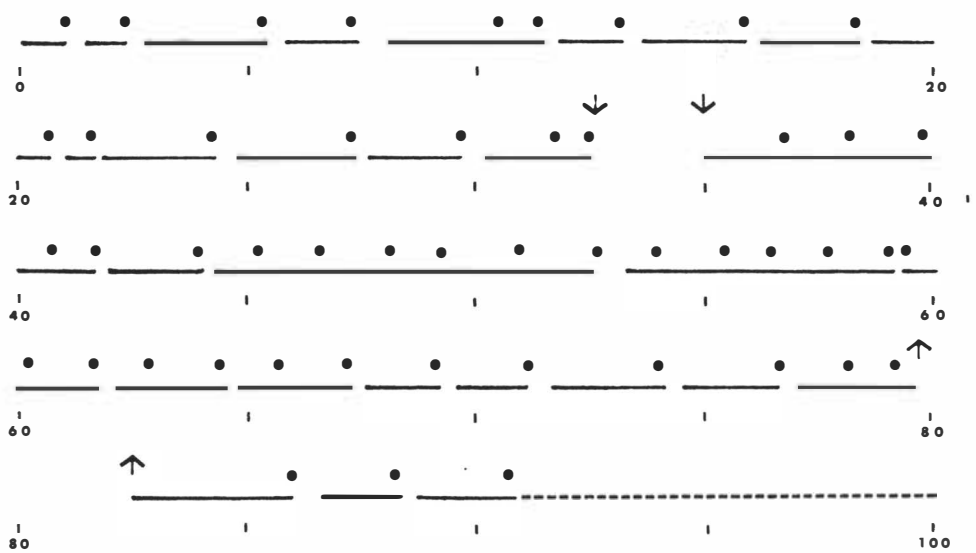
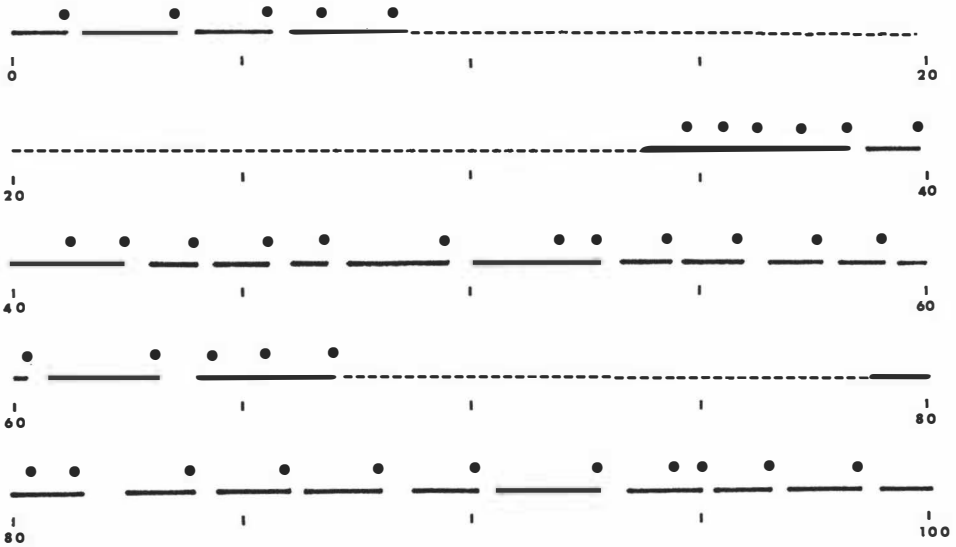


FIGURE 11

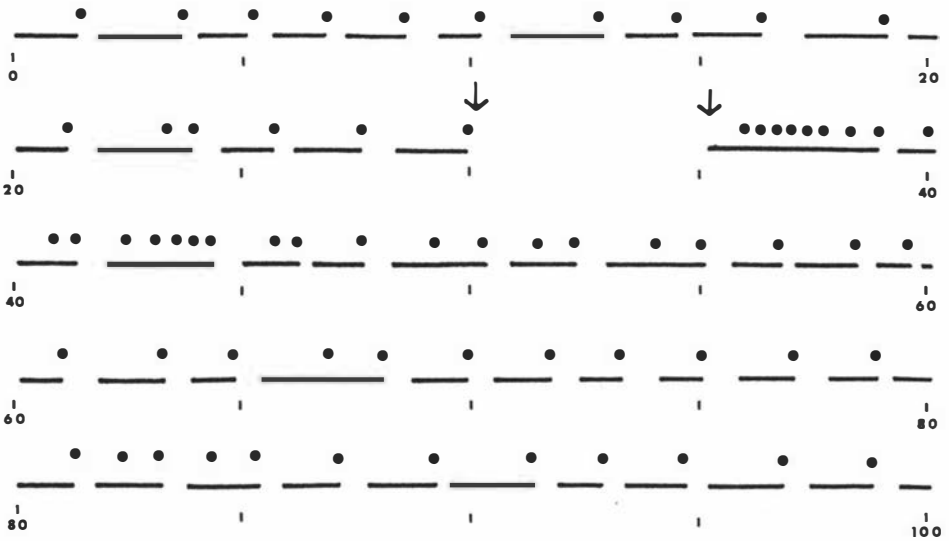
Depiction of the relationship between abomasal pyloric antral activity (solid line), onward passage of a bolus from the duodenal bulb (dots) and rhythmic segmental activity in the jejunum (broken line). Time scale in minutes.

Graph A after bottle feeding 50 ml of $BaSO_4$: graph B bottle feed 50 ml $BaSO_4$ mixed with 500 ml milk over time marked with arrows.

SHEEP No. 21 GRAPH A



SHEEP No. 21 GRAPH B



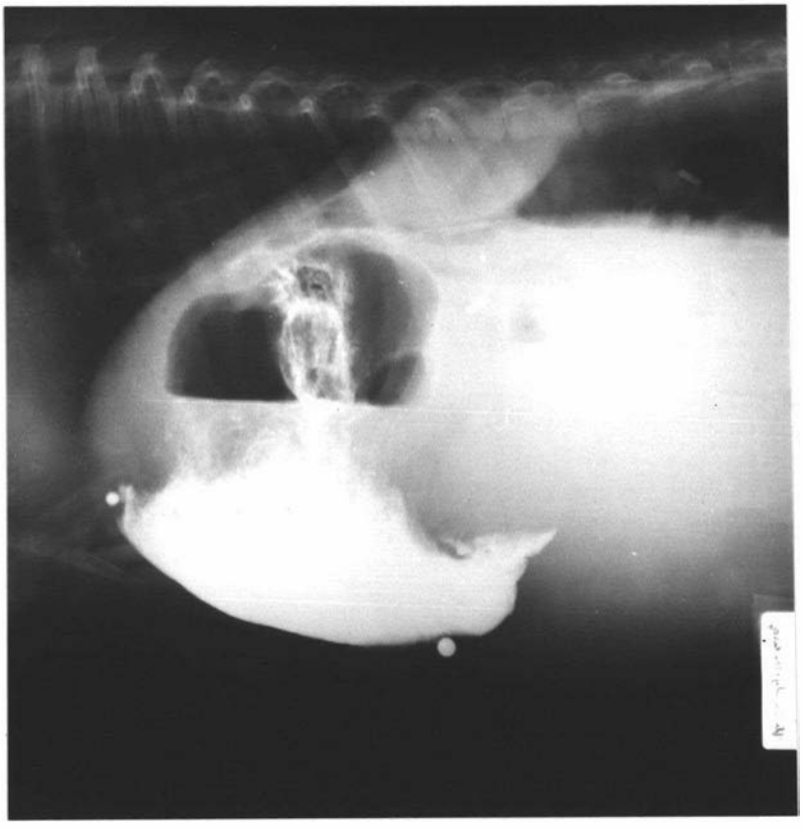
of peristaltic contractions at the pylorus during periods of abomasal activity was consistent within sheep and within breeds so the pyloric antrum acted as a pump with a constant stroke frequency but a variable stroke volume. The duodenal bulb and initial ascending part of the duodenum gradually became filled with digesta; then contraction of the duodenal bulb initiated a wave of contraction which rapidly propelled the digesta to the jejunum. The number of peristaltic waves arriving at the pylorus required to push enough digesta into the duodenum to initiate a contraction was variable. The only type of activity which did not fit into this pattern were the static waves seen in the body of the abomasum.

During this series of observations, two isolated but interesting events were recorded. The first of these occurred in Sheep 21 when it was 12 weeks old. At this time, it had not been weaned and was fed cow's milk from a bottle 3 times per day. It was housed in a pen on a bedding of sawdust, separated from its neighbours by a slatted wooden partition. From time to time, it had been observed to push its head between the slats and nibble at the wool of its companions on either side. At one session, after being fed 500 ml of cow's milk mixed with 50 ml of barium sulphate suspension, a radiolucent object outlined with barium was seen within the omasum. This object approximated the omasum in size and shape (Plate 46). Over the following 5 minutes, it was seen to be slowly extruded from the omasum eventually to drop into the abomasum, where it floated at the interface between the gas cap and the liquid abomasal contents. This object was still visible floating at the interface the following day (Plate 47). Seven days later it had sunk through the digesta to lie on the abomasal floor (Plate 48), where it was still visible 6 weeks later. The second event was observed in Sheep 23, which was 3 weeks old and was maintained by bottle-feeding with 120 ml of cow's milk every three hours. It had been bottle-fed with 120 ml of cow's milk mixed with 50 ml of barium sulphate and had swallowed some, but not an excessive volume, of gas. Video-tape recording of abomasal motility was commenced immediately feeding had finished. A large piece of what appeared to be curdled milk mixed with barium caused an obstruction in the pyloric antrum, so when the gas cap was displaced round from the fundic region, it was unable to escape through the pylorus. The result of this was

PLATE 46

Later radiograph of the abdomen of Sheep 21 taken immediately after bottle-feeding with 50 ml of $BaSO_4$ mixed with 500 ml of milk. An object outlined with $BaSO_4$, can be seen being extruded from the omasum.

Ab abomasum, B ball-bearings, DRu dorsal rumen, E electrodes, G gas caps, H object being extruded, O omasum, Re reticulum, VRu ventral rumen.



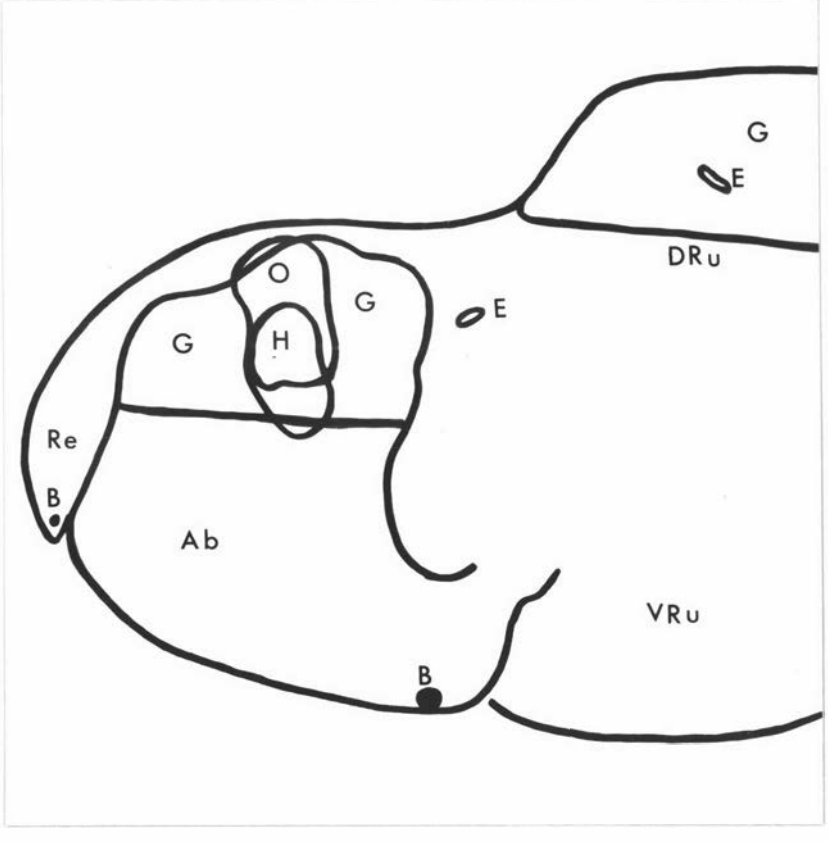
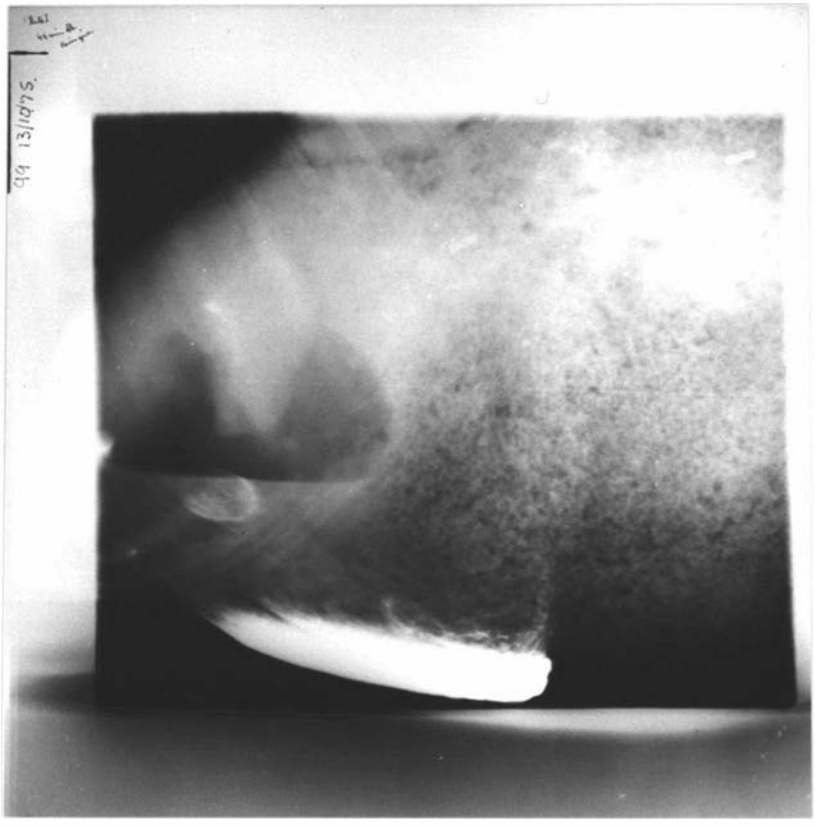

G
E
DRu
O
G
E
G
H
Re
B
Ab
VRu
B

PLATE 47

Lateral radiograph of the abdomen of Sheep 21 taken the day following the radiograph in Plate 46. The extruded object can be seen floating in the abomasum.

Ab abomasum, DRu dorsal rumen, E electrodes, G gas cap, H extruded object, O omasum, VRu ventral rumen.


99 13/1075.

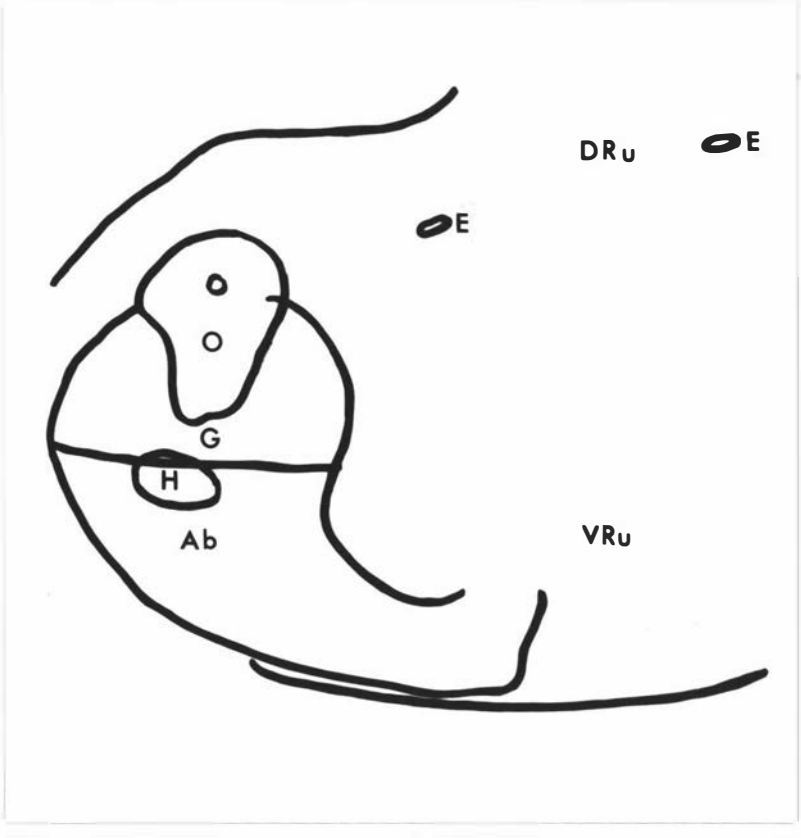
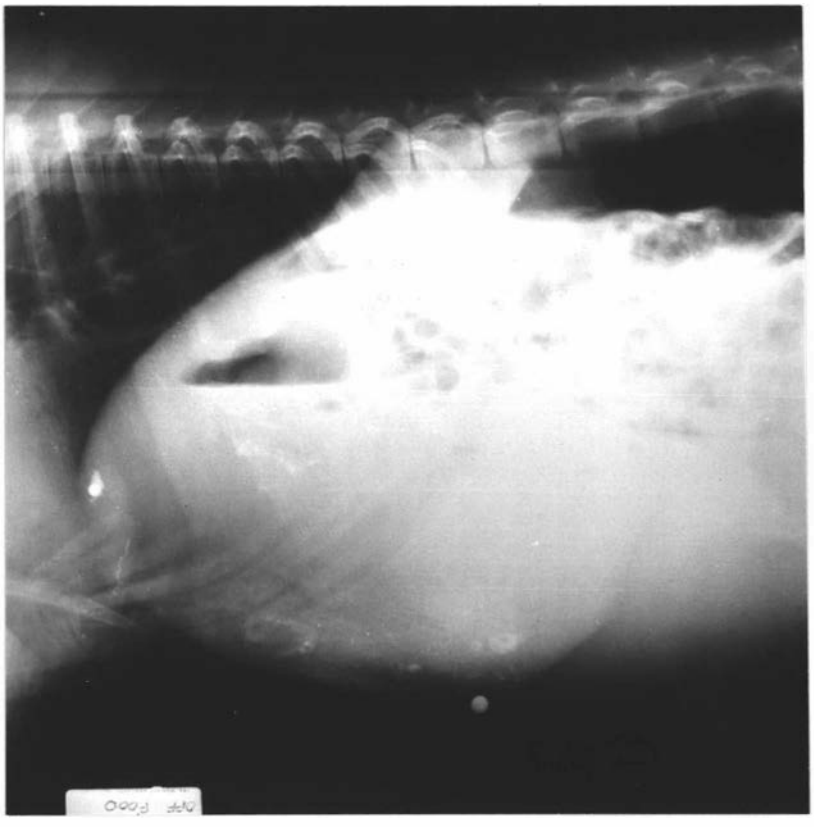
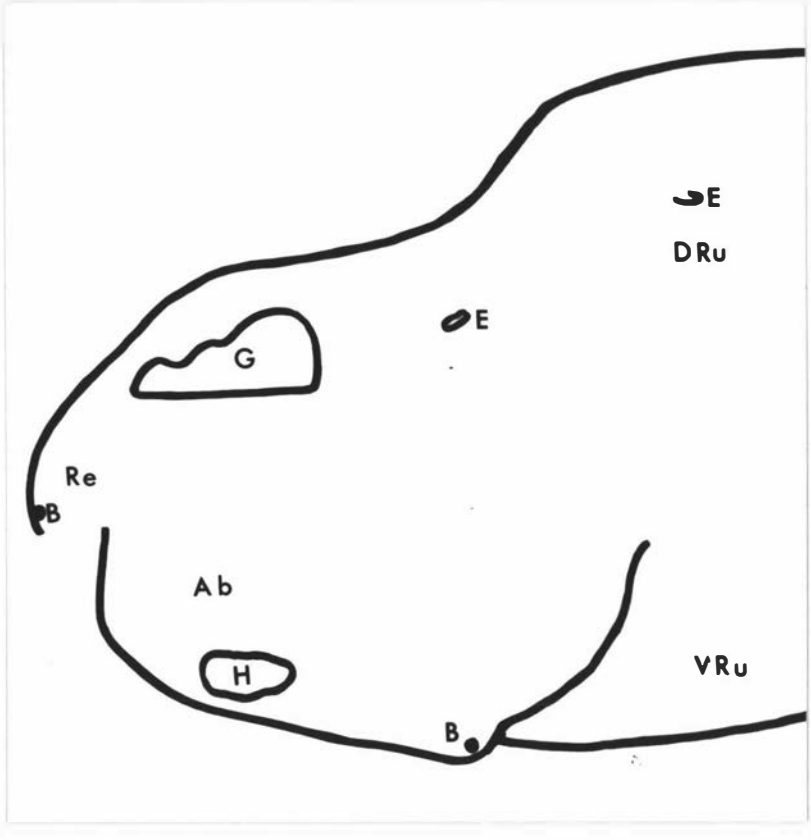

DRu
E
E
O
O
G
H
Ab
VRu

PLATE 48

Lateral radiograph of the abdomen of Sheep 21 taken 7 days after the radiograph in Plate 46. The extruded object has now sunk to the greater curvature of the abomasum.

Ab abomasum, B ball bearings, DRu dorsal rumen,
E electrodes, G gas cap, H extruded object, Re reticulum
VRu ventral rumen.




E
DRu
E
G
Re
B
Ab
H
VRu
B

that the gas-filled body of the abomasum floated dorsally (Fig. 12). This movement displaced the obstructing object from the pyloric antrum and allowed the gas to be eliminated through the pylorus, and as this happened, the body of the abomasum slowly returned to its normal position.

A marked relationship between meal frequency, meal size and abomasal activity after feeding was observed. In Sheep 21 which was bottle-fed three times a day, the abomasum was distended with milk and gas and the pattern of motility observed in the abomasum and duodenum (Fig. 11) was altered for a considerable time. In Sheep 22 and 23 which were fed smaller amounts every 3 hours the changes to the pattern of motility after feeding were minimal (Fig. 13). The two lambs which were suckling their mother had no detectable change in the pattern of motility following suckling.

4:4 DISCUSSION

Ehrlein and Hill (1969) found there was no detectable change in size or shape of the omasum during its contraction sequences. In the present study no radiographic evidence of the sequences of contraction described by other workers (Ogha *et al*., 1965; Ehrlein and Hill, 1969; Bueno *et al*., 1972, Bueno and Ruckebusch, 1974; Bueno, 1975) was seen. It seems probable therefore that these contractions - which were demonstrated by means such as balloons, strain gauges and electromyography - are isometric rather than isotonic in nature.

The movement of the omasum towards the cardia, and the small dorsal movement of the pole of the reticulum which occurred when bottle-fed sheep sighted the feeding bottle would most likely indicate closure of the reticular groove (Titchen and Newhook, 1975). This supports the observation made by Wise (1939) and Orskov *et al*. (1970) that the sight or smell of milk was sufficient to cause closure of the groove in trained animals. Further evidence that closure of the groove can be evoked by the anticipation of suckling was given by two other observations: air that was swallowed during the period of excitement just before the bottle was given passed directly into the abomasum, and orally administered ball bearings passed directly into the

FIGURE 12

Drawings taken from video-tape recording of the abomasal function of Sheep 23. Dotted area represents gas.

A. Immediately following feeding with a moderate gas cap in the abomasal fundus.

B. Gas has been displaced into the body region causing it to displace dorsally.

C. Dorsal displacement of the body region of the abomasum.

Du duodenum, P pylorus.

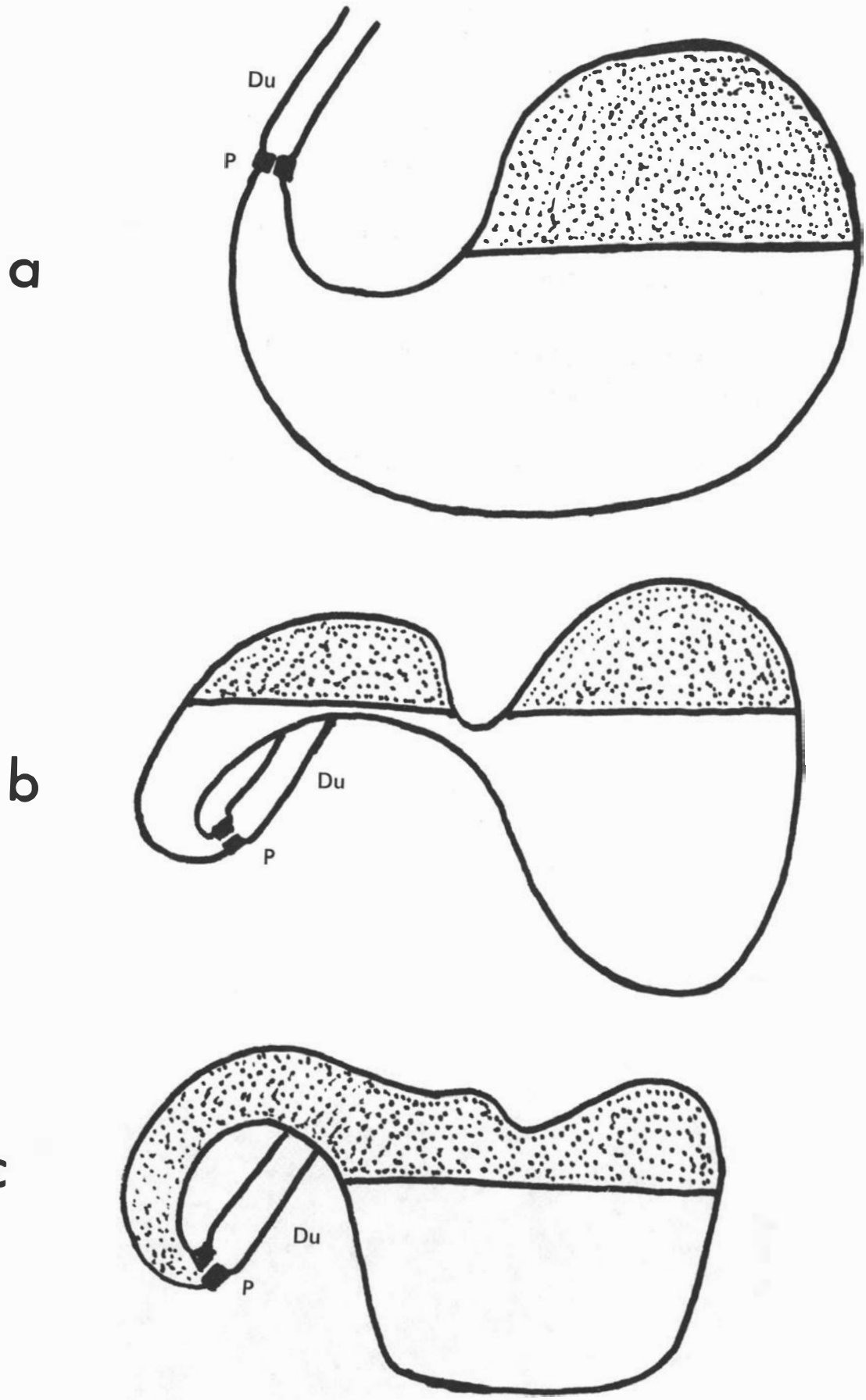
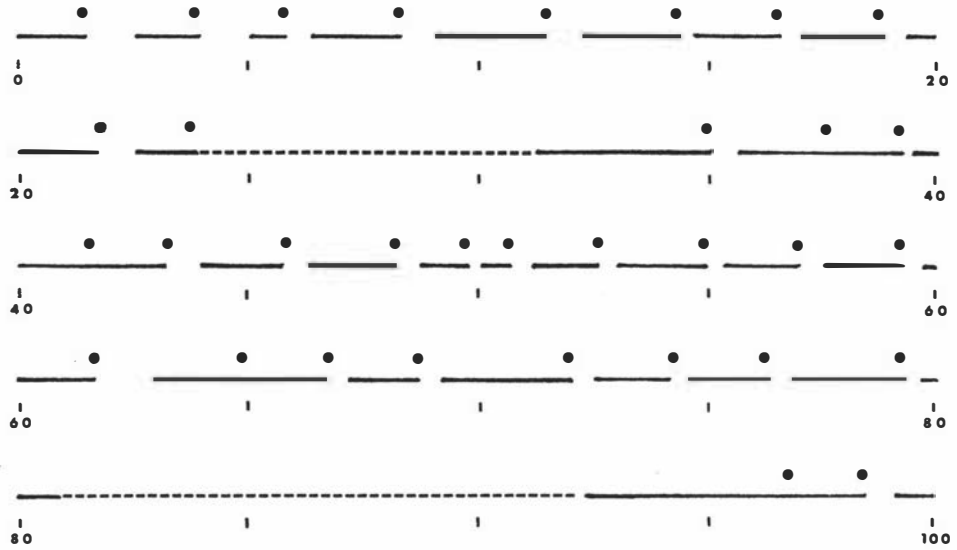

a
Du
P
b
Du
P
c
Du
P

FIGURE 13

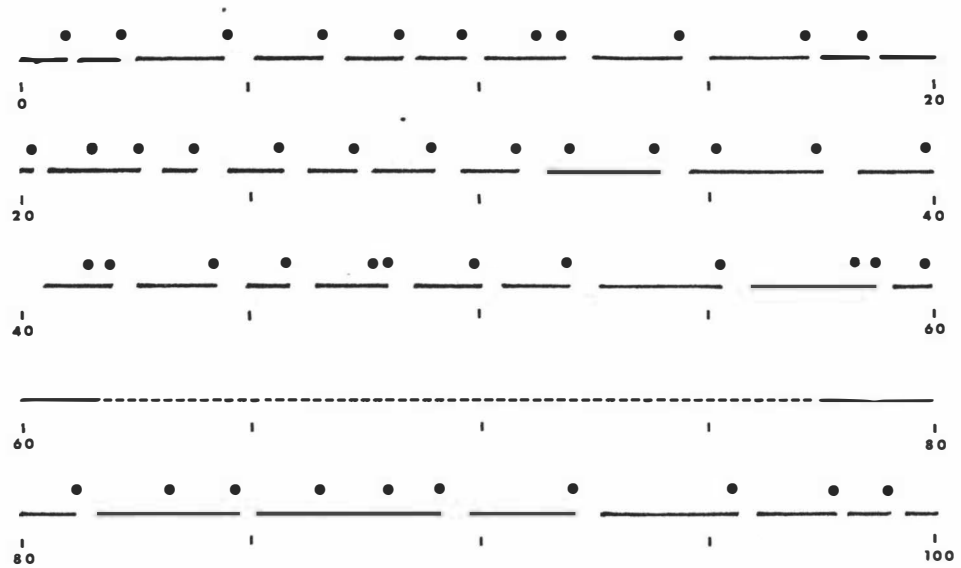
Depiction of the relationship between pyloric antral activity (solid line), onward passage of a bolus from the duodenal bulb (dots) and rhythmic segmental activity in the jejunum (broken line). Time scale in minutes.

Both graphs of activity after feeding 120 ml of milk mixed with 50 ml of $BaSO_4$ in 24 day-old lambs (22, 23) fed 150 ml milk 8 times each 24 hours.

SHEEP No. 23 GRAPH A



SHEEP No. 22 GRAPH A



abomasum when they were given by the individual who bottle-fed the sheep. This suggests that in bottle-fed animals the reflex closure of the reticular groove can be cortically mediated by the anticipation of feeding, before there is a response to buccopharyngeal stimulation as demonstrated by Comline and Titchen (1951).

The large volume of air swallowed by bottle-fed animals has been demonstrated previously (Benzie and Phillipson, 1957) and is probably the result of a combination of factors. The design of the teat and the bottle would be expected to have the largest influence. The lambs suckling from their mothers swallowed a much smaller volume of air because they could form a better seal on the teat and they did not have to let air back up into the bottle to break the vacuum. Also the feeding regimen imposed on bottle-fed animals meant that they were hungry and drank more avidly than their ad libitum-fed counterparts suckling their mother. The distension of the abomasum in bottle-fed sheep, resulting from the ingestion of a large volume of liquid and air, caused marked changes in the patterns of both abomasal and small intestinal motility. This suggests that the changes in these patterns reported by Ruckebusch and Bueno (1973) when calves are weaned off a bottle are a result of decreasing abomasal distension rather than a direct effect of weaning. Normal motility patterns of abomasum and small intestine similar to those in the weaned animal were found in lambs fed every three hours and in lambs suckling normally from their mothers. These findings indicate that if young ruminants have to be fed artificially, a more normal state of alimentary tract function would be achieved by feeding at frequent intervals and by using teats and bottles designed to keep the amount of swallowed air to a minimum.

The passive displacement of the fundic region of the abomasum associated with reticular contractions was first reported by Czepa and Stigler (1926) and has been remarked on since by a number of authors including Benzie and Phillipson (1957) and Ehrlein and Hill (1970). No function has so far been ascribed to this movement. Possibly it plays some part in sucking or washing digesta out of the omasum as most of the flow from omasum to abomasum also occurred during its course. The slow flow of contrast material seen would suggest a washing rather than a sucking action. Another function could be to

mix abomasal contents during periods of quiescence in the motility of the organ.

The radiographic observations of the regular rhythmic contractions migrating across the pyloric antrum and the integrated action of the pylorus, are similar to those previously described (Magee, 1932; Phillipson, 1939; Benzie and Phillipson, 1957; Ehrlein and Hill, 1970; Ehrlein, 1976). The timing of relaxation of the pyloric sphincter relative to the approaching rings of contraction controlled the amount of digesta passed through to the duodenum. No radiological evidence could be found to support the suggestion made by Lauwers et al. (1979) that a plug formed by mucosal folds close to the pylorus acts to prevent passage of digesta.

The frequency of contractions was found to be 8.3 $\pm$ 0.2/minute for the Soay breed of sheep and 7.2 $\pm$ 0.2/minute for the other breeds. This significant between-breed difference ($P < 0.01$) may explain the discrepancy between the present results and those of Ehrlein (1970) (5.6 $\pm$ 0.3/minute), Bolton et al. (1976) (6.6 $\pm$ 0.05/minute) and Ruckebusch and Bueno (1977) (5.6 $\pm$ 0.3/minute) working with other breeds of sheep. However, this difference could also be the result of other factors. The slight pause seen in abomasal contractions after a bolus was propelled down the duodenum has not been described previously and if it is not taken into account when calculating the frequency the figure derived would be lower. Normally boluses pass down the duodenum at approximately two minute intervals. During each two minute period therefore there is liable to be a period of about 30 seconds when contractions of the abomasal antrum cease. The frequencies reported here were calculated from counts taken over time intervals that did not include short periods without contractions. If the frequency of contractions in the breeds other than Soay is calculated from counts taken over time intervals that included such a period every two minutes, the frequency calculated would be within the figures previously quoted by Ehrlein (1970), Bolton et al. (1976) and Ruckebusch and Bueno (1977). Whichever way frequencies are calculated, there would remain a difference between the Soay and the other breeds used here.

Extended periods of inactivity were reported by Ehrlein (1970), and the observation that these periods were related to a migrating phase of rhythmic segmental activity on the jejunum confirms the findings of Ruckebusch and Bueno (1977).

Previous investigations of abomasal activity (Magee, 1932; Phillipson, 1939; Benzie and Phillipson, 1957; Kay, 1965; Ehrlein, 1970; Ruckebusch and Bueno, 1977) have found no contractions in the fundic region. It has been suggested that the fundic region of the abomasum, like the corresponding region of the simple stomach, acts as a reservoir and applies a tonic contraction pushing digesta towards the pyloric antrum (Ehrlein, 1976). This may well be so most of the time in sheep. However, in the present study, under certain circumstances peristaltic waves of contraction started up in the fundic region and migrated towards the pylorus. When the abomasum was relatively empty, as in bottle-fed sheep following an overnight fast, the first contractions of the abomasum that occurred following a period of inactivity started in the fundic region, but the site of origin then rapidly moved aborad as the pyloric antrum was filled. It would appear that the abomasal wall orad of the pyloric antrum is capable of peristaltic contraction but that distension of the antrum exerts an inhibitory effect which varies in degree in relation to the degree of antral fill. The stimulus for the contraction of the fundus seen after bottle-feeding appeared to be gaseous distension of the fundic region. These contractions displaced the gas cap round the lesser curvature effectively transporting it to the pylorus for elimination. On only one occasion out of nineteen was the gas cap seen to return through the omasum to the reticulo-rumen as reported by Phillipson (1939).

The static contractions of the ventral wall of the abomasum have not been reported previously. The possibility that these were "end on" views of the abomasal vela was considered but their orientation and distribution did not match those expected for vela. They also appeared and disappeared without any change in the position of the abomasum relative to the x-ray beam. They were narrow bands of contraction which occurred at infrequent intervals and were maintained for 2 to 4 minutes. No explanation of the cause or function of these

contractions can be offered.

The effect of abomasal distension on the flow through the omasum has been reported (Phillipson, 1939; Weiss, 1953; Titchen, 1958a, 1960) and on contraction sequences of the reticulo-rumen (Titchen, 1958a; Briggs, 1961; Ash, 1962, 1962a; Carr, 1970) but there is little information on the effect of the flow of digesta through the pylorus to the duodenum. The observation of a great increase in the number of boluses passing down the duodenum and the disappearance of periods of abomasal inactivity resulting from abomasal distension would indicate a marked increase in flow out of the abomasum. This increase in flow was not accomplished by an increase in motility as was suggested by Ehrlein and Hill (1970). There was no demonstrable increase in frequency of the contractions of the pyloric antrum: the effect appeared to be achieved by passing a greater volume of digesta into the duodenum with each antral contraction.

The object observed being extruded into the abomasum from the omasum was almost certainly a "hair ball". It was only outlined by the barium sulphate whereas if it had been a clot of milk the barium sulphate would have been dispersed evenly through it. Also the prolonged survival in the acid environment of the abomasum indicates material considerably more insoluble than milk. This observation would suggest that the omasum does act to filter out some material but it would appear to be of little purpose if a conglomorate of the collected material is eventually passed on to the abomasum.

The second observation of a dorsal displacement of the abomasum suggests how displaced abomasum in cattle might occur. It would appear that the accumulation of a large volume of gas coupled with either a mechanical or physiological obstruction to the flow of the gas out through the pylorus would cause abomasal displacement. This displacement then can result in a partial rotation causing a total obstruction so the situation cannot resolve itself as it did in the present instance.

Chapter V

MOTILITY OF THE SMALL INTESTINE

5:1 LITERATURE REVIEW

In 1899 Bayliss and Starling summed up the then current knowledge of motility of the small intestine as follows. "On no one subject in physiology do we meet with so many discrepancies of fact and opinion as in that of the physiology of intestinal movements. Among factors contributing to such divergencies must doubtless be included the varying behaviour of the gut in different animals, the varying conditions of the animal with regard to feeding, or conditions of experiment such as exposure and cooling of intestines. Although in many cases we have been able to explain the results obtained by previous observers by reference to one or other of the disturbing conditions mentioned above, we must confess that in some instances we have been absolutely unable to reproduce effects described by physiologists of repute, however we might vary our method of experiment; and we have had to come to the unsatisfactory conclusion that these results are due to fallacy of observation or experimental methods".

These two authors carried out their research into intestinal motility with dogs which were anaesthetised using morphia and a mixture of air, chloroform and ether, stating that the effect of morphia on intestinal motility was so slight that it was better to give a large dose of morphia than to rely completely on the gaseous mixture. The contractions of the intestine were observed directly by opening the abdomen when the dog was immersed in a warm saline bath. Graphic recordings were also made using a piece of apparatus which they designed and called an 'enterograph' which allowed the independent recording of contractions of the longitudinal and the circular muscle of the intestine. Their investigations were carried out on both intact intestine *in vivo* and isolated intestine *in vitro*. They came to the conclusion that two basic types of motility occurred in the small intestine. The first of these was a pendular movement which was rhythmical and resulted from simultaneous contraction of the circular

and longitudinal muscles. Pendular movements occurred with a frequency of 12 to 13 per minute and moved along the intestine at 2 to 5 cm/second. Bayliss and Starling claimed that these contractions were myogenic in origin. The second type of motility was a peristaltic contraction which was a wave of constriction that travelled only in an aborad direction. The peristaltic contraction was a reflex event which was initiated by mechanical stimulation and controlled through Auerbach's plexus. Bayliss and Starling demonstrated that the reflex could be abolished by the topical application of a local anaesthetic, and that it was not controlled by higher nerve centres. From their observations they formulated "A law of the intestine", which states "Local stimulation of the gut produces excitation above and inhibition below the excited area" (Bayliss and Starling, 1899). Although the effects were dependent on the local nervous system, Bayliss and Starling also demonstrated the existence of some central nervous control over intestinal motility. Stimulation of the splanchnic nerves was shown to cause inhibition of motility while stimulation of the vagal nerves was shown to cause an initial inhibition of short duration, followed by a period of augmentation.

The earliest publication on the use of x-rays to investigate alimentary tract function is that of Cannon (1898). He studied the movements of the stomach in cats, using subnitrate of bismuth as a contrast agent. In 1901 he reported to the Boston Society of Medical Sciences on his studies on the motility of the intestines, again using x-rays as the method of observation. This remarkable paper, published in 1902, records his observations of intestinal motility in cats after they had been fed a mixture of canned salmon and subnitrate of bismuth; he concluded that there were three different types of movement to be seen in the small intestine of cats (Cannon, 1902). The first type of movement described was a pendular or swaying movement which corresponded to the pendular movement seen by Bayliss and Starling (1899). Also like Bayliss and Starling, he described peristaltic waves of contractions but he subdivided these into two different types. The first type of peristaltic activity was seen mainly when digesta was passed on from the duodenum. It was a rapidly progressing wave of contraction which propelled the gut contents continuously through a number of loops of intestine. The second type of peristalsis was much slower

and passed the contents along for only a few centimeters before stopping. It could take several forms one of which could be associated with rhythmic segmental contractions, the most common type of activity seen in the small intestine of cats. When rhythmic segmental contractions were initiated, a column of digesta was broken up into segments which were subdivided and reformed. He noted that digesta progressed very slowly under this type of activity and suggested it to be a mixing movement bringing the digesta into contact with the intestinal wall, so facilitating absorption as well.

Cannon (1902), continued with some important observations on the movement of digesta through the alimentary tract. Food material did not pass through the pylorus with every contraction of the pyloric antrum; but when the pylorus did relax digesta was pushed through into the duodenum where it joined, or was then joined by, other ejections from the pylorus. When the duodenum was filled with digesta, rhythmic segmentation of the duodenum started up, usually with the intervals between each segment being long so that the digesta was shunted back and forth over a distance of some centimeters. A peristaltic contraction then occurred, carrying some of the gut contents for a considerable distance down into the small intestine where they sometimes remained static for several hours. Following this period of quiescence, rhythmic segmentation started at this site and was followed by peristalsis which propelled the contents towards the ileo-caecal valve. The transit time from pylorus to ileo-caecal valve was usually 4 - 5 hours, but depended on the nature of the ingesta.

Although the present review is concerned with the motility of the small intestine, Cannon's (1902) observations on the function of the large intestine deserve note. He stated that the ileo-caecal valve was always competent, never allowing the back flow of material from the large intestine. Using his fluoroscopic screen he watched the radio-opaque material passing through the ileo-caecal valve into an empty colon and saw that antiperistaltic waves carried it back up into the caecum. The contents built-up in the colon to the level of transverse and descending regions. As the faecal material moved down the colon, tonic contractions divided it into globular masses. During the act of defaecation the entire colon moved around so that the ascending

part came to lie in the position of the transverse part and a ring of contraction occurred in the descending colon which moved towards the anus, expressing all the material caudal to it. This comprehensive report of Cannon's (1902) concludes with yet another interesting observation: if an animal was at all distressed the movements of both the large and small intestines were entirely inhibited.

Following on from Cannon's work it might have been expected that radiology would have become one of the main methods of investigating motility of the small intestine, but this has not been the case. Only a few investigations since have used radiology as a means of observing intestinal motility; Liljedahl et al. (1958), Mattsson et al. (1960) and Friedman et al. (1965) are amongst the most important of these. Most investigations of the muscular activity of gut and its control have been made using other methods. Direct observations were carried out either by opening the abdomen (Alvarez, 1914; Hukuhara, 1930-31; Dukes and Sampson, 1937) or by exteriorising loops surgically prepared to various designs (Biebl, 1930; Douglas and Mann, 1939; Hiatt et al., 1966). Some work was carried out using isolated segments of gut (Alvarez, 1914; Diament et al., 1961).

Many methods of making graphic recordings of contractions of the gut have been developed. Changes in intraluminal pressure have been recorded using balloons either singly or in series (Templeton and Lawson, 1931; Rowlands et al., 1950; Code et al., 1952; Hightower, 1952; Smith, 1959), open tipped catheters (Brody and Quigley, 1951; Coombe, 1966) and pressure sensitive radiopills (Farrar and Bernstein, 1958; Ramorino and Colagrande, 1964). Information on the strength and direction of contractions has been obtained using small strain gauges (Bass et al., 1961; Reinke et al., 1967; Ruckebusch, 1970; Grivel and Ruckebusch, 1972). However the method that has become widely used to investigate intestinal motility has been that of recording of the electrical activity of the muscles of the gut wall (Alvarez and Mahoney, 1922; Berkson, 1933; Bozler, 1946; Milton et al., 1955; Armstrong et al., 1956; Holaday, 1958; Daniel et al., 1960, 1960a; Bass et al., 1961; Bortoff, 1961; Coombe, 1966; Ruckebusch, 1970; Grivel, 1971; Grivel and Ruckebusch, 1972; Ruckebusch and Bueno, 1973).

Alvarez and Mahoney (1922) were the first to demonstrate electrical activity of the gut wall. Research done since then has established that this electrical activity has two components. One component which is always present is a slow change in potential occurring regularly over the length of the small intestine. This has been variously called the "slow wave", "pacesetter potential" or "basic electrical rhythm". Bozler (1946) suggested that this slow wave acted as the pacemaker for contractions of the gut wall, a hypothesis also supported by Code et al. (1968). Bortoff (1961) found that this rhythmic change in electrical potential occurred in the longitudinal muscle, and that the frequency and rate of propagation decreased from duodenum to ileum. The slow wave frequency and rate of propagation has been shown to be consistent at a given site for each species but to vary between species (Grivel and Ruckebusch, 1972). The frequency and rate of propagation also change with temperature in such a way as to suggest they are a function of the metabolic rate (Christensen et al., 1966). The other component of intestinal electrical activity is a rapid change in potential, called a "spike" or "action" potential, which is superimposed on the slow wave. This spike potential is the action potential of a contraction of the circular muscle (Milton et al., 1955; Bass et al., 1961) and is associated with both a visible contraction of the gut wall and a rise in intraluminal pressure (Daniel et al., 1960; Ruckebusch et al., 1968). The value of electrical recordings as a means of monitoring gut motility lies in the fact that the different forms of gut contractions are associated with specific patterns of electrical activity.

The different forms of contraction of the small intestine were observed and described by early workers, for example Bayliss and Starling (1899) and Cannon (1902) as noted above; more recent descriptions of the three basic forms have been given by a number of authors (Ramorina and Colagrande, 1964; Grivel, 1971; Grivel and Ruckebusch, 1972). The first form of contraction consists of irregularly occurring, small, random, contractions of the circular muscle which take place throughout the small intestine. These are seen electromyographically as randomly distributed spiking potentials: this form of contraction is thus associated with, and is known as, irregular spiking activity (ISA) (Ruckebusch and Bueno, 1975). The second form of contraction is

a regular, rhythmic series of circular muscle contractions which travel aborad as a group: it is called rhythmic segmentation and is associated with regular occurring spiking activity (RSA). Rhythmic segmentation was first recognised by Alvarez (1914) and he noticed that the frequency of these contractions decreased as they moved aborad, an observation which led to the concept of the "intestinal gradient". The presence of the gradient was firmly established and was shown to be independent of an extrinsic nerve supply (Code et al., 1968). It was, however, partly dependent on continuity with the orad parts of the small intestine (Douglas and Mann, 1930; Douglas, 1948, 1949). The third form of contraction is a ring-like contraction of the lumen of the gut which is progressive and moves continuously over a variable distance (Ruckebusch, 1970). This is peristalsis and is a manifestation of the peristaltic reflex, the stimulus for which is stretch of the gut wall or tactile stimulation of its lining. The first step in peristalsis is a contraction of the longitudinal muscle distal to the stimulus which is then followed, 90^{o} - 180^{o} out of phase, by an aborad moving contraction of the circular muscle (Farrar and Zfass, 1967). The electrical activity associated with peristalsis is a burst of spike potentials which is seen to migrate rapidly across a series of electrodes placed along the small intestine (Ruckebusch, 1970).

The concept of a migrating myoelectrical complex (MMC) of the small intestine common to all species has been proposed (Code and Schlegel, 1974; Bueno et al., 1975). The MMC is comprised of three periods - a period of quiescence, a period of ISA and a period of RSA. The amount of time spent in each period is variable, as is the frequency of occurrence of MMCs.

In the sheep and the dog, MMCs occur at intervals of about 90 minutes. The ratio of inactive to active periods in an MMC is 1:2 while during the period of activity itself the ratio of ISA to RSA is 8.9:1 (Szurszewski, 1969; Ruckebusch and Bueno, 1975). However, this regular occurrence of the MMC has been shown to be modified by many factors. In sheep and weaned calves the MMC is always present and is not abolished by feeding (Grivel and Ruckebusch, 1972; Ruckebusch and Bueno, 1973) but in the dog it is replaced by ISA for over seven hours

after feeding (Code and Marlett, 1975). With pigs the pattern is altered depending on the feeding routine. If the food is given ad lib., the MMC is not affected by eating, but if a single meal is presented the MMC is disrupted as it is in the dog after eating (Ruckebusch and Bueno, 1976).

There is still considerable debate as to the control mechanisms of the MMC and there is evidence of both neurological and hormonal control. Although it has been shown that MMCs will occur over neurologically isolated loops of bowel (Aeberhard et al., 1980) this conflicts with the evidence for an extrinsic neural control presented by Carlson et al. (1972). The pattern of the MMC is not significantly altered by vagotomy, splanchnicectomy or both (Ruckebusch and Bueno, 1975; Ruckebusch and Bueno, 1977, 1977a) so the role of the extrinsic nerve supply remains unclear. The inhibition of the MMC that occurs following opening of the abdominal cavity is abolished by splanchnicectomy (Bueno et al., 1978) which does demonstrate that extrinsic nerves influence the MMC.

It was demonstrated by Wingate et al. (1976) that the intravenous infusion of the hormone motilin induced an MMC. This effect was confirmed by Vantrappen et al. (1978) who showed that plasma levels of motilin peak about 15 minutes before the RSA occurred in the orad part of the jejunum. The relationship could not be demonstrated in the pig (Borody et al., 1981). Insulin has also been shown to affect the MMC particularly in the dog. In the dog the administration of insulin abolishes the MMC and causes ISA to persist for 4 - 5 hours while in sheep there is a lesser but still obvious effect. Gastrin has a similar effect in dogs but this lasts for only about one hour and has no effect in sheep (Bueno and Ruckebusch, 1976, 1976a).

Carlson et al. (1972) reported that in dogs with Thiry-Vella loops the MMC passed across the loop of small intestine as if it were still an integral part of the small intestine, a finding supported by the work of Grivel and Ruckebusch (1972). It has been suggested that the MMC is controlled from an extrinsic centre possibly located in the prevertebral ganglia (Wingate et al., 1976). However, this is disputed

by Ruckebusch and Bueno (1977) who found that denervating a length of gut had no effect on the MMC in sheep. Recent work suggests that the MMC is intrinsic to the small intestine and will occur in neurologically totally isolated segments (Aeberhard et al., 1980).

The pattern of motor activity of the small intestine is the MMC (Bueno and Ruckebusch, 1973) but it remains unclear whether its control is extrinsic, intrinsic or a combination of both. Code et al. (1968) suggested a hypothesis to explain the relationships between the patterns of electrical activity of the intestinal wall and the patterns of digesta movement. To test this hypothesis a correlation had to be established between the electrical activity of the intestinal wall and the movement of digesta. In the course of these observations the hypothesis was suggested that the form of contractions of the gut wall was directly related to the volume of digesta present so a further series of experiments was formulated to test this.

5:2 MATERIALS AND METHODS

This study of the movement of digesta in the small intestine of sheep involved the following observations and experiments:

Radiological observations of digesta movements in the normal small intestine (5:2:1);

Radiological observations of the effects on digesta movements caused by the insertion of cannulae in the small intestine (5:2:2);

Measurement of the volume and length of boluses in the duodenum and proximal jejunum (5:2:3);

Experimental initiation of contractions of the small intestine by the introduction of digesta into the lumen (5:2:4);

Recording of myoelectric potentials in the wall of the proximal jejunum (5:2:5);

Simultaneous radiological observations and electrical recordings for correlation of digesta movements with

myoelectrical activity (5:2:6);

Observation of the effects on the myoelectrical activity of the small intestine of removal of digesta or the introduction of digesta (5:2:7).

Animals and their preparation: Details of the 14 sheep used are given in Table XIII. The animals were housed and fed as described in Chapter 3.

Sheep 1, 4, 5, 21 and 28 had abomasal cannulae inserted (Chapter 3:2) 2 months before being used in these experiments. After the first series of observations (5:2:1) were made, all the sheep except 22, 23, 30, 32, 33 and 34, had duodenal catheters inserted. Sheep 1, 2, 3, 4 and 5 had re-entrant cannulae inserted at different sites in the small intestine. Sheep 28, 30, 31, 32, 33 and 34 had T cannulae inserted in the proximal jejunum and an array of electrodes implanted in the wall above and below the site of cannulation.

Catheterisation: The catheters were 300 mm long. They were silastic medical grade tubing (Dow Corning) with an internal diameter of 1.7 mm and an external diameter of 2.75 mm. Polypropylene discs, 15 mm in diameter, were glued on 3 mm and 8 mm back from the tip, using silastic medical adhesive silicone type A (Dow Corning). Fixed to the outer end was the plastic boss from an 18 gauge hypodermic needle (Plate 50).

Following preparation of the site, a low right flank para-costal incision was made into the peritoneal cavity. The pylorus and ascending duodenum were identified and brought out through the incision. Great care was taken to control all haemorrhage and to handle tissues carefully to minimise the formation of adhesions. Rubber-shod bowel clamps were placed across the abomasal antrum just orad of the pylorus and on the ascending duodenum close to the sigmoid flexure. The region of the duodenal bulb was then identified and a purse-string suture, passing down to the submucosal region, placed on its anti-mesenteric edge. An incision into the duodenum was made within the purse-string and the first disc of the catheter passed through into

TABLE XIII

SHEEP USED FOR THE INVESTIGATION OF THE MOTILITY OF THE SMALL INTESTINE

Sheep No.	Age (months)	Breed	Sex	Where housed	Surgical Preparation	Comments
1	7	Soay	F	Rowett	V,W,X.	
2	7	Soay	F	Rowett	W,X.	Bottle-trained
3	7	Soay	F	Rowett	W,X.	Bottle-trained
4	9	Dorset/ Suffolk	F	Rowett	V,W,X.	
5	9	Dorset/ Suffolk	F	Rowett	V,W,X.	
21	3	Dorset/ Finnish	M	Rowett	V,W.	Bottle-fed
22	0.75	Dorset/ Finnish	M	Rowett		Bottle-fed
23	0.75	Dorset/ Finnish	F	Rowett		Bottle-fed
28	8	Romney	F	Massey	V,W,Y,Z.	
30	9	Romney	F	Massey	Y,Z.	
31	10	Romney	F	Massey	W,Y,Z.	
32	11	Romney	F	Massey	Y,Z.	
33	10	Romney	F	Massey	Y,Z.	
34	10	Romney	F	Massey	Y,Z.	

F - female

M = male

V = abomasal fistula or catheter

W = duodenal catheter

X = re-entrant cannula

Y = T cannulae

Z = electrodes

the lumen. The purse-string was then pulled up bringing the duodenal wall between the two discs, care being taken to ensure the wall was inverted. A second purse-string suture was then placed as close to the first as the discs would allow and this was also pulled tight, again making sure that the duodenal wall was inverted. The catheter was fed across the peritoneal cavity and brought out through the abdominal wall high on the right flank. A loose loop of catheter was left close to the duodenum to allow for subsequent movement. The laparotomy was closed in the normal manner, layer by layer. The catheter was attached to the outside of the animal by wrapping 6" elastoplast (Johnson and Johnson) loosely round the caudal part of the thorax and sticking the catheter to this using Sleek adhesive tape (Smith and Nephew) (Plate 49). The catheter was flushed daily with 5 ml isotonic saline to keep it patent.

Re-entrant cannulation: The re-entrant cannulae used were of the Ash type (Ash, 1962b). They were made from polyvinylchloride and had an internal diameter of 10 mm (Plate 51). The cannula was placed in the duodenum of sheep 50, 70 mm aborad from the pylorus. It was positioned vertically so that digesta from the duodenal bulb passed upwards. The sites of the other cannulae, all of which were positioned horizontally, were: in the duodenum just as it passed around the root of the mesentery (sheep 4); in the jejunum just aborad of the duodeno-jejunal junction (sheep 3); in the jejunum 800 mm aborad of the duodeno-jejunal junction (sheep 1); and in the ileum 400 mm orad of the ileo-caecal junction (sheep 2).

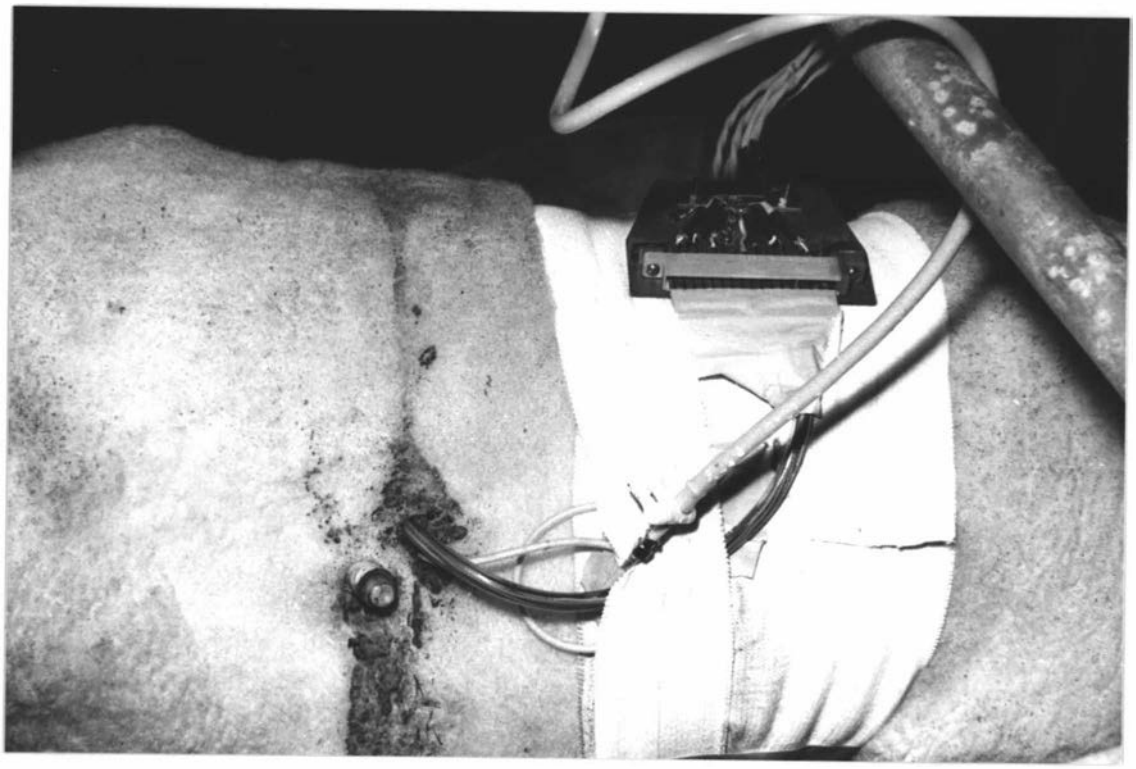
A low right flank laparotomy was performed and the region of small intestine to be cannulated identified and exteriorised. After the digesta had been gently massaged away the region was isolated from the rest of the intestine with 2 pairs of rubber-shod bowel clamps. The intestine was then transected and the two ends closed with an inverting suture of 2/0 chromic gut. The mesentery was split to allow mobility and easy separation of the two ends. Purse string sutures were placed 30 mm back from the transections on the antimesenteric edges. These were large enough to allow an incision to be made within them which would admit the shoes of the half cannula. The two halves of the cannula were then inserted, one on each side of the

PLATE 49

The right flank of sheep 31 photographed during a recording session. Starting from the left: the T cannula (end on) from the jejunum, the electrode cables encased in a length of polyvinylchloride tubing, and the duodenal catheter entering the body below the cable tubing. The cables lead up to the plug system seen on the animal's back which connects them to the pen recorder. The duodenal catheter is connected by a length of tubing (light tubing passing round horizontal bar) to a peristaltic pump. The adhesive tape round the thorax is used to hold the cables and catheter in position.

PLATE 50

The duodenal and abomasal catheters were made up from silastic tubing with polypropylene discs fixed to the end to be implanted. The boss from an 18 gauge hypodermic needle was fixed at the outer end.



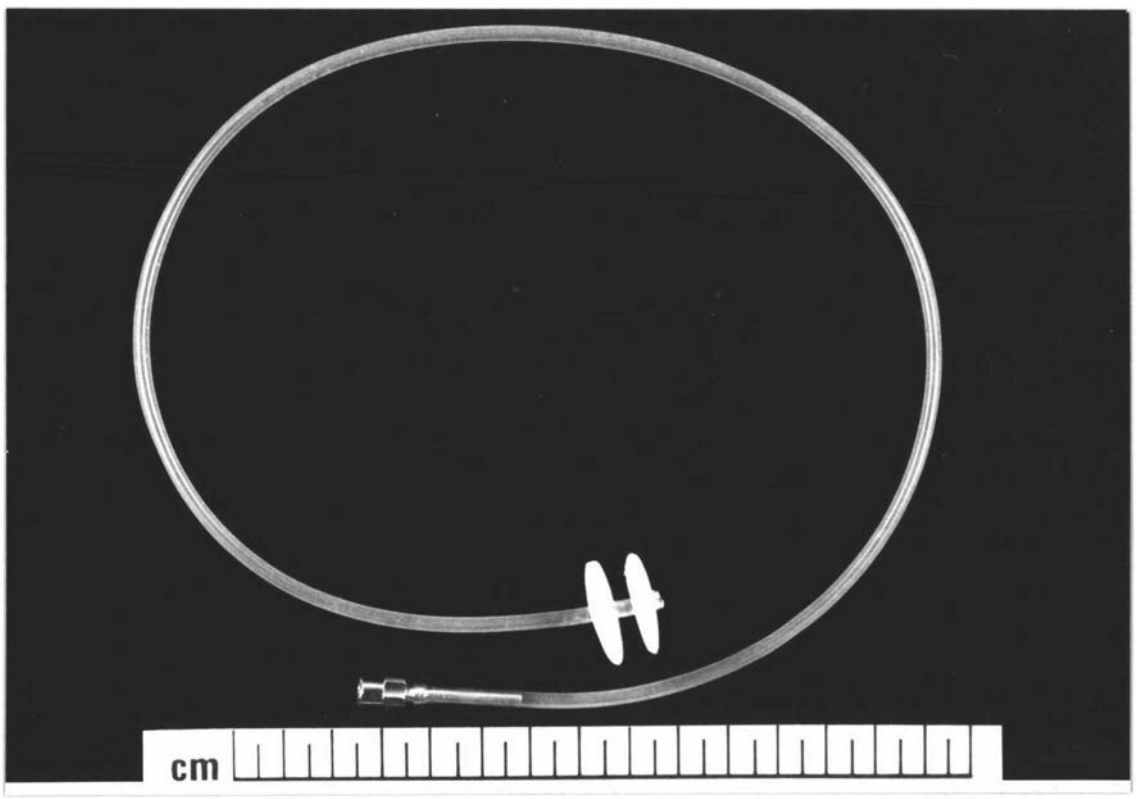

cm

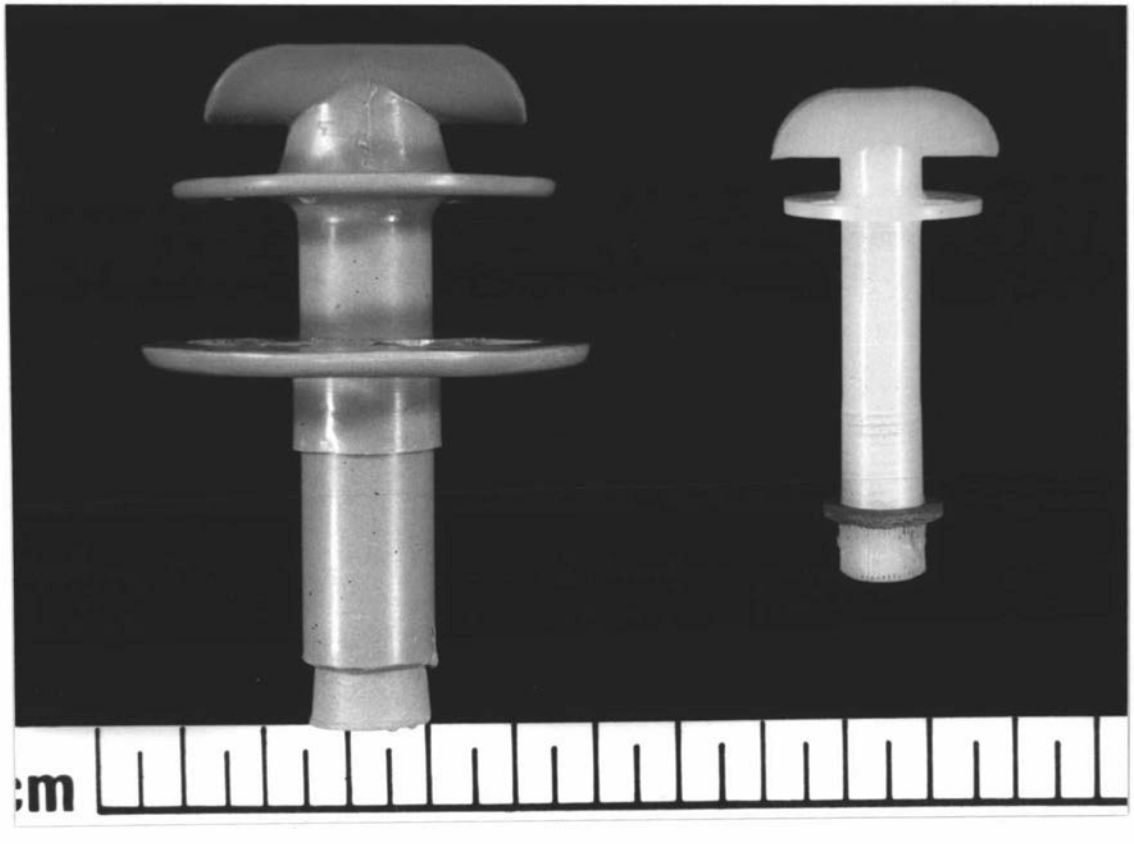
PLATE 51

The 'Ash type' re-entrant cannula used in all re-entrant cannulations. The transparent piece of polyvinylchloride tubing allows the flow of digesta across the re-entrant cannula to be checked.

PLATE 52

The two types of T cannula used in the small intestine. The one on the left was found to have too large a shoe for easy insertion into the aborad small intestine. The cannula on the right was the one used in all the sheep from which results were obtained. The cannula on the right, with its shoe (which is uppermost) flattened out, was also used as an abomasal fistula.


cm
0 1 2 3 4 5 6 7 8 9 10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transection. The purse-string sutures were drawn tight making sure that the intestinal wall was inverted. Two stab incisions were made on the right abdominal wall through which the arms of the half cannula were passed. The sites for making these stab wounds were selected by taking the following criteria into account: the intestine was as little displaced from its normal position as possible; the two arms of the cannula had to be close enough for easy approximation; the exterior part of the cannula had to be situated where it would cause as little inconvenience as possible, that is, well cranial of the hind limb and high enough up the flank to allow the animal to lie down. The two arms of the cannuala were then connected with a piece of polyvinylchlordie tubing.

Insertion of T cannulae: Two types of T cannulae were used (Plate 52), having internal diameters 8 mm and 5 mm. Both were made from polypropylene. The bigger was found to be too large for the jejunum, causing marked stretching and distension, with ulceration of the mucous membrane. In one sheep the intestinal wall perforated resulting in severe peritonitis. None of the animals fitted with these larger cannulae were included in the experimental series. The smaller cannula was completely satisfactory.

A right flank laparotomy was performed and the site for cannulation identified and exteriorised. The digesta was gently massaged away and the region isolated with 2 pairs of rubber-shod bowel clamps. A purse-string suture was placed on the antimesenteric wall of the intestine and an incision made into the lumen within the suture. After the shoe of the cannula was inserted into the lumen, the purse-string was drawn tight, making sure the gut wall was inverted. After the cannula was in place a zone of the intestine extending 500 mm orad and aborad of the cannula was encased in a polyester fibre mesh (Mersilene, Ethicon). The mesh was applied loosely around the intestine and was held in position by a number of single simple sutures, some of which passed through the mesentery. The object of placing this mesh was so that a small balloon could be inserted down the cannula and inflated to obstruct the flow of digesta without causing gross distension of the intestine which would itself initiate peristalsis (Kosterlitz and Robinson, 1959). The cannula was brought

out through a stab incision made in the right flank as high as possible without displacing the intestine unduly. The cannula was maintained in position by encasing the exteriorised part of the barrel in adhesive tape (Sleek, Smith and Nephew). The laparotomy wound was then closed in the normal manner.

Implantation of electrodes: This was carried out at the time of cannulation of the jejunum. The details of the electrodes and leads are described below (Page 122). An attempt was made to locate the electrodes along the intestine at measured intervals orad and aborad of the cannula. However, measurement was difficult because of the convolutions of the intestine. The method adopted was to measure out 50 mm lengths of intestine while holding it with as little tension as possible. Each electrode disc was positioned on the site selected, with the electrodes aligned along the long axis of the intestine. After applying slight pressure to ensure the electrodes penetrated the serosal surface they were sutured in place using 2/0 chromic gut passed through holes in the disc holding the electrodes. A double reference electrode (in case one failed) was inserted by suturing the stainless steel wire of the reference leads to the peritoneum at the edge of the abdominal wound. All leads were brought together in a 200 mm length of polyvinylchloride tubing (Portex Plastics) (Plate 54) and brought out through a stab wound high in the right flank. The outer end of the tube was then packed with sterile paraffin wax to seal it. The leads and connecting board were attached to the Elasto-plast wrapped loosely round the thorax (Plate 49).

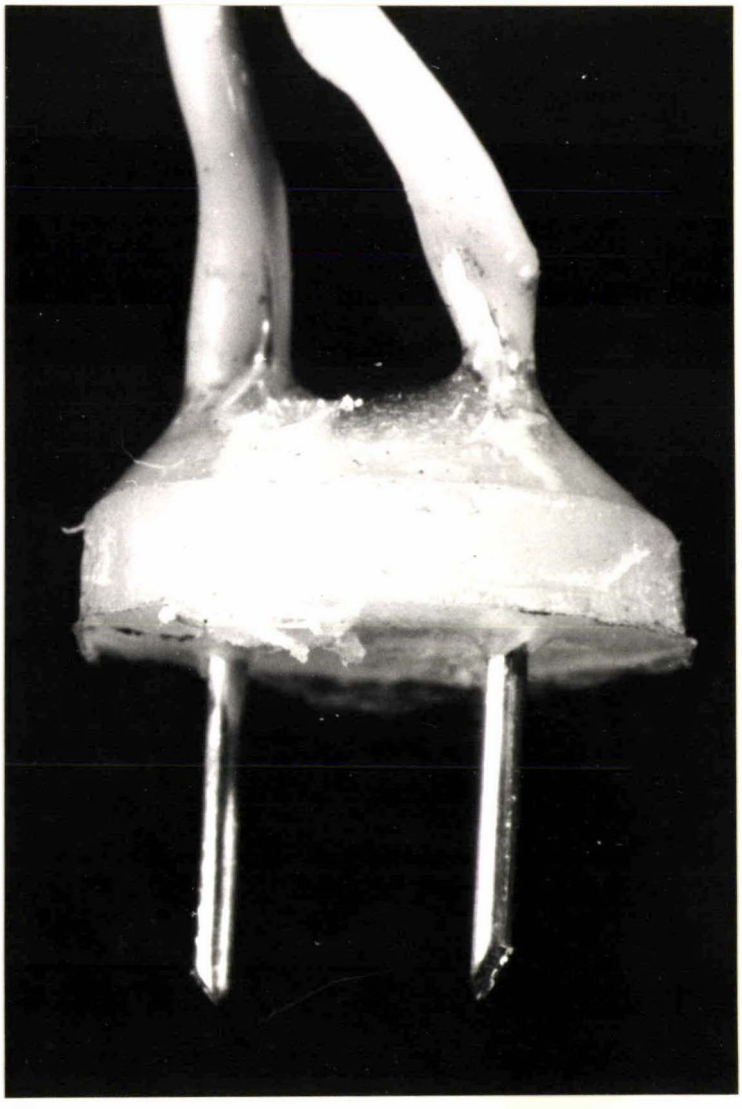
At the conclusion of the investigations sheep 30, 32, 33 and 34 were killed by an overdose of anaesthetic and a postmortem examination carried out. The sites of the electrodes were checked as follows. The small intestine was removed, carefully preserving the mesenteric attachment, and laid out (Plates 55, 56). A piece of string was then placed along the convolutions and the measurements between electrodes and to the cannula were made. The mesenteric attachment was then broken down and the intestine laid out again (Plates 57, 58) and the measurements repeated. The measurements made at surgery and the two sets made at postmortem are given in Table XIV.

PLATE 53

The electrodes which were implanted in the wall of the small intestine. The circular base of the disc is 8 mm in diameter and the electrodes are 5 mm apart. The disc is made of nylon and the electrodes from 24 S.W.G. stainless steel suture wire. The wires were cut off at 2 mm above the disc just before they were implanted into the muscle of the wall of the small intestine.

PLATE 54

The harness of electrodes and leads as it was prepared to implant in the sheep. There are six double electrodes on nylon discs and two reference electrodes made from braided stainless steel suture wire. The leads are fed through a length of polyvinylchloride tubing and are colour coded for ease of identification.



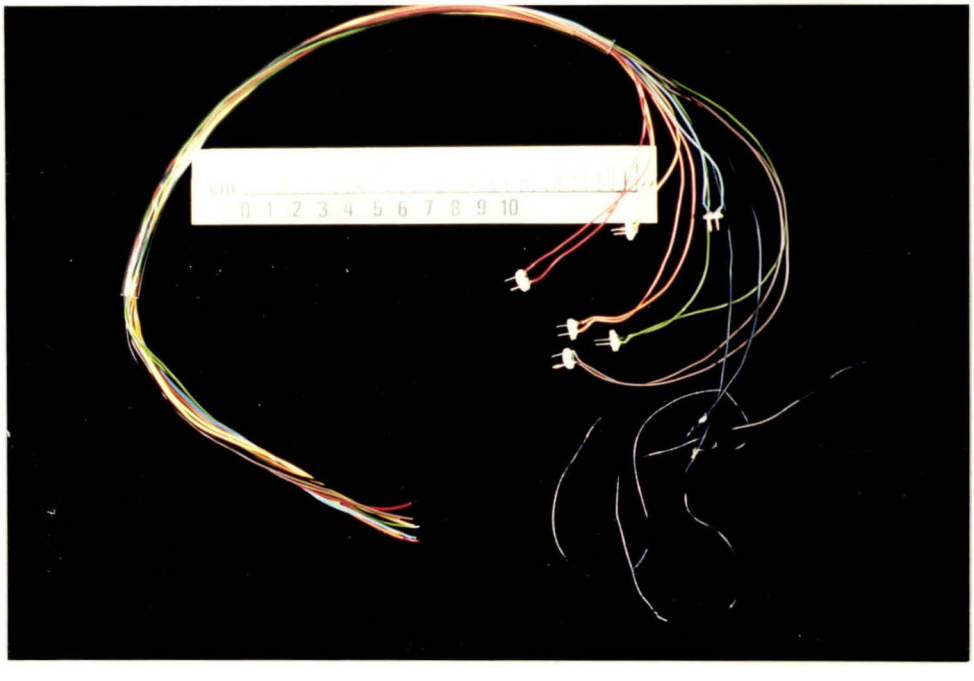

cm
0 1 2 3 4 5 6 7 8 9 10

PLATE 55

The duodenum and orad jejunum of sheep 35 after removal from the animal postmortem. The position of the electrodes and T cannula relative to the duodenum and to each other is illustrated. The mesenteric attachment of the orad jejunum has not been broken down.

E electrodes, H hepatic flexure of the duodenum, P pylorus, T T cannula.

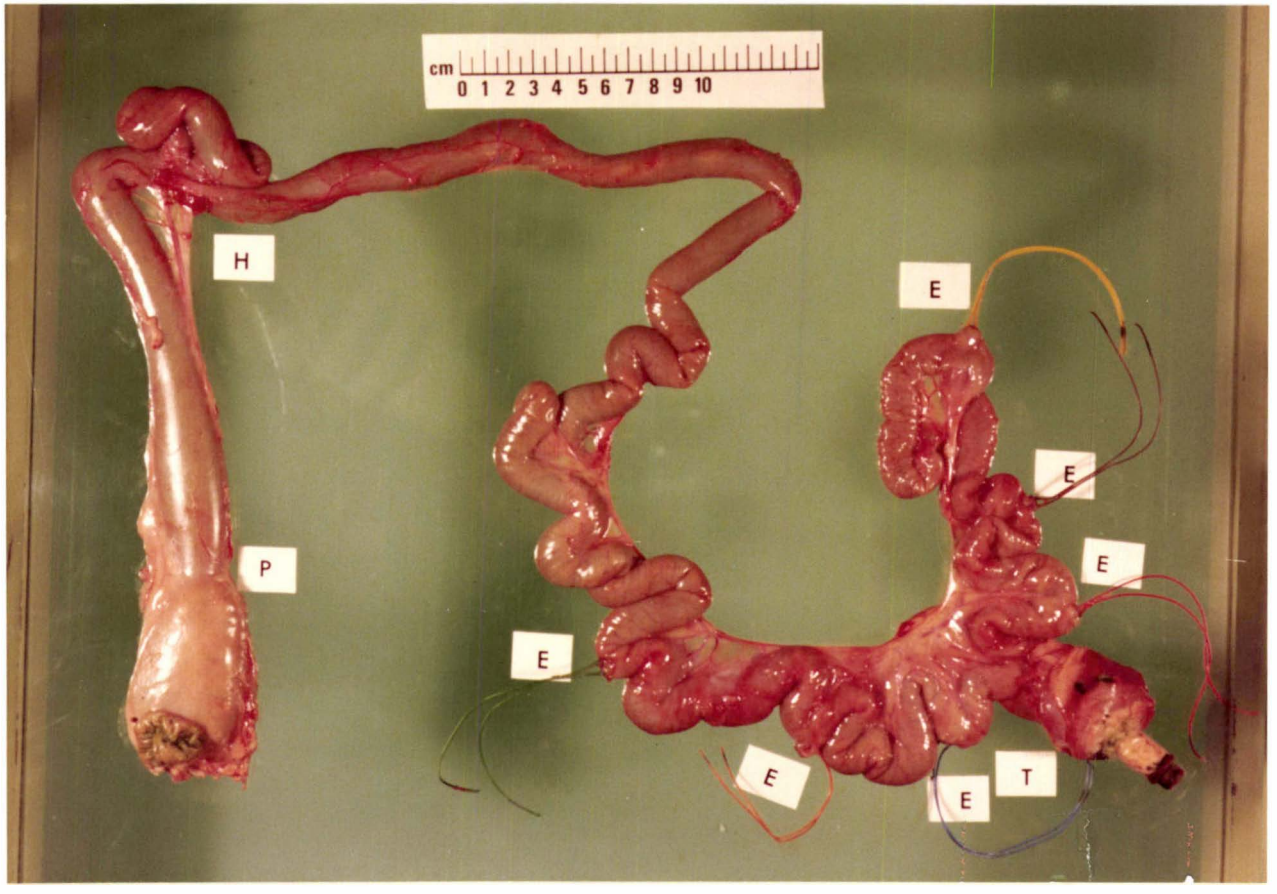

cm
0 1 2 3 4 5 6 7 8 9 10
H
P
E
E
E
E
E
E
T

PLATE 56

The duodenum and orad jejunum of sheep 32 after removal from the animal postmortem. The position of the electrodes and T cannula relative to the duodenum and to each other is illustrated. The mesenteric attachment of the orad jejunum has not been broken down.

E electrodes, H hepatic flexure of the duodenum, P pylorus, T T cannula.

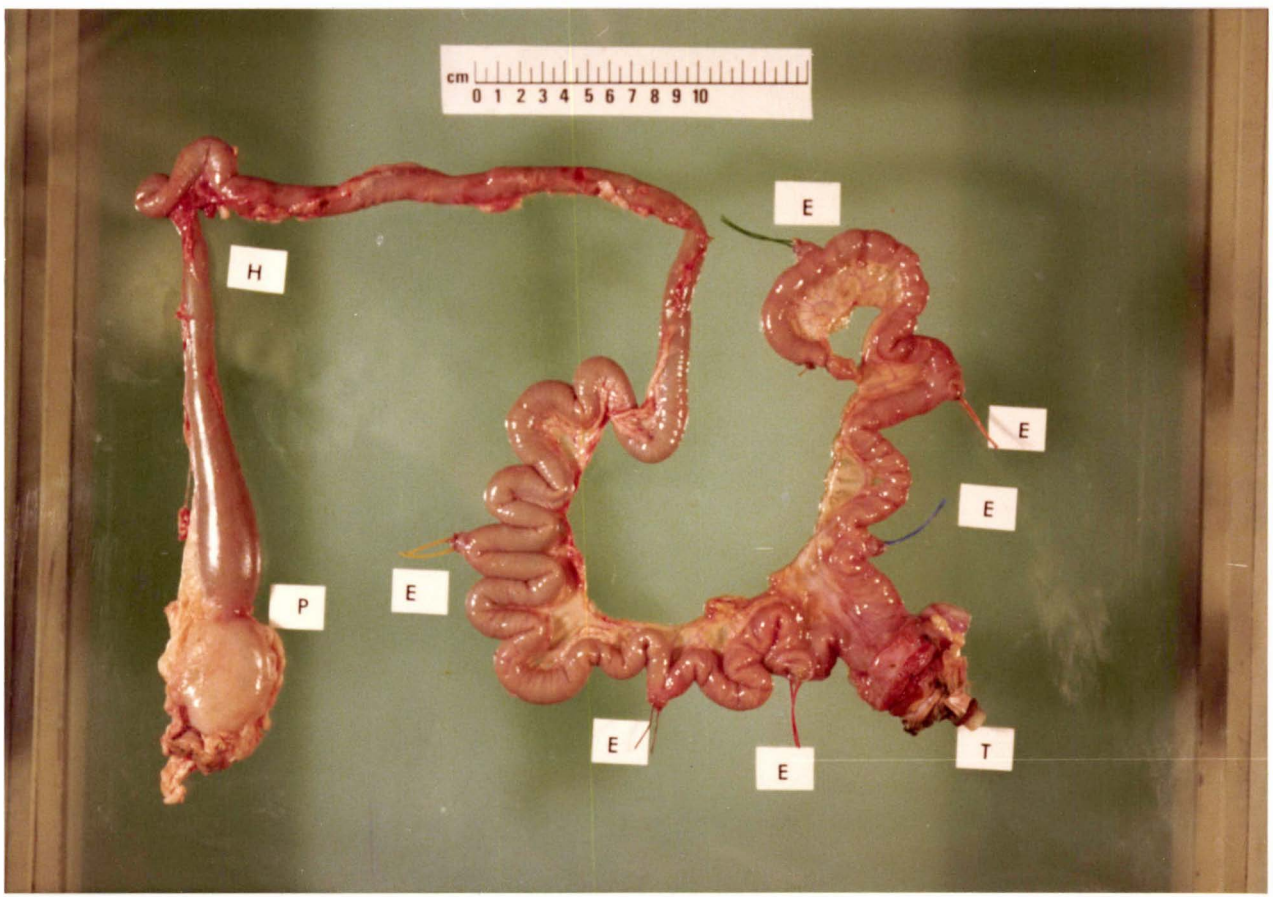

cm
0 1 2 3 4 5 6 7 8 9 10
H
P
E
E
E
E
E
E
E
T

PLATE 57

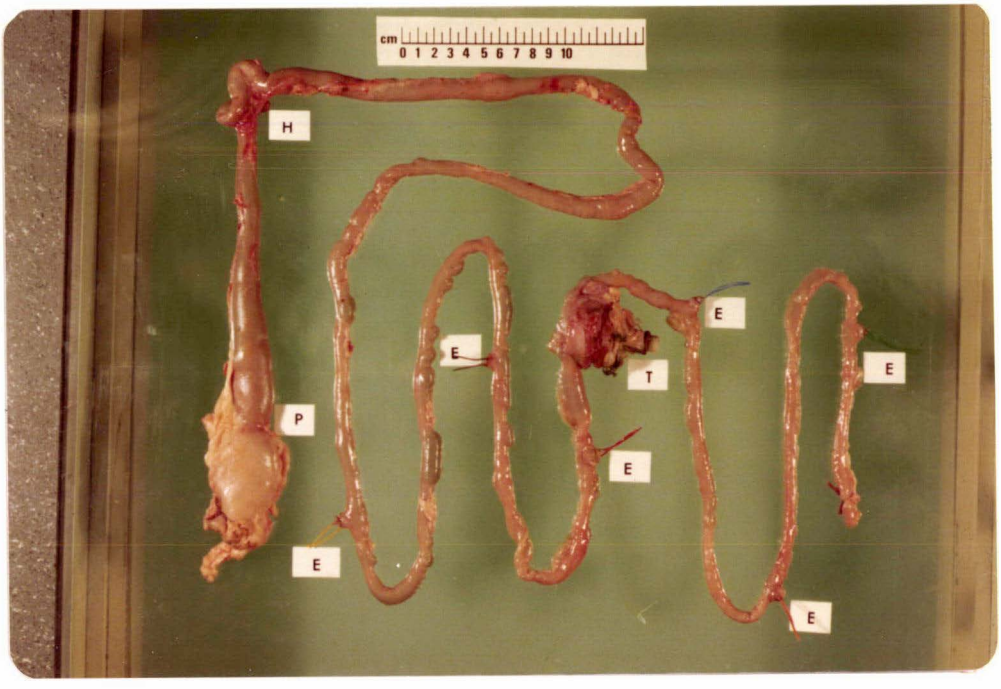
The duodenum and orad jejunum of sheep 33 after removal postmortem and breaking down of the mesenteric attachment. This shows the distances between the electrodes and the T cannula. The raised areas of the gut wall particularly noticeable between the two most orad electrodes are postmortem artifacts caused by tearing of the mesenteric attachment.

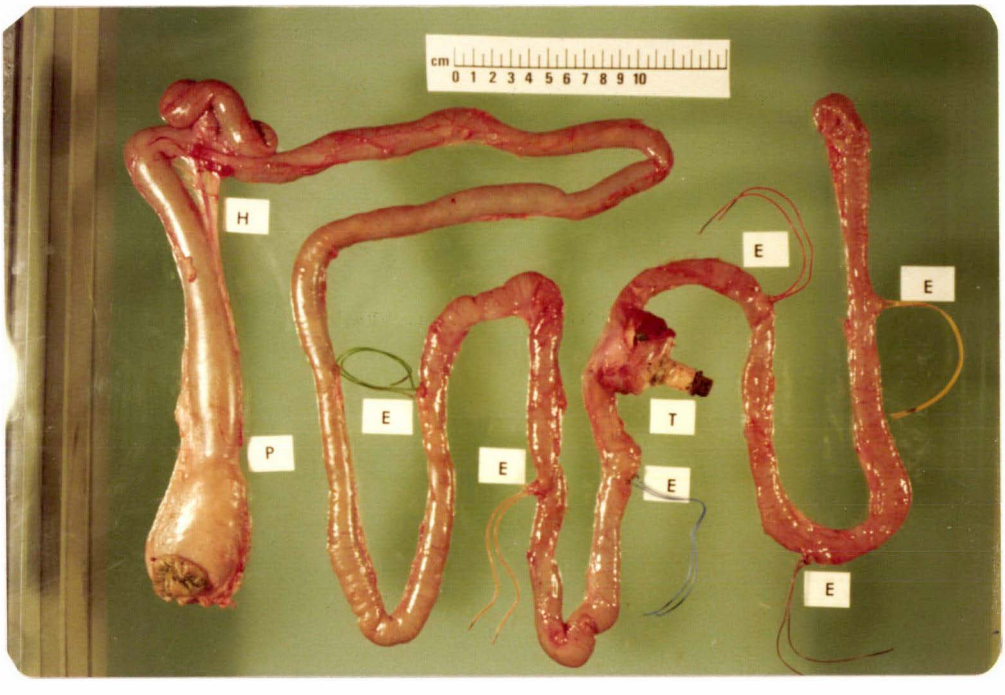
E electrode, H hepatic flexure of duodenum, P pylorus,
T T cannula.

PLATE 58

The duodenum and orad jejunum of sheep 32 after the removal postmortem and breaking down of the mesenteric attachment. This shows the distances between electrodes and the T cannula.

E electrode, H hepatic flexure of duodenum, P pylorus,
T T cannula.


cm
0 1 2 3 4 5 6 7 8 9 10
H
E
E
T
E
P
E
E
E


cm
0 1 2 3 4 5 6 7 8 9 10
H
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E

TABLE XIV

DISTANCES* (mm) BETWEEN ELECTRODES AND CANNULA

Electrodes & Cannula	Sheep 30			Sheep 32			Sheep 33			Sheep 34		
	a	b	c	a	b	c	a	b	c	a	b	c
1 - 2	400	420	430	300	270	340	300	320	360	300	320	360
2 - 3	400	420	430	300	250	330	300	280	380	300	280	370
3 - cannula	100	90	100	100	120	150	100	90	100	100	90	110
cannula - 4	100	120	110	100	160	200	100	100	100	100	90	130
4 - 5	400	500	520	300	300	290	300	270	320	300	270	380
5 - 6	400	500	550	300	350	350	300	330	350	300	350	370

* (a) measured at surgery,

(b) postmortem with mesentery intact,

(c) and with mesenteric attachment broken down.

Radiological procedures: Because of the complex stomach, it is difficult to introduce sufficient contrast material into the small intestine of ruminants to make it adequately visible radiographically. Initially the barium sulphate was introduced into the abomasum either by using bottle-fed or bottle-trained animals, or by infusing it through an abomasal cannula. This gave reasonable contrast in the proximal small intestine in most animals but was unreliable, and failed to give useful contrast in the more distal regions. Duodenal catheters were therefore used, implanted in the duodenal bulb. Contrast media infused through these consistently gave good contrast to digesta in the small intestine at all levels. Observations were carried out to determine whether or not the method of administering barium sulphate had an effect on the motility patterns seen.

The animals were screened for long periods (up to 3 hours). These sessions were recorded on video-tape and the sequences analysed later.

During each recording period, the leading edge of contrast material was followed through from the duodenum to the ileo-caecal junction. Only by doing this could each region of the small intestine be identified: once all the coils of small intestine had been filled with contrast material it became difficult to recognise the different regions with any certainty. The activity of the small intestine was observed overall at the time of screening and the specific motility patterns seen in different regions were studied in detail when reviewing the video-tape recordings. To overcome the viewing speed restrictions imposed by the video-tape play-back system, parts of the recordings which illustrated specific motility patterns were copied onto 16 mm cine-film. This cine-film was then projected through a variable speed projector.

Recording small intestinal myoelectric potentials: Initially, electrodes similar to those described by Ruckebusch (1968) were used except that they were made from multifilament 5 gauge stainless steel suture wire (ST-50 Ethicon) because this material is inert in body tissues. Generally a good signal was obtained but when a contraction of the intestinal wall occurred the electrodes short-circuited,

causing violent deflections of the recorder pen. The sheep in which these electrodes were implanted were used only for developing techniques: they were not used for deriving data used in subsequent analyses. To overcome the shorting problem, new electrodes were devised which gave satisfactory results for the life of the animals. These electrodes were assembled on a nylon disc 8 mm in diameter and 1 mm thick (Plate 53). The electrodes themselves were two pieces of 24 SWG stainless steel suture wire (Zimmer UK) passing through the disc 5 mm apart. On the side of the disc to be applied to the small intestine the electrodes projected 2 mm. On the other side they were soldered to leads, the joint being "potted" in Araldite (CIBA UK). These leads were colour-coded 10/0.1 mini-strand wires with polyvinyl-chloride insulation (Barlow Electronics). There were two holes in the nylon disc to facilitate suturing it in position on the intestinal wall. The reference electrodes were 5 gauge multifilament stainless steel wires soldered to the same type of lead wires. All the leads were brought together in a 200 mm length of polyvinylchloride tubing (Portex Plastics) to pass through the abdominal wall. Once the electrodes had been implanted and the leads exteriorised, they were soldered onto a contact board made of synthetic-resin-based paper, allowing 16 contacts at a 3.81 mm matrix (Part No. 242/2503, Vero-Electronics Ltd). When recording, this board was connected to a matching socket-edge connector (Part No. 2211/3066/1 Vero-Electronics Ltd) (Plates 59, 60), and shielded cables that led to the pen recorder.

Six electrodes were implanted along the small intestine of each animal, this being the maximum number of recording channels available.

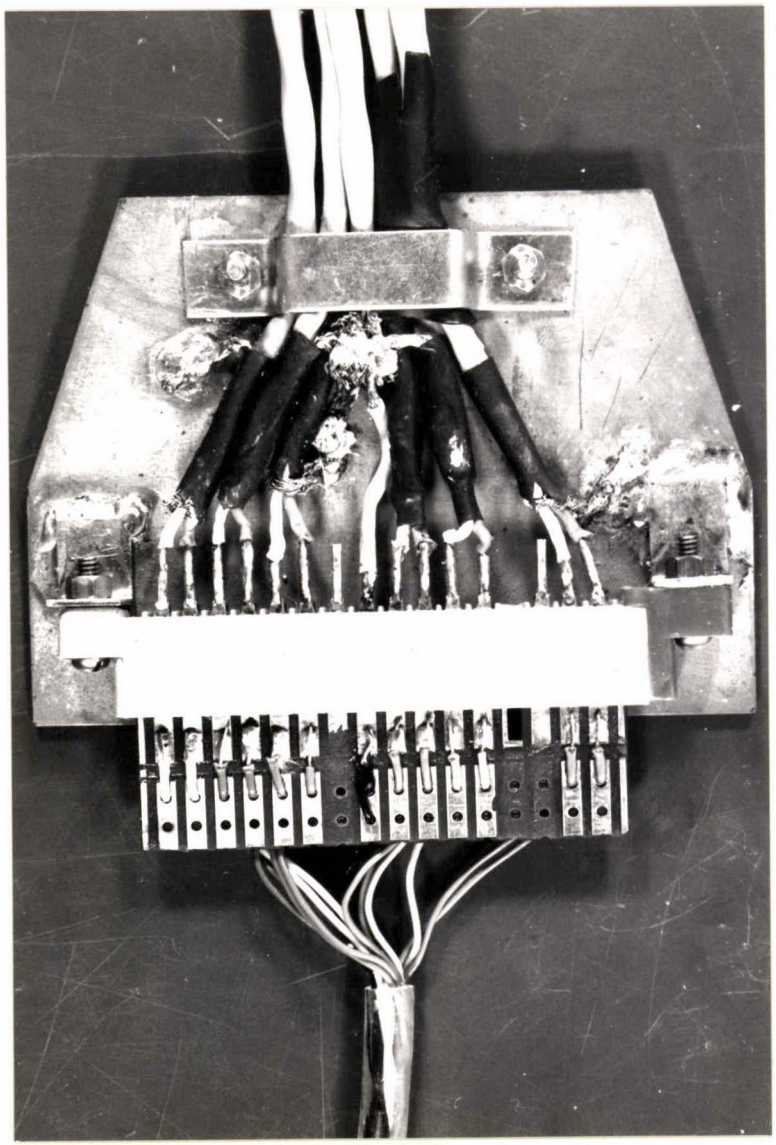
Simultaneous records were made from the six sites on the small intestine. The signals were fed into AC7 preamplifiers (Devices Ltd) used in the differential mode, and the outputs recorded with a six channel heated-stylus pen recorder (Devices Ltd). The settings on the preamplifiers which gave the optimum trace were: time constant, 0.03 seconds; filter, 70Hz; range, 250μv. The paper speed selected was 50 mm/minute. Plugged into the marker pen circuit was a small power pack which activated the light-emitting diode in the cine-camera when the marker button was depressed. It was observed when trying to correlate the pen recording with the cine-film that the paper speed

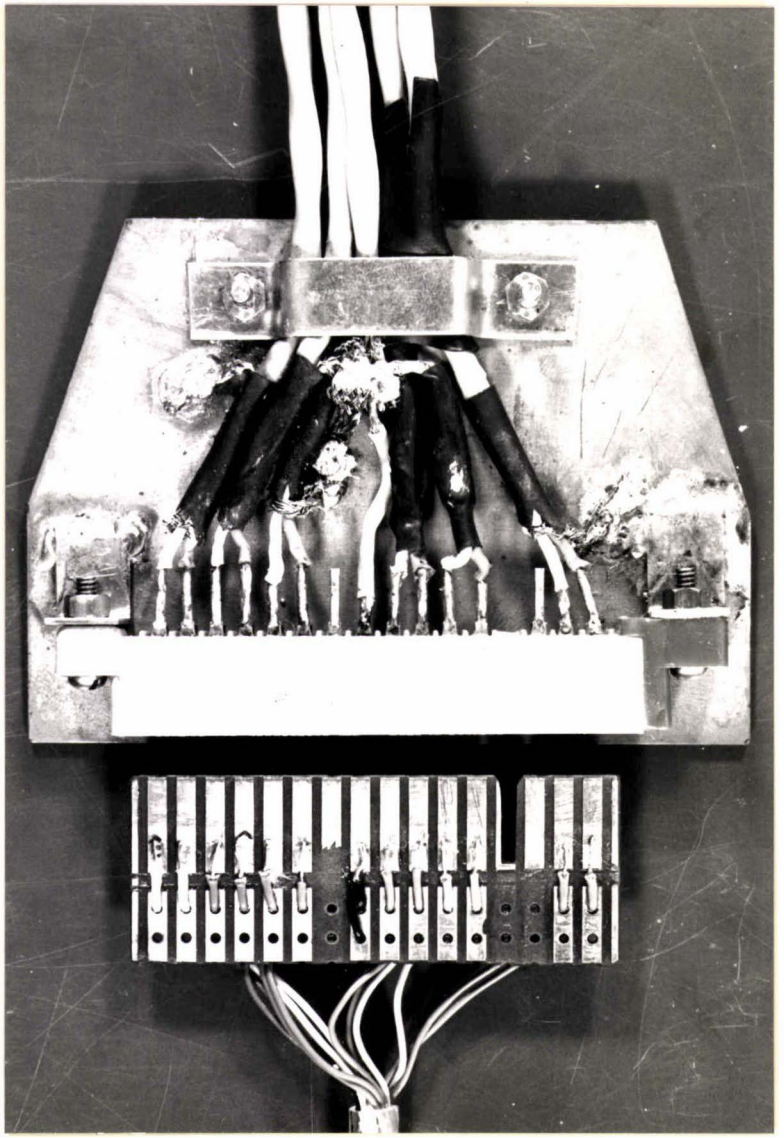
PLATE 59

The external end of the electrode leads are connected onto a circuit board (right) which can be plugged into a socket edge-connector (left). The socket edge-connector is fixed to a shaped piece of copper backed with synthetic resin based paper, and all the earth leads are soldered to it.

PLATE 60

The circuit board and socket edge-connector have been plugged together to show the key in the circuit board which corresponds to a plug in the socket-edge connector so that they cannot be connected the wrong way round.





and time marker were not exactly as specified. On checking with a stop watch it was found that the paper speed was 55 mm/min and that the minute marker was in fact marking at 61 second intervals; hence the time intervals on all reproductions of pen recordings are 61 seconds.

Analyses of myoelectrical recordings: Recordings of electrical activity were taken over periods of up to 6 hours at each session. The recordings obtained were analysed in the following ways:

(1) The frequency of the slow-wave at each electrode site was determined by counting the waves in 30 randomly selected minute intervals spread over the different recording sessions. The results were expressed as a mean and standard error.

(2) The time taken for a continuous, rapidly aborad-moving contraction to migrate between successive electrodes was measured at 30 randomly selected times spread over the different recording sessions. The results were expressed as a mean and standard error. From these figures the speed of migration was calculated by using the distances between electrodes as measured postmortem before the mesentery was stripped (Table XIV).

(3) The time interval between the recurrence of the RSA phase was measured and the results expressed diagrammatically.

(4) The time taken for each phase of RSA to pass each electrode was taken at 10 randomly selected times spread over the different recording sessions and the results expressed as a mean and standard error. (Only ten readings were taken of events associated with the RSA phase because it occurred at widely spaced intervals).

(5) The time taken for the RSA phase to migrate between electrodes was taken at ten randomly selected times spread over the different recording sessions and the results expressed as a mean and standard error. The speed of migration was calculated as in (2) above.

(6) The wavelength of the slow wave was calculated from the frequency and velocity of propagation by using the formula wavelength = velocity x frequency.

Correlation of radiologically observed digesta movements with small intestinal myoelectrical records: To establish the relationship between the radiographically observed patterns of activity and electrical activity, radiographic cine-film was taken when a specific type of electrical activity was occurring at, or was passing between, specific electrodes. Correlation was possible because (a) the marker on the pen recorder was linked to the frame marker in the cine-camera, allowing synchronisation of record and film and (b) the electrodes were visible on the cine-film (Plate 61), allowing correlation between signals and digesta movement at the electrode sites. To carry out the correlation, the cine-film was viewed with a variable speed projector using the linked frame marker and frame counting for cross reference and timing.

Results of postmortem examinations: All sheep were examined postmortem at the completion of the experiment. At the site of insertion of the T cannula, the small intestine had become adherent to the abdominal wall but no adhesions had formed to any other region (Plate 62). The polyester film mesh was completely buried in fibrous tissue but this had not caused any detectable constriction of the lumen (Plate 63). The mucous membrane and wall of the small intestine at the cannulation site appeared normal at gross examination (Plates 64, 65) but on histological examination a narrow band of chronic inflammation was found surrounding the entry point of the cannula.

The leads to the electrodes were covered with a thin layer of fibrous

PLATE 61

A lateral radiograph of sheep 32 showing a balloon, filled with contrast media, just inside the T cannula. The picture is somewhat confused by the leads going to the electrodes on the small intestine so no attempt was made to make a labelled line drawing of this radiograph.

Reading from the left of the radiograph the curving white shadow running in the vertical plane is the harness of electrode wires as it passes out through the sheeps flank. The circular white shadow to the right of this is the T cannula in the jejunum and the dense shadow to the right and below this is the contrast-filled balloon. The balloon was normally inflated with air but was filled with contrast media on this occasion to make it show up better in the radiograph. The tubing connected to the balloon is also filled with contrast and can be seen running out through the open cannula. The remaining white shadows on this photograph are the electrodes and their leads.

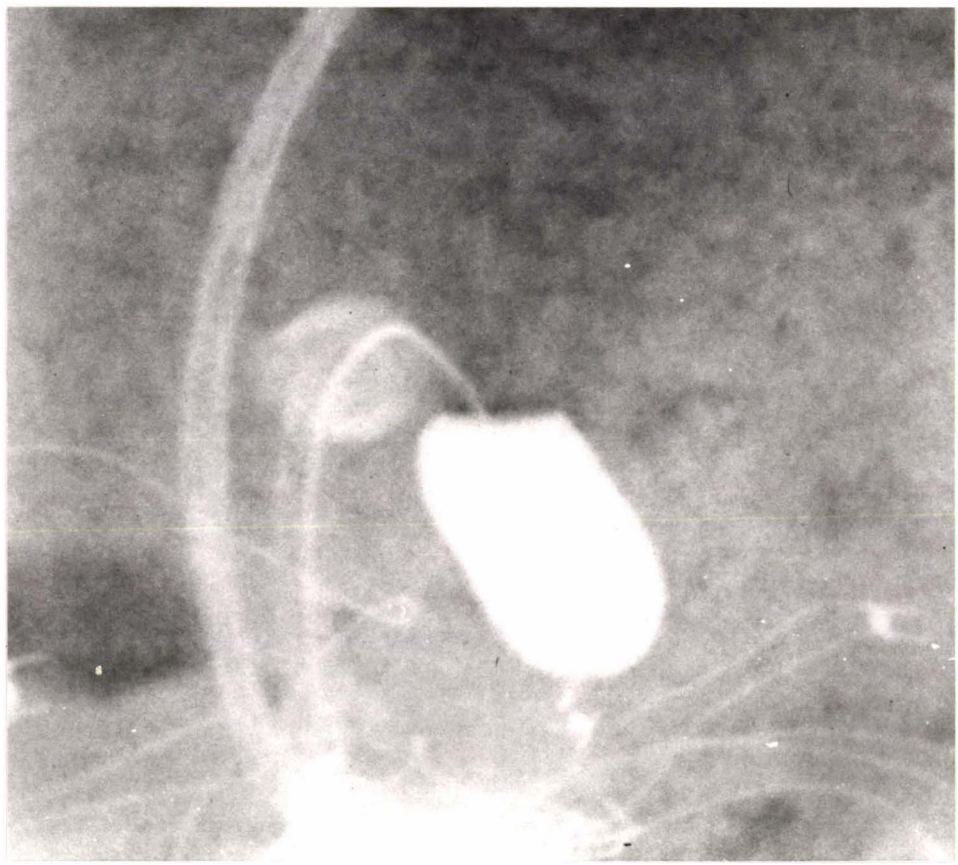
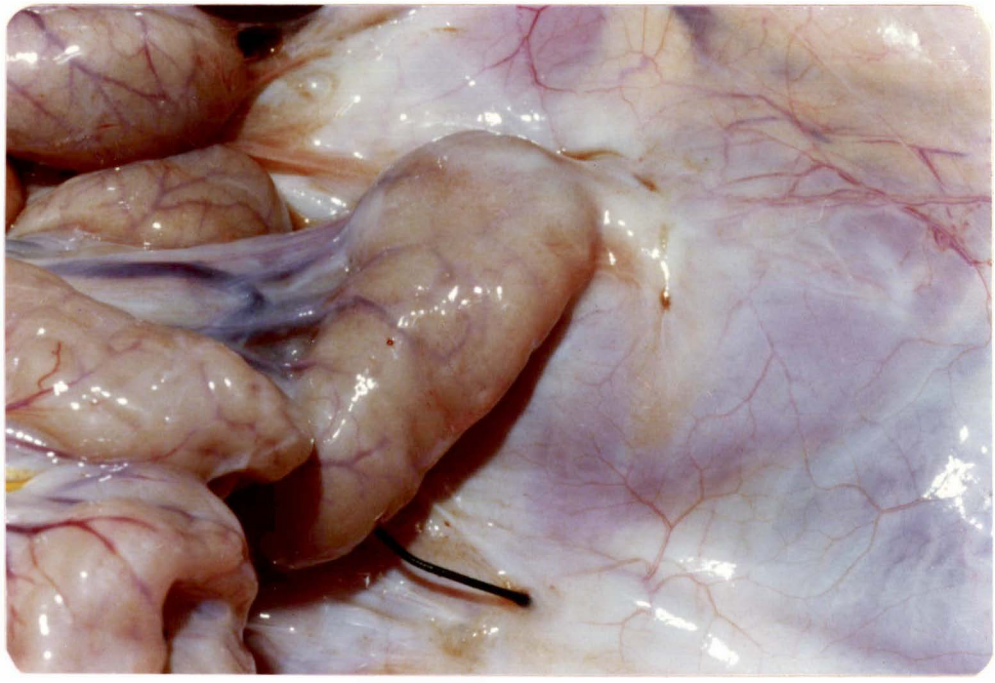


PLATE 62

The site of exit of the T cannula from the abdominal cavity where an adhesion between the jejunum and abdominal wall has occurred (sheep 33). The black lead is one of the two reference electrodes which were placed below the parietal peritoneum. The yellow lead came from a jejunal electrode.

PLATE 63

The site of insertion of the T cannula after removal postmortem (sheep 32). The T cannula is directed towards the top of the picture with the jejunum running across the bottom. The large central fibrous mass is the adhesion between the jejunal wall and the abdominal wall. The jejunum on either side of the cannula is encased in mesh which has become covered with a layer of fibrous tissue.



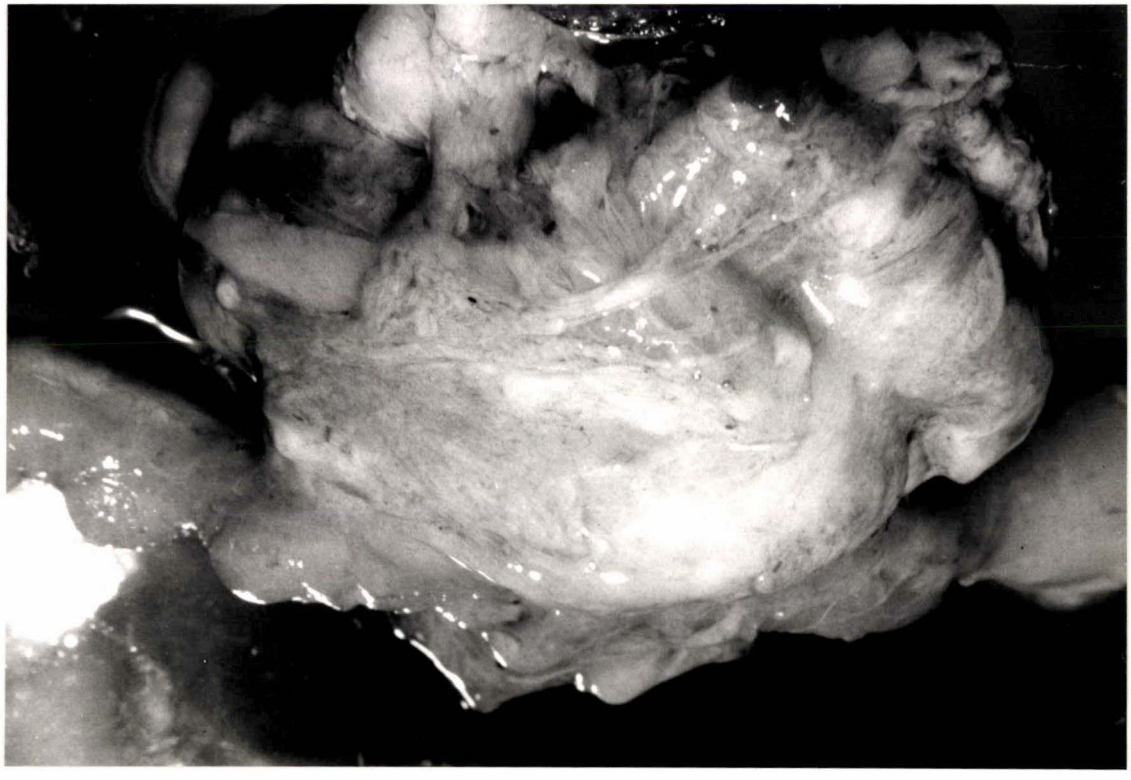
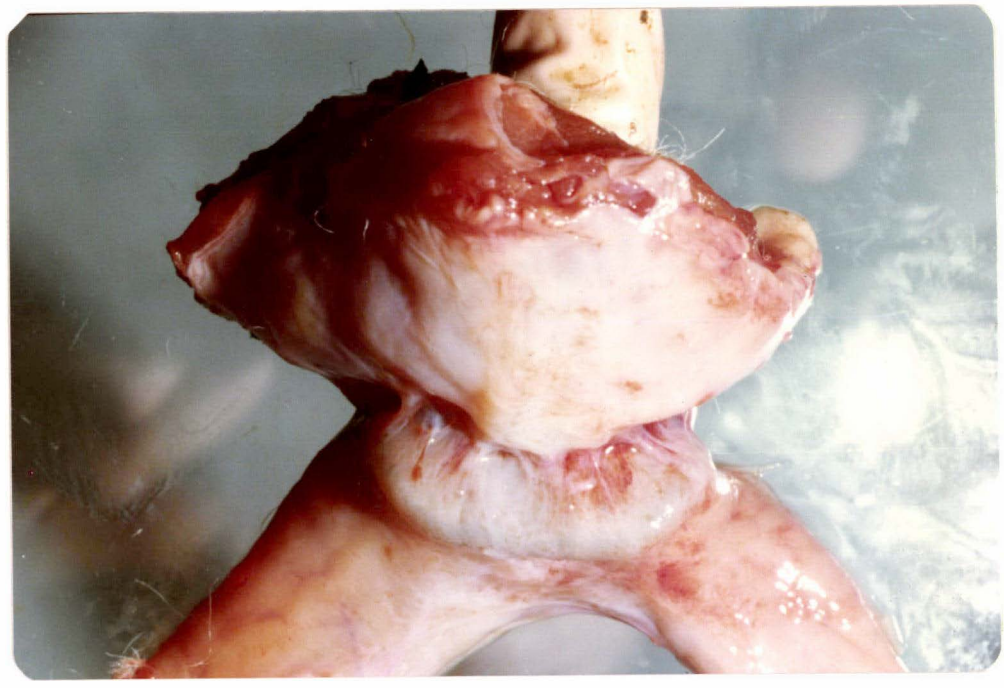


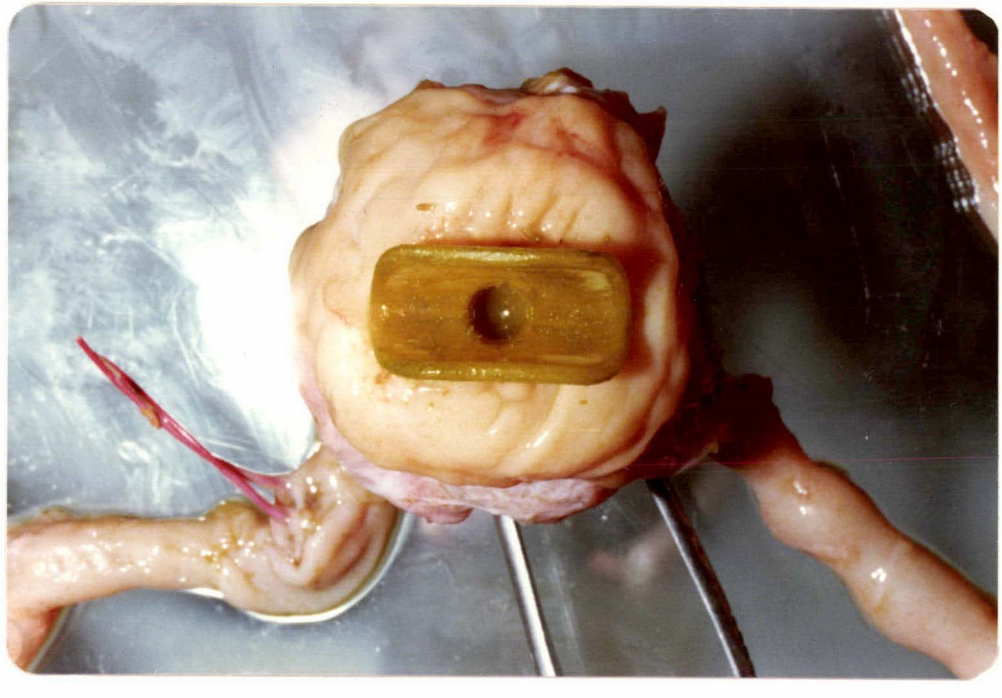
PLATE 64

The site of insertion of the T cannula and the resultant adhesion to the abdominal wall after removal postmortem (sheep 33). The mesh round the wall of the small intestine on either side of the T cannula has become completely covered by a thin layer of fibrous tissue and has caused some thickening and stiffening of the jejunal wall on both sides of the cannula.

PLATE 65

The site of insertion of the T cannula after removal postmortem. The lumen has been opened and the wall reflected, revealing the shoe of the cannula (sheep 32). There is no gross indication of inflammatory response nor is there any ulceration of the mucosa.





tissue and in a few animals there were small adhesions between the leads and a contiguous loop of small intestine. Grossly there was no abnormality at the site of attachment of the electrodes to the wall of the intestine nor where the muscle layers were penetrated (Plates 66, 67, 68, 69). On histological examination there was a small zone of chronic inflammation around each electrode.

5:2:1 Radiological observation of the digesta movements in the normal small intestine.

Digesta movements in the small intestine of 9 sheep were observed following the administration of contrast material. Sheep 2, 3, 21, 22 and 23 were bottle-fed with a mixture of 25 ml barium sulphate suspension and 25 ml cow's milk. Sheep 1, 4, 5 and 28 had a mixture of 25 ml barium sulphate and 25 ml water introduced through their abomasal cannulae. Following administration, each sheep was placed in the crush between the x-ray tube and the image intensifier and digesta movement in the small intestine observed and recorded for 120 minutes.

Each of the sheep then had a duodenal catheter implanted. Two weeks later they were again placed in the crush between the x-ray tube and image intensifier. Barium sulphate suspension warmed to 37^{o} C in a constant temperature bath was infused through the catheter at 0.8 ml/minute by means of a continuous infusion pump (Proportioning Pump Technicon). The movement of the marked digesta in the small intestine was observed and recorded for 120 - 300 minutes. The video-tapes were compared between animals and between sessions to establish a normal pattern of activity and to look for any effects that might be related to the route of administration of contrast media.

5:2:2 Radiological observations of the effects on digesta movement caused by insertion of cannulae in the small intestine.

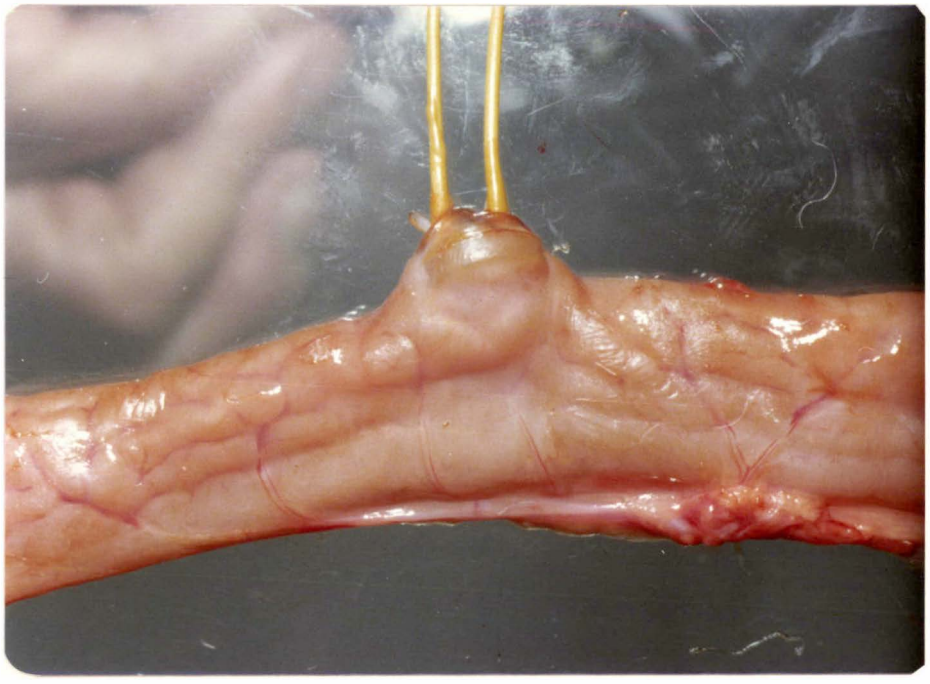
Two weeks following the insertion of re-entrant cannulae in the small intestine of sheep 1, 2, 3, 4 and 5, and T cannulae in the jejunum of sheep 28 and 31, digesta movement in the small intestine was observed

PLATE 66

An electrode in place in the jejunal wall postmortem (sheep 32). The disc and part of the leads have become encased in a thin layer of fibrous tissue. There are no indications of inflammation or stricture of the intestinal wall.

PLATE 67

An electrode in place in the jejunal wall postmortem (sheep 33). The lumen has been opened. There is no indication of an inflammatory response to the electrode and no ulceration of the mucosa. The two small spots of discolouration are where the two electrodes are lying just below the mucosal surface.



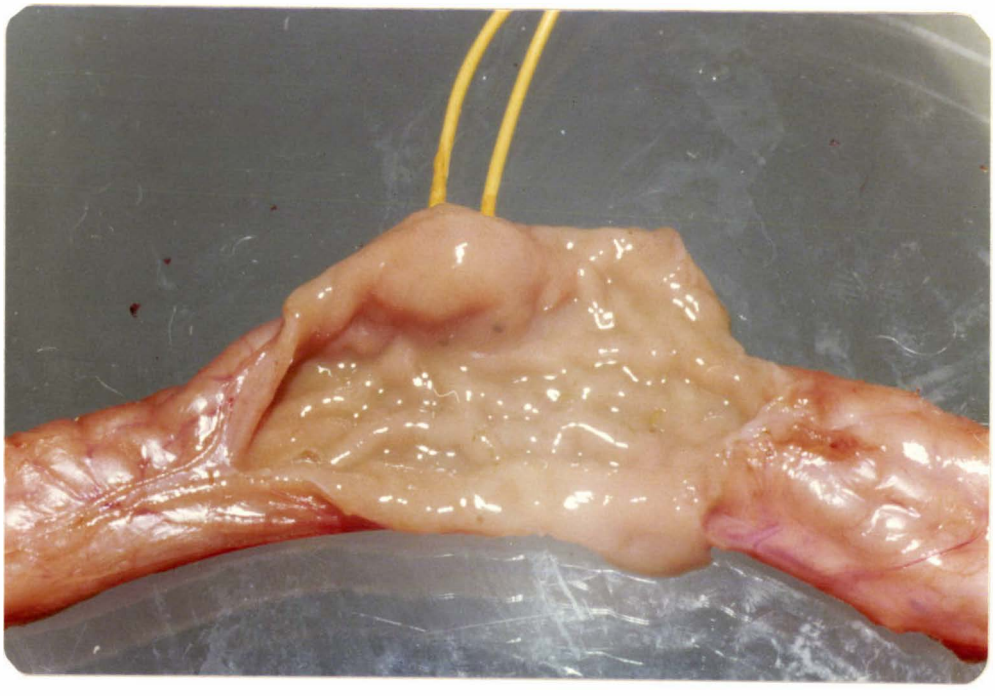
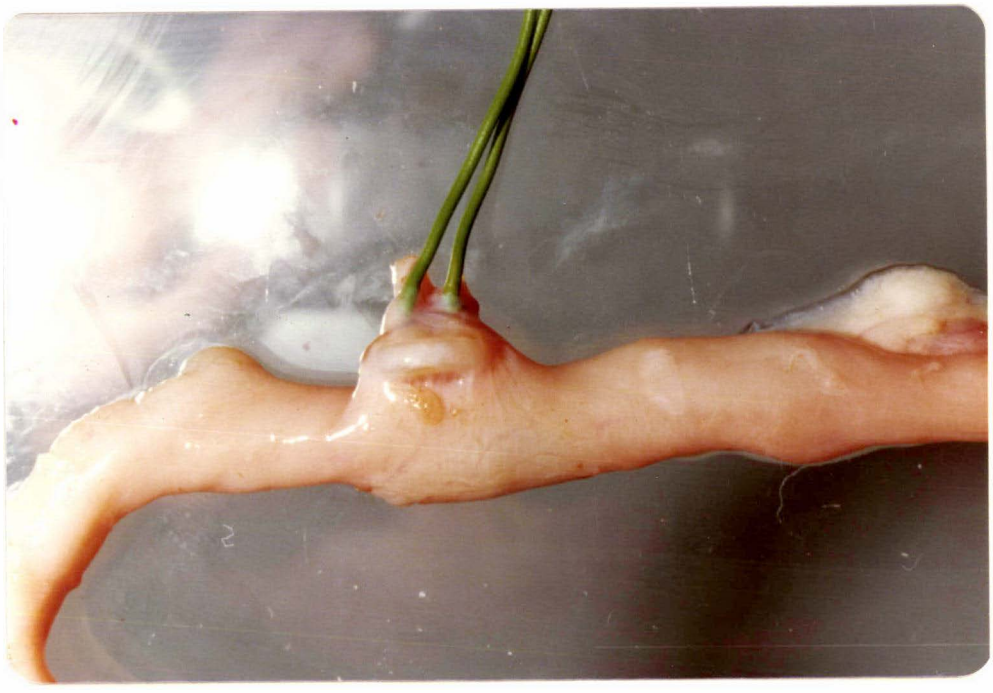


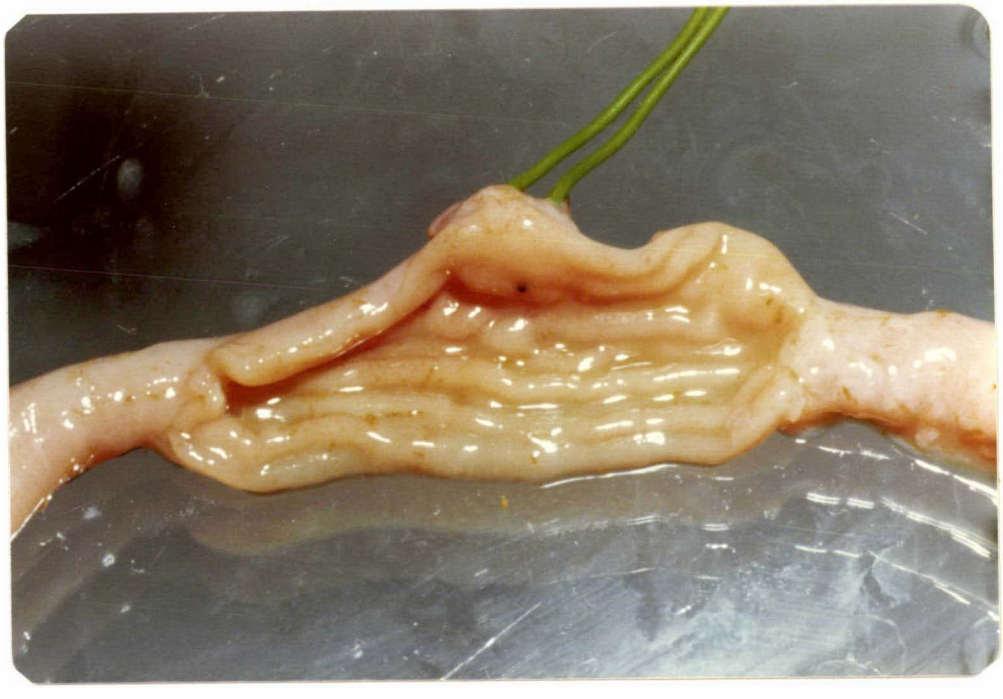
PLATE 68

An electrode in place in the jejunal wall postmortem (sheep 32). The disc and electrode wires have become encased in fibrous tissue. There are no indications of inflammation or stricture of the intestinal wall. The small blister just below the disc is a postmortem artifact caused by a small serosal tear made when the mesentery was removed.

PLATE 69

An electrode in place in the jejunal wall postmortem (sheep 33). The lumen has been opened. There is no gross indication of an inflammatory response to the electrode and no ulceration of the mucosa. The small spot of discolouration of the mucous membrane is where an electrode is lying just beneath the mucosal surface.





radiologically and recorded on video-tape. Barium sulphate suspension was introduced through the duodenal catheters at 0.8 ml/ minute. Each session was limited to 120 minutes and was repeated at 2, 3 and 4 weeks and 2 months.

5:2:3 Measurement of the volume and length of boluses in the duodenum and proximal jejunum.

The volume of boluses in the proximal and distal duodenum and in the jejunum were measured in sheep 3, 4 and 5 which had re-entrant cannulae. After each session in experiment 5:2:2 at 2, 3 and 4 weeks and 2 months after cannulation the cannula was opened for 30 minutes and the digesta collected. The volume of digesta was measured and the number of boluses in which it was delivered was counted from the video-tape recording of the activity of the small intestine.

Measurements were made of the lengths of 3 rapidly aborad moving boluses in each of three sheep (32, 33 and 34). To make these measurements the assumption had to be made that the bolus was normal to the x-ray beam, an assumption that was almost certainly incorrect. Allowance was made for geometric enlargement using the system described in Appendix 2.

5:2:4 Experimental initiation of contractions of the small intestine by the introduction of digesta into the lumen.

During the collection of digesta for volume measurement (5:2:3), 5 ml of barium sulphate suspension was run under gravity from the aborad arm of the cannula into the intestine so that any movement could be detected radiographically. Following the collection of digesta a mixture, of 50% barium sulphate and 50% digesta (V/V), warmed to 37^{o} C, was introduced into the aborad limb of the cannulae in volumes of 5 ml, 10 ml and 15ml, either slowly (by letting it run down the arm of the cannulae under gravity) or quickly (by injection from a syringe through a short tube in the cannula bung). The movement of introduced digesta was observed and recorded on video-tape.

5:2:5 Recording of myoelectric potentials in the wall of the proximal jejunum.

Continuous recordings of myoelectrical potentials were made from 4 sheep (30, 32, 33 and 34) prepared with a T cannula and electrodes in the small intestine. Each recording session lasted 6 hours and each sheep was recorded from three times - 3 weeks after surgery and at two successive 2 week intervals. The records were analysed as described above.

5:2:6 Simultaneous radiological observations and electrical recordings for correlation of digesta movements with myoelectrical activity.

Simultaneous radiological (video-tape) and myoelectrical potential records were made from two sheep (28 and 31) having a duodenal catheter and T cannula with implanted electrodes in the jejunum. Each sheep was subjected to 4 x 120 minutes recording sessions separated by at least 7 days, the first being carried out 3 weeks after surgery. At each session barium sulphate suspension, warmed to 37^{o} C was introduced through the duodenal catheter at a rate of 0.8 ml/minute and the small intestine observed radiologically by screening. A continuous video-tape recording was made and simultaneously, a continuous record of myoelectrical potentials. As specific types of electrical activity were recognised, radiographic cine-film was taken. Correlations were made as described earlier.

5:2:7 Observation of the effects on the myoelectrical activity of the small intestine of removal of digesta or the introduction of digesta.

During 6 hour sessions of continuous recording of myoelectrical potentials, the effects of diversion or introduction of digesta were observed in sheep 30, 32, 33 and 34. Each animal was subjected to 3 such sessions at weekly intervals. At each session observations were made of the effects on the electrical activity of the following manipulations:

(1) The jejunal cannula was left open;

(2) The cannula was open and a balloon made from a latex rubber finger stall with a capacity of approximately 5 ml inserted aborad from the cannula was inflated for a variable period. The balloon was positioned so that it remained within the region of the small intestine covered by gauze;

(3) Digesta warmed to 37^{o} C, was introduced through a catheter passed 20 mm aborad of the cannula at a rate of 2.2 ml/minute using a constant infusion pump.

5:3 RESULTS

5:3:1 Radiological observations of digesta movements in the normal small intestine.

Only slight variations were found between individuals in the time of, and between, various events in the small intestine. There was no difference between animals which had barium sulphate administered by bottle-feeding and those which had it introduced through an abomasal catheter or cannula, nor was there a difference in the pattern of activity seen when the barium sulphate was introduced either to the abomasum or constantly infused into the duodenum.

Two basic types of digesta movement were observed. The first was characteristic of a particular region and has been called here "the regional pattern of movement". The second was a pattern of activity that moved over the length of the small intestine and has been called "the migrating pattern of movement".

The regional pattern of movement was recognised to occur in three basic forms, related to different regions of the small intestine:

(1) continuous rapid aborad progression of a large bolus, seen typically in the duodenum and proximal jejunum,

(2) intermittent aborad progression of small boluses, seen typically in the distal jejunum, and

(3) division and coalescing of small boluses, seen typically in the ileum.

The initiation of contractions of the duodenal bulb appeared to be dependent on the degree of filling of the proximal duodenum. When a critical volume of digesta had accumulated in the proximal duodenum, a contraction of the bulb propelled it aborad. Such a contraction is shown on Plate 70 which is compiled from a series of spot-films. No direct relationship between contractions of the pyloric antrum and the duodenal bulb could be established. An apparent relationship occurred when the last of a series of deliveries of digesta through the pylorus increased the amount present in the proximal duodenum above the critical volume. Once an individual animal had been observed for some time, it was possible to determine visually the critical degree of filling and to predict when the next contraction of the bulb would occur.

The number of contractions of the pyloric antrum that were required to deliver the critical volume of digesta through the pylorus was variable. On most occasions that digesta passed through, there was no associated contraction of the duodenal bulb; however contractions of the duodenal bulb were observed from time to time that were unrelated to the passage of digesta through the pylorus.

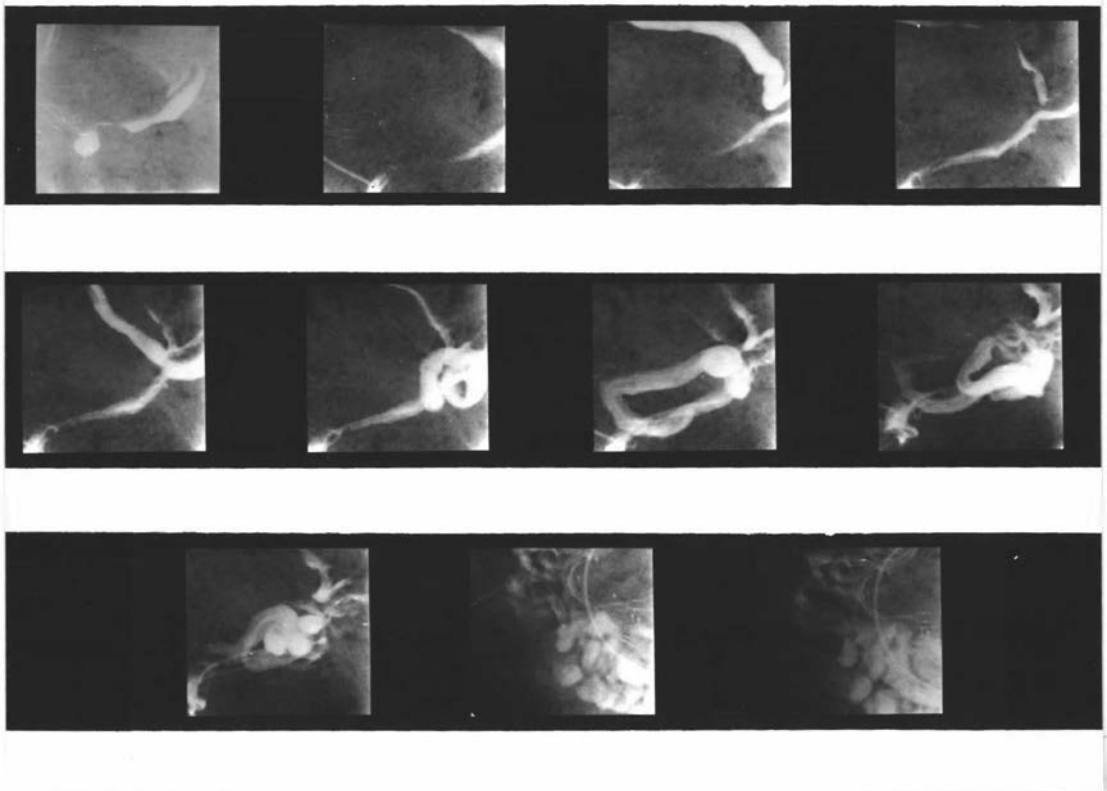
Infrequently, contraction of the duodenal bulb was not followed by contraction of the proximal duodenum. On these occasions digesta was pushed to the sigmoid flexure then returned as the bulb relaxed, occasionally passing back through the pylorus into the abomasum. Usually, however, contraction of the bulb was followed by contraction of the duodenum, which propelled digesta through the duodenum into the jejunum as a continuous rapid aborad progression of a large bolus (Plate 70). The time taken for the bolus to traverse the duodenum did not exceed 15 seconds and no digesta could be detected remaining behind. Most often when a bolus was propelled through the duodenum there was a brief pause (up to 30 seconds) in the contractions of the

PLATE 70

This series of frames from 70 mm spot-films taken at 1 second intervals illustrates the migration of a bolus from the ascending duodenum to its eventual fragmentation in the jejunum. The animals head is to the right.

The bolus was formed by the rapid infusion of 15 ml of barium sulphate into a duodenal catheter 1 minute after the previous bolus had passed down the duodenum. The amount of barium sulphate left behind in the duodenum is not usual when the propulsion of the bolus is initiated without interference.

In the first frame in the top row a contraction of the duodenum is occurring just above the circular shadow caused by the discs on the end of the duodenal catheter. The rate of travel of the bolus makes it very difficult to pan after it with the heavy x-ray equipment so in the second frame the bolus can be seen disappearing off the right of the frame to pass round the sigmoid flexure and reappear higher up on the right of this frame. The third frame shows the bolus travelling horizontally in the duodenum towards the ligament of Trietz. By the fourth frame the bolus has disappeared caudally leaving some slight traces in the duodenum. In the first frame of the second row the bolus has reappeared from the top of the picture and from then onwards is travelling in coils of jejunum. In the first frame of the third row the bolus has started to break up and by the last two frames it has been completely fragmented.



pyloric antrum.

Because of the many convolutions of the jejunum, it was difficult to judge exactly how far each bolus travelled (Plate 70). However, there was a tendency for those boluses arriving immediately after the quiescent phase of the MMC to travel a shorter distance.

As the long bolus from the duodenum moved through the jejunum, it was gradually reduced in length by dropping digesta off its trailing edge, a process which continued until the original bolus was divided into a number of smaller, almost equal-sized boluses. The next bolus arriving from the duodenum would then pick up one or more of these smaller boluses on its leading edge and as the new aggregated bolus continued to move, it too dropped boluses off its trailing edge. In this way the short, discrete boluses typical of the digesta distribution in the jejunum were formed. Once formed, the smaller boluses continued to move aborad at a slower and much less constant pace (Plate 70) than that of the long bolus delivered from the duodenum. Occasionally, a number of the smaller boluses would coalesce forming a single large bolus which would then move rapidly and continuously aborad for some distance before dividing into smaller boluses again. In the distal jejunum the boluses continued to move slowly aborad, but with frequent short stops. Occasionally they also subdivided and coalesced (Fig. 14). This behaviour, subdividing and coalescing, became increasingly prominent as the boluses passed towards the ileum. When the boluses reached the ileum they were smaller and closer together than in the jejunum, with some digesta moving a short distance orad as subdivisions took place (Fig. 15). The net speed of aborad progression of digesta continued to decrease towards the ileo-caecal junction. As a result of this slow rate of passage, digesta spent longer in the ileum than in other regions of the smaller intestine.

The migrating pattern of movement was seen to involve all regions. At intervals, a distinct aborad migrating pattern of bolus movement was seen to become established in the proximal jejunum. The first changes observed were (1) that the boluses in the train became equal in size and (2) evenly spaced and (3) the train commenced to move aborad at a constant speed. As they were observed passing a given point in the

FIGURE 14

This diagram is derived from radiographic cine-film of bolus movement in the jejunum.

From (a) through to (h) represents the sequence of events observed in the same length of gut over a short time interval.

(a) 1, 2, 3 and 4 are four evenly sized boluses but they are not equally spaced.

(b) 1 remains static, 2 starts to move, 3 and 4 started to move later.

(c) 1 starts to move, 2 stops, 3 and 4 continue to move.

(d) 5, a new bolus, moves into the observed section. 1, 2 and 3 stop moving.

(e) 5 stops moving, 1 moves on and amalgamates with 2, 3 stops moving.

(f) 5 starts to move again, (1 + 2) move while 3 remains static.

(g) Another new bolus (7 + 6) moves into the observed section, 5 moves and (1 + 2) move.

(h) Bolus (7 + 6) splits with part 7 moving a short distance and stopping while part 6 continues to move, 5 and (1 + 2) continue to move.

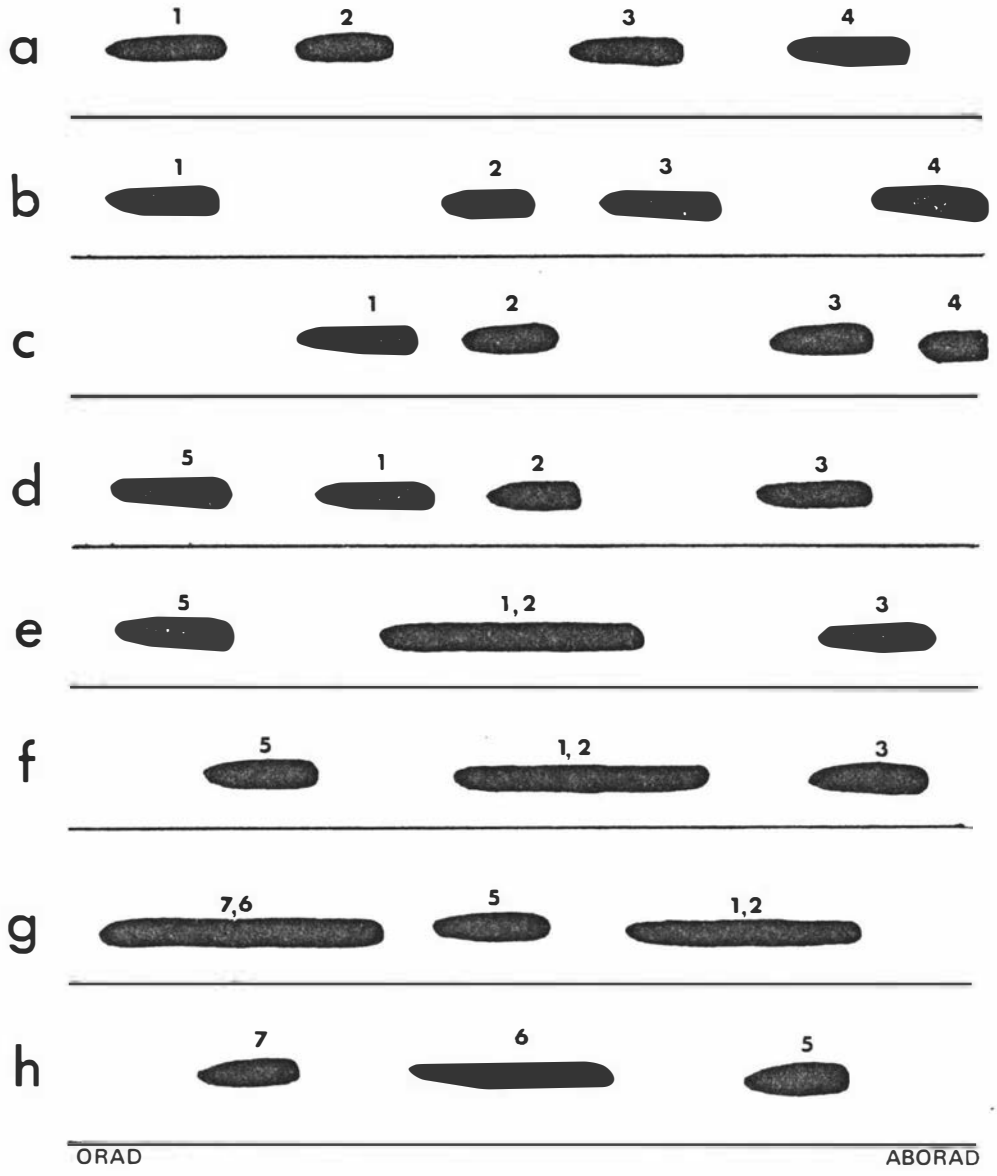

a
1
2
3
4
b
1
2
3
4
c
1
2
3
4
d
5
1
2
3
e
5
1, 2
3
f
5
1, 2
3
g
7,6
5
1,2
h
7
6
5
ORAD
ABORAD

FIGURE 15

This diagram is derived from radiographic cine-film of bolus movement in the ileum.

From (a) through to (e) represents the activity seen in the same length of ileum over a short time interval.

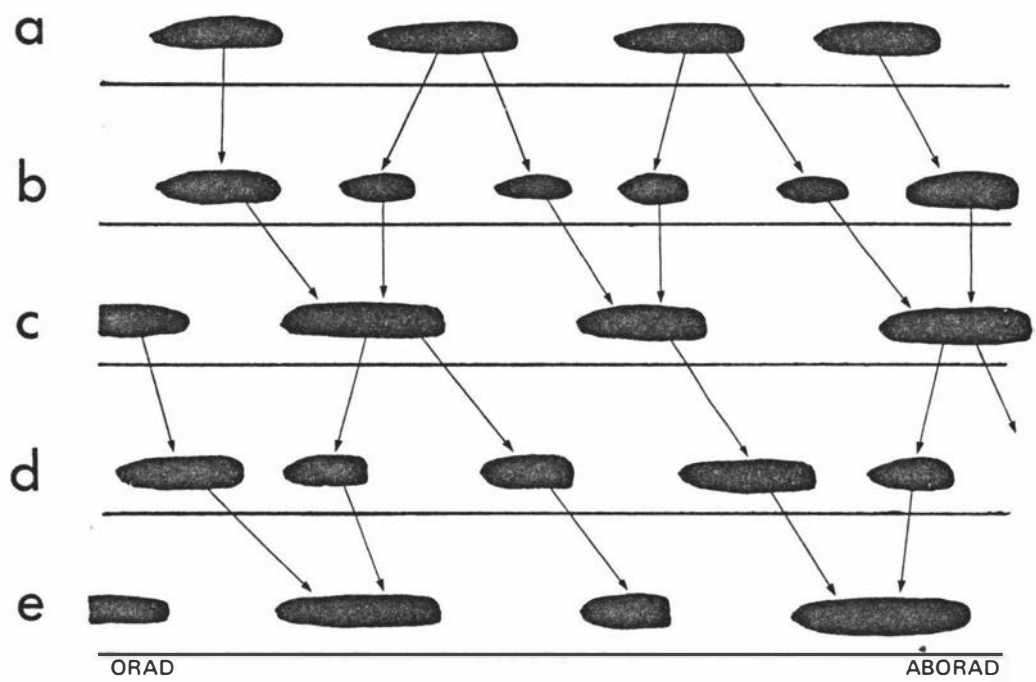
(a) Four boluses of approximately the same size and equally spaced.

(b) The middle two boluses are split into two parts with the orad parts of the divisions moving a short distance orad and the aborad parts moving aborad.

(c) Amalgamation of some boluses occurs as is indicated by the arrows.

(d) Splitting of two of the boluses occurs again as is shown by the arrows.

(e) Some reamalgamation occurs as is shown by the arrows.


a
b
c
d
e
ORAD
ABORAD

small intestine, the boluses became smaller and further apart but the distances between their centres remained the same (Fig. 16). The boluses continued to decrease in size until they were no longer visible, leaving behind a zone of emptied small intestine. These distinctive patterns migrated slowly along the small intestine taking from 70 - 90 minutes to pass from the jejunum to the ileo-caecal junction. Not all of them travelled the full length of the small intestine. The migrating patterns occurred every 35 - 70 minutes so that there were frequently two progressing along the small intestine at any one time. Following the passing of a migrating pattern, digesta was pushed into the empty section of intestine by one of the forms of regional patterns of movement. The cycle was then repeated. Examples of the succession of regional and migrating patterns in the ileum can be seen in Plate 71.

As described in 4:3:2 there was a clear relationship between abomasal activity and the establishment of a migrating pattern of movement in the proximal jejunum. This appeared to depend on the passage of digesta from the stomach to the small intestine. Accurate measurement of the flow rate of digesta through the pylorus was not possible from radiological observation. However some assessment of the flow rate could be made if it was assumed that each bolus propelled aborad in the duodenum by contraction of the duodenal bulb contained the same volume of digesta, a reasonable assumption (see 5:3:3). Data from Chapter 4 (Figs. 10, 11, 12) suggest a 5-fold variation in the number of boluses passing aborad in the duodenum, from 1/minute to 5/minute, and therefore a 5-fold variation in the flow rate through the pylorus.

5:3:2 Radiological observations of the effects on digesta movement caused by insertion of cannulae in the small intestine.

(1) Duodenum.

Proximal duodenum: The effects on the movement of digesta of placing a re-entrant cannula in the duodenum just aborad of the duodenal bulb were only slight. When a contraction of the duodenal bulb occurred, sufficient digesta was usually propelled through the cannula to

FIGURE 16

This diagram is derived from radiographic cine-film of the onset of an aborad migrating pattern of bolus movement.

The arrows indicate the direction of bolus movement and the three lines represent the same region of small intestine at short time intervals.

A train of boluses move aborad at a constant speed. As the boluses are observed passing a point in the small intestine they become smaller and spaced further apart but their central points remain equally spaced as is illustrated with the broken line.

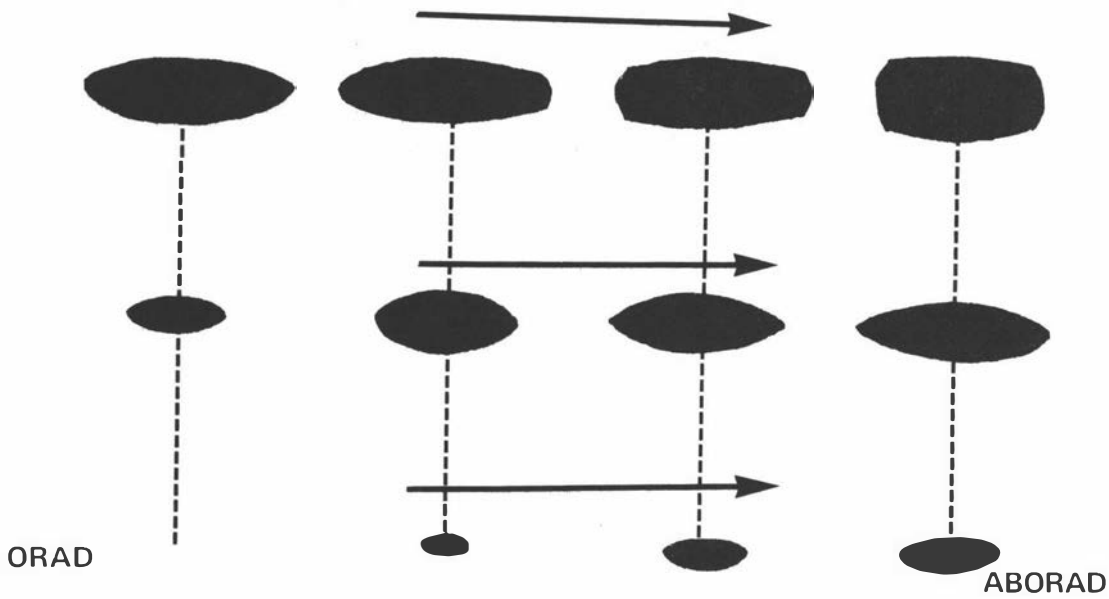
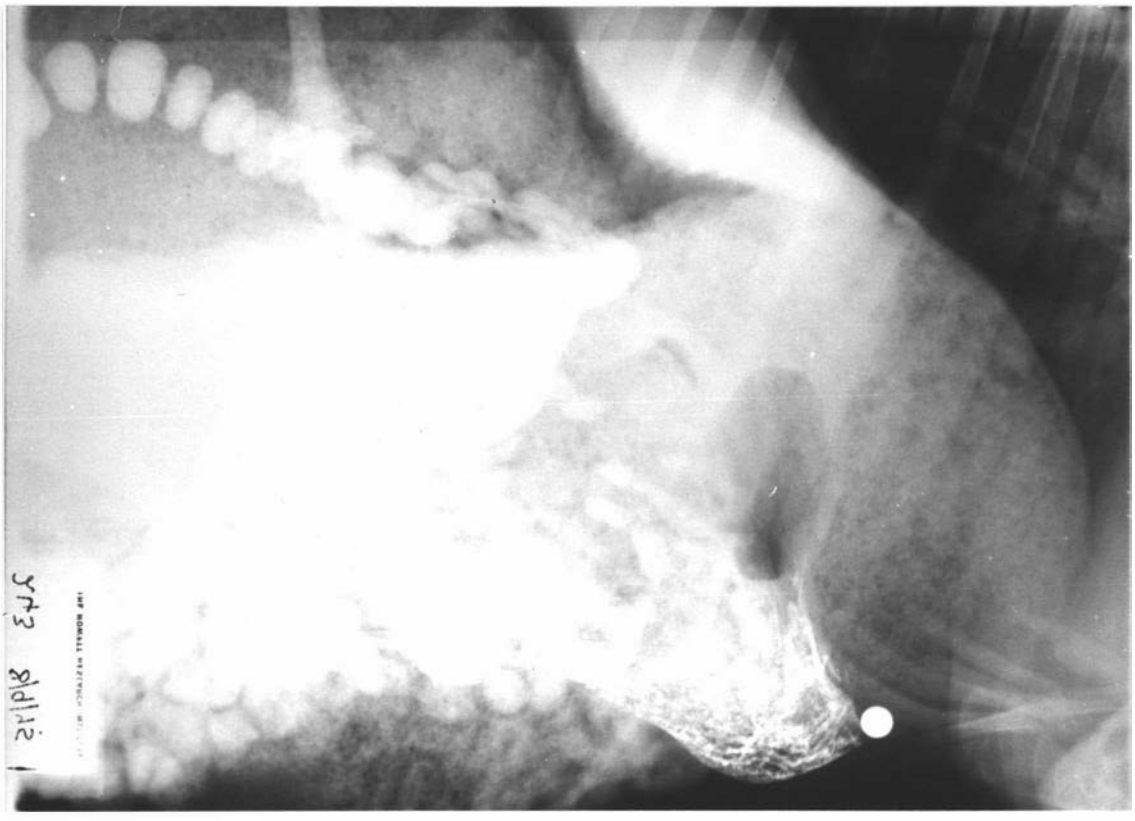
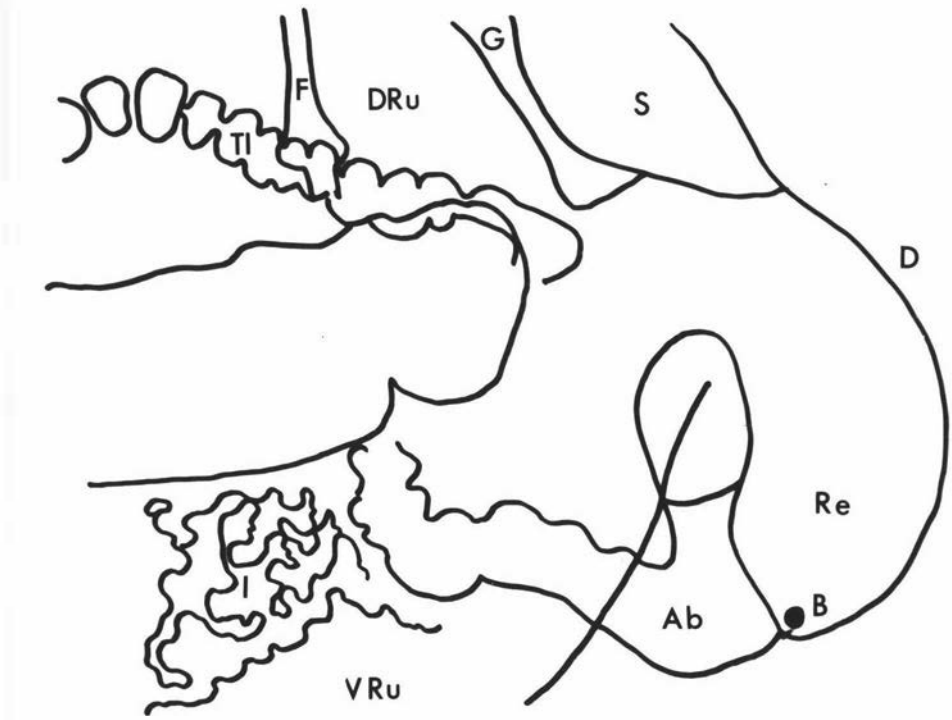

ORAD
ABORAD

PLATE 71

Although there are many features visible on this radiograph the main point of interest is the leading edge of a migrating pattern of bolus movement that can be seen in the terminal ileum. It is moving from left to right towards the ileo-caecal valve. The increasingly regular spacing of the boluses can be seen. The other features on this radiograph are the outline of a rather empty abomasum and the irregularly sized boluses in other parts of the small intestine.

Ab abomasum, B ball bearing, D diaphragm, DRu dorsal rumen, F abomasal catheter, G gas cap, I ileum, Re reticulum, S spleen, T terminal ileum, VRu ventral rumen.




G
F
DRu
S
TI
D
Re
I
Ab
B
VRu

initiate, at the aborad side, a continuous rapid aborad progression of a long bolus. On the occasions when this did not occur, digesta returned orad through the cannula back into the relaxed duodenal bulb region and sometimes even passed back through the pylorus into the abomasum. The aborad migrating pattern still appeared to begin in the jejunum. Four months after the cannula was inserted the only change detected was an increase in the diameter of the duodenal bulb region.

Distal duodenum: The insertion of a re-entrant cannula in the horizontal duodenum just aborad of the sigmoid flexure caused considerable disruption to the normal passage of digesta. The boluses of digesta being delivered from the duodenal bulb rarely passed through the cannula intact and some digesta, frequently a large amount, remained orad of the cannula, causing distension of the duodenum. The arrival of successive boluses would gradually push this digesta through the cannula. At the aborad side of the cannula, the digesta on some occasions formed another long bolus which then continued rapidly aborad into the jejunum. More frequently, a number of smaller boluses were formed and moved aborad at a much slower and irregular pace. The aborad migrating pattern was still seen to start up in the jejunum at a frequency that could not be distinguished from that in the non-cannulated animal.

(2) Jejunum.

Re-entrant cannulae inserted in either the proximal or distal jejunum caused marked interference to the normal passage of digesta. Digesta was held up on the orad side of the cannula and within the cannula itself. Usually it was pushed through the cannula slowly and small boluses were then seen to pass slowly aborad. Only rarely did a single bolus push through enough digesta to form a long bolus on the aborad side of the cannual - when this occurred the bolus would progress rapidly aborad. The net effect was that whereas in the normal animal digesta passed the site cannulated in a few seconds, in the cannulated animal digesta was delayed for more than 30 minutes. Migrating patterns of boluses occurred orad and aborad of the cannula. The patterns which started up orad to the cannula stopped at the

cannula and were never seen to "cross" it. Aborad of the cannula other migrating patterns started up independently.

Simple T cannulae had almost no effect on the movement of digesta. The only detected consequence was that a small amount of digesta remained around the shoe of the cannula all the time. The migrating patterns passed without change.

(3) Ileum.

A re-entrant cannula inserted in the terminal ileum caused gross interference to the passage of digesta. In this region the size of the boluses was such that an individual bolus displaced only a small amount of digesta into the cannula. Digesta collected in the ileum dilating it for 150 - 220 mm orad of the cannula. Eventually some digesta was pushed through, only to pool on the aborad side. Transport to the ileo-caecal junction was usually delayed until a migrating pattern of movement arrived orad to the cannula pushing through most of the pooled digesta. However, the migrating pattern usually faded out 100 mm - 500 mm orad of the ileo-caecal junction leaving some digesta on the orad side of the cannula. Migrating patterns of bolus movements were never seen at the aborad side of the cannula. The digesta mass aborad of the cannula was moved to the ileo-caecal junction by the normal regional pattern of bolus movement. After the cannula had been in place for 4 months there was marked dilation of the ileum for 150 mm to 200 mm orad of the cannula.

5:3:3 Measurement of the volume and length of boluses in the duodenum and proximal jejunum.

Volume: In sheep with re-entrant cannulae in the proximal small intestine, the volume of digesta collected over 30 minutes from the orad arm of the re-entrant cannulae and the number of boluses which delivered it are given in Table XV. The mean volume of 147 boluses was 13.3 ml.

Length: The measurements of 3 boluses in the duodenums of each of

TABLE XV

THE VOLUME OF RAPIDLY ABORAD MIGRATING BOLUSES IN THE PROXIMAL SMALL INTESTINE

Sheep No.	Cannulation Site	Session*	Volume Collected** (ml)	No. of Boluses***	Bolus Volume (ml)	Mean Bolus Volume (ml)
			a	b	a/b	
5	Duodenum 70 mm from pylorus	1 2 3 4	93 169 193 224	6 11 13 15	16 15 15 15	15.1
4	Duodenum distal to hepatic flexure	1 2 3 4	99 197 140 171	10 13 12 16	10 15 12 11	11.9
6	Jejunum, immediately aborad of duodenum	1 2 3 4	97 268 156 192	8 17 11 15	12 16 14 13	14.0
	All sheep		1949	147		13.3

(*) Session 1 - 2 weeks after surgery; 2 - 3 weeks after surgery; 3 - 4 weeks after surgery; 4 - 2 months after surgery.

(**) Collected from open orad arm of re-entrant cannula over period of 30 minutes.

(***) Determined from radiological observation (video-tape).

three sheep are given in Table XVI. The mean of these was 115 mm with a range of 89 - 134 mm.

5:3:4 Experimental initiation of contractions of the small intestine by the introduction of digesta into the lumen.

If digesta arriving at the orad side of the re-entrant cannula was withdrawn by allowing it to escape from the opened cannula, no digesta movement at the aborad side of the cannula could be detected radiographically. This was true even when large volumes of digesta were delivered at the orad fistula. Activity of the intestine at the aborad side of the cannula could readily be initiated by the reintroduction of digesta at the aborad arm of the cannula. Rapid injection of 15 ml initiated a continuous rapid aborad progression of a long bolus. Injections of lower volumes or at a slower rate caused the formation of a number of smaller boluses which moved aborad in a slow and irregular manner.

5:3:5 Recording of myoelectric potentials in the wall of the proximal jejunum.

The basic forms of electrical activity recorded were regular slow changes of potential (slow waves) and sharp transient changes of potential (spiking). The sharp potential changes of spiking activity were superimposed on slow waves and varied in occurrence, intensity and size. These basic forms were organised into patterns of activity the most conspicuous of which was a rhythmic spiking activity (RSA) which migrated slowly aborad. Another pattern was that of rapid aborad migrating spike potentials(RAMS).

Migrating myoelectrical complexes (MMC): The MMC was a regularly recurring pattern of activity which passed aborad over the array of electrodes at intervals of 30 - 70 minutes. Three phases could be distinguished, a quiescent phase, a phase of irregular spiking activity (ISA) and a phase of rhythmic spiking activity (RSA).

(1) Quiescent phase: At each electrode there was a period when the

TABLE XVI

THE LENGTH (mm) OF RAPIDLY ABORAD MIGRATING BOLUSES IN THE DUODENUM.

Sheep No.	Bolus No.	Length mm
3	1	118
	2	109
	3	112
		mean 113.0
4	1	89
	2	117
	3	122
		mean 109.3
5	1	131
	2	134
	3	105
		mean 123.3
All sheep		mean 115.2

only activity recorded was the slow wave or pace-setter potential. The amplitude of the slow wave waxed and waned but not apparently in any regular manner (Plate 72). The mean frequency of the slow wave at each electrode is given in Table XVII. A general trend for the frequency to decrease aborally along the small intestine can be seen. Also there were consistent animal differences: the ranking of the animals in terms of the slow wave frequency at each individual electrode site was identical at 5 of the 6 sites. The overall mean frequency (all sheep, all electrodes) was 21.09/minute, range 19.8 - 22.7/minute.

(2) Irregular spiking activity phase: When an ISA phase affected an electrode and spiking potentials appeared on some of the slow waves (Plate 73), the number of slow waves with superimposed spike potentials tended to increase as the ISA phase moved across the electrode. It was not possible to establish whether or not spiking potentials migrated along the small intestine, because of the spacing of electrodes used and the random nature of the spiking activity.

(3) Regular spiking activity phase: In the RSA phase large spike potentials occurred on every slow wave migrating aborad across the electrodes (Plate 74). As an RSA phase approached an electrode, first the amplitude of the slow wave increased, then spike potentials appeared regularly on every slow wave and covered an increasing segment of the slow wave (Plate 75). These patterns of activity usually migrated aborad across all the electrodes (Plate 76) but occasionally one would start up between electrodes and then migrate aborad (Plate 77). The speed at which the RSA phase migrated was variable (Plates 76, 78). The times taken for the RSA phase to pass between successive electrodes is given in Table XVIII and the calculated speed of migration in Table XIX. The time taken for an RSA phase to pass each electrode is given in Table XX. The standard error is not quoted because this would be the same as for the time taken for the RSA phase of the MMC to migrate between electrodes (Table XVIII).

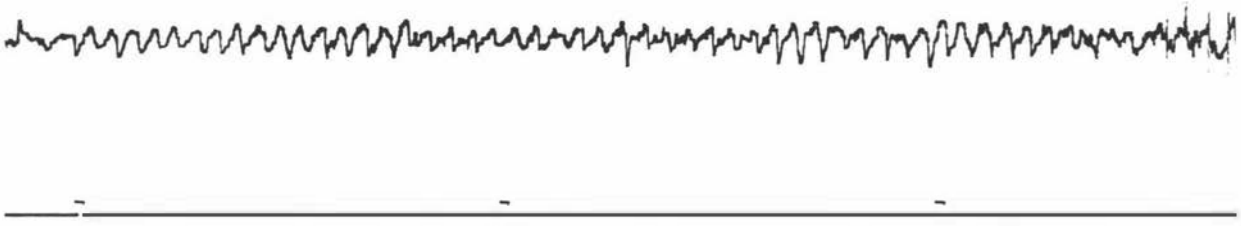
In two of the animals (sheep 30, 32) the speed of migration appeared to decrease as the RSA phase moved aborally (Table XIX). However, in none of the animals were trends consistent. The duration of the RSA

PLATE 72

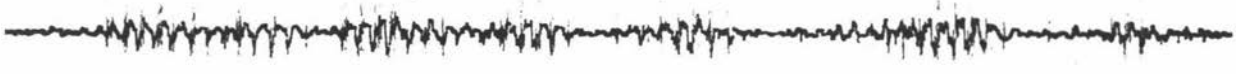
Electromyogram from an electrode on the jejunum during the quiescent phase (sheep 34). There are no spiking potentials only slow waves which wax and wane in amplitude but have a constant frequency.

PLATE 73

Electromyogram from an electrode on the jejunum during ISA phase (sheep 32). Bursts of spiking potentials are superimposed on the slow waves at irregular intervals.



mins



mins

TABLE XVII

SLOW WAVE FREQUENCY

Electrode	Number per minute							
	Sheep 30		Sheep 32		Sheep 33		Sheep 34	
	Mean ±	S.E.	Mean ±	S.E.	Mean ±	S.E.	Mean ±	S.E.
1	20.8 ±	0.2*	20.1 ±	0.1	22.1 ±	0.2	22.7 ±	0.2
2	20.8	0.2	20.1	0.1	21.9	0.2	22.1	0.1
3	21.0	0.1	19.9	0.1	21.9	0.3	22.0	0.2
4	20.9	0.1	20.0	0.1	21.5	0.2	21.1	0.2
5	20.9	0.1	19.8	0.1	21.2	0.2	21.4	0.2
6	20.9	0.1	19.8	0.1	21.8	0.3	21.7	0.2

* Mean and standard error (S.E.) of 30 readings at each electrode site for each sheep.

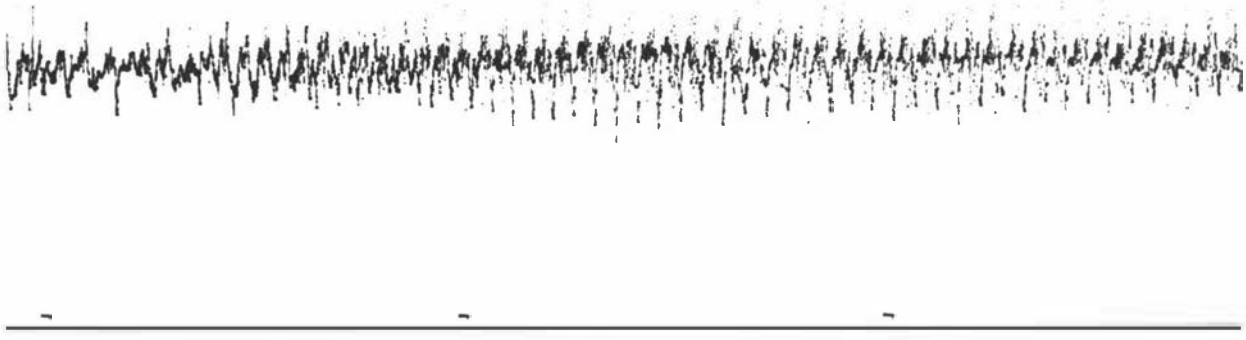
Note: The individual readings are not given because there is a large number of them. The readings taken for one sheep are given in Appendix III as an example.

PLATE 74

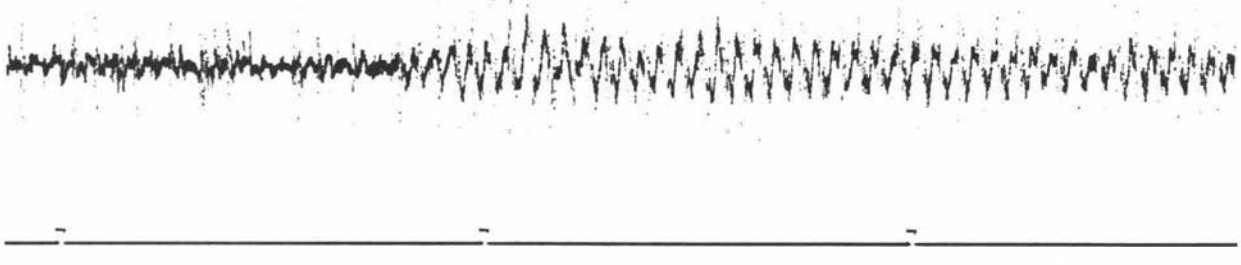
Electromyogram from an electrode on the jejunum during the RSA phase. Large amplitude spiking potentials occur superimposed on every slow wave (sheep 30).

PLATE 75

Electromyogram from an electrode on the jejunum as the RSA phase becomes established (sheep 30). The amplitude of the slow waves increases then spike potentials appear on every slow wave and are superimposed on an increasing segment of the slow wave.



mins



mins

PLATE 76

Electromyograms from six electrodes on the jejunum (sheep 34). Electrode 1 is the most orad and there is 300 mm between each electrode except 3 and 4 where the spacing is 200 mm. A T cannula is located midway between electrodes 3 and 4. The RSA phase migrates across all the electrodes with the slope of line connecting the approximate midpoints of the phase at each electrode representing the speed of migration. Note the quiescent phase that follows the RSA phase at each electrode.

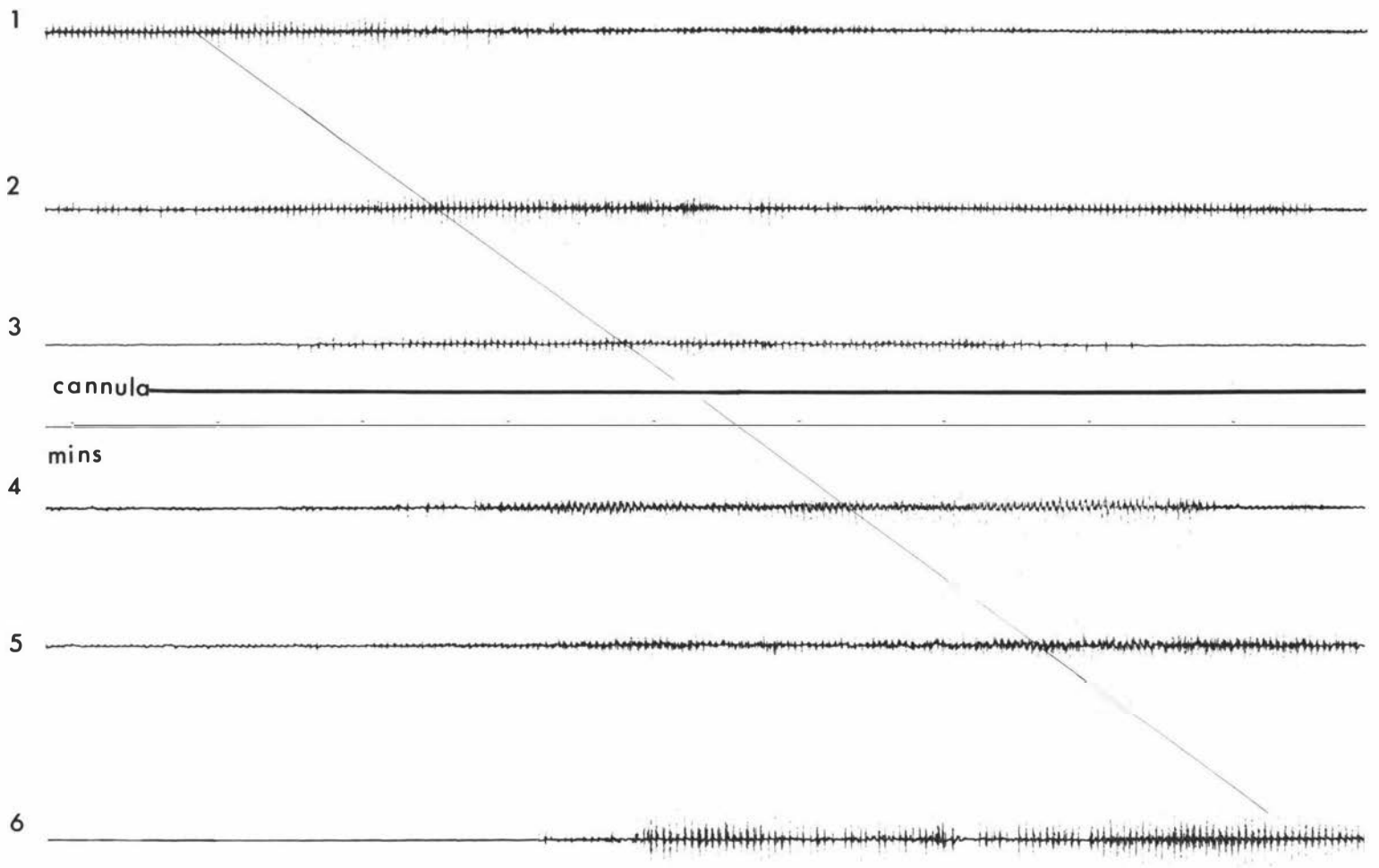

1
2
3
cannula
mins
4
5
6

PLATE 77

Electromyogram from six electrodes on the jejunum with the same distribution as those on Plate 76 (sheep 34). The RSA phase does not appear at electrode 1 so it must have started somewhere between electrodes 1 and 2. The activity at electrode 1 is only slow wave, there are no spiking potentials.

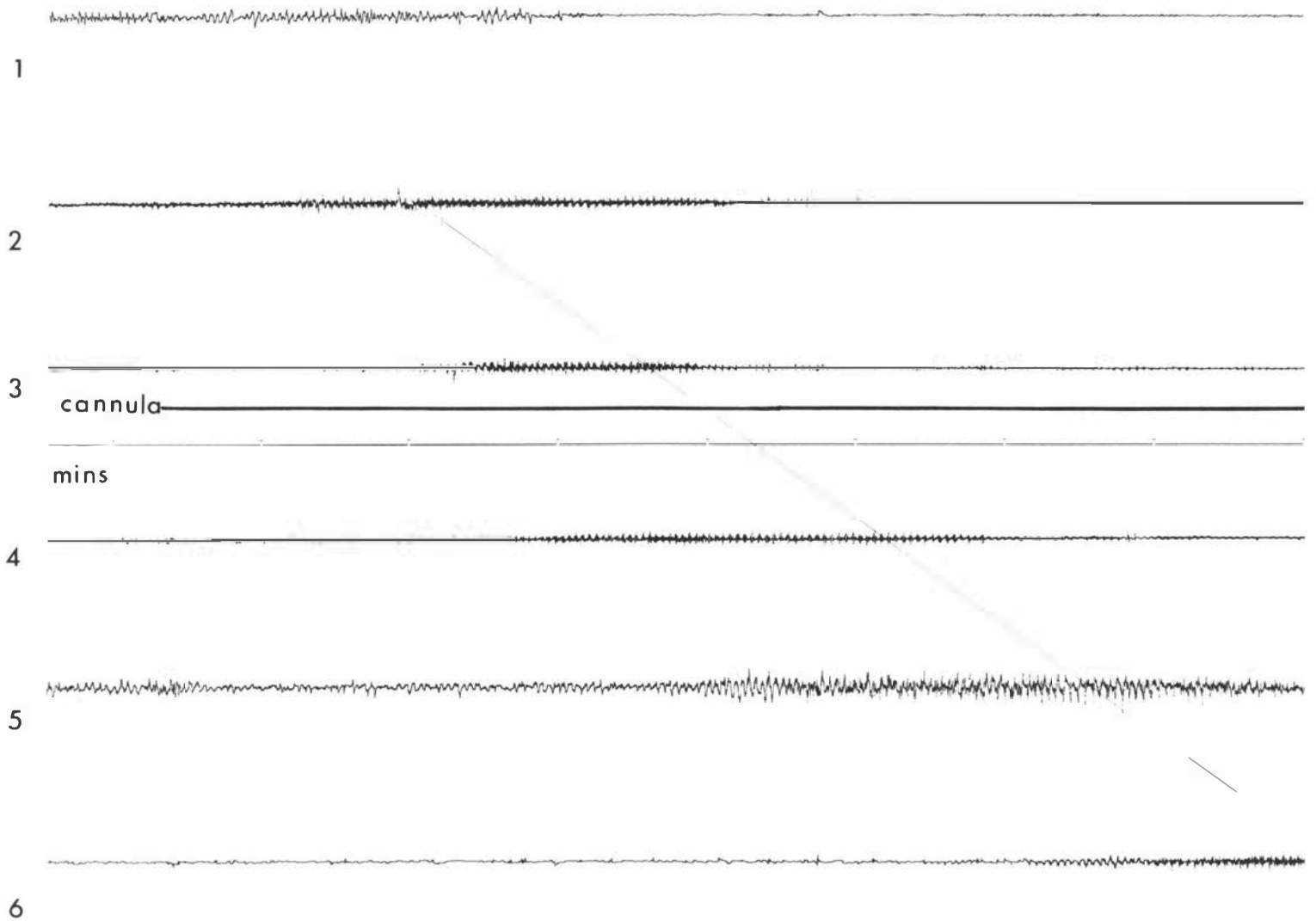

1
2
3
cannula
mins
4
5
6

PLATE 78

Electromyograms from six electrodes of the jejunum from the same sheep as Plate 76. The slope of the line joining the approximate midpoints of the RSA phase at each electrode is steeper than on Plate 76 indicating an increase in the speed of migration.

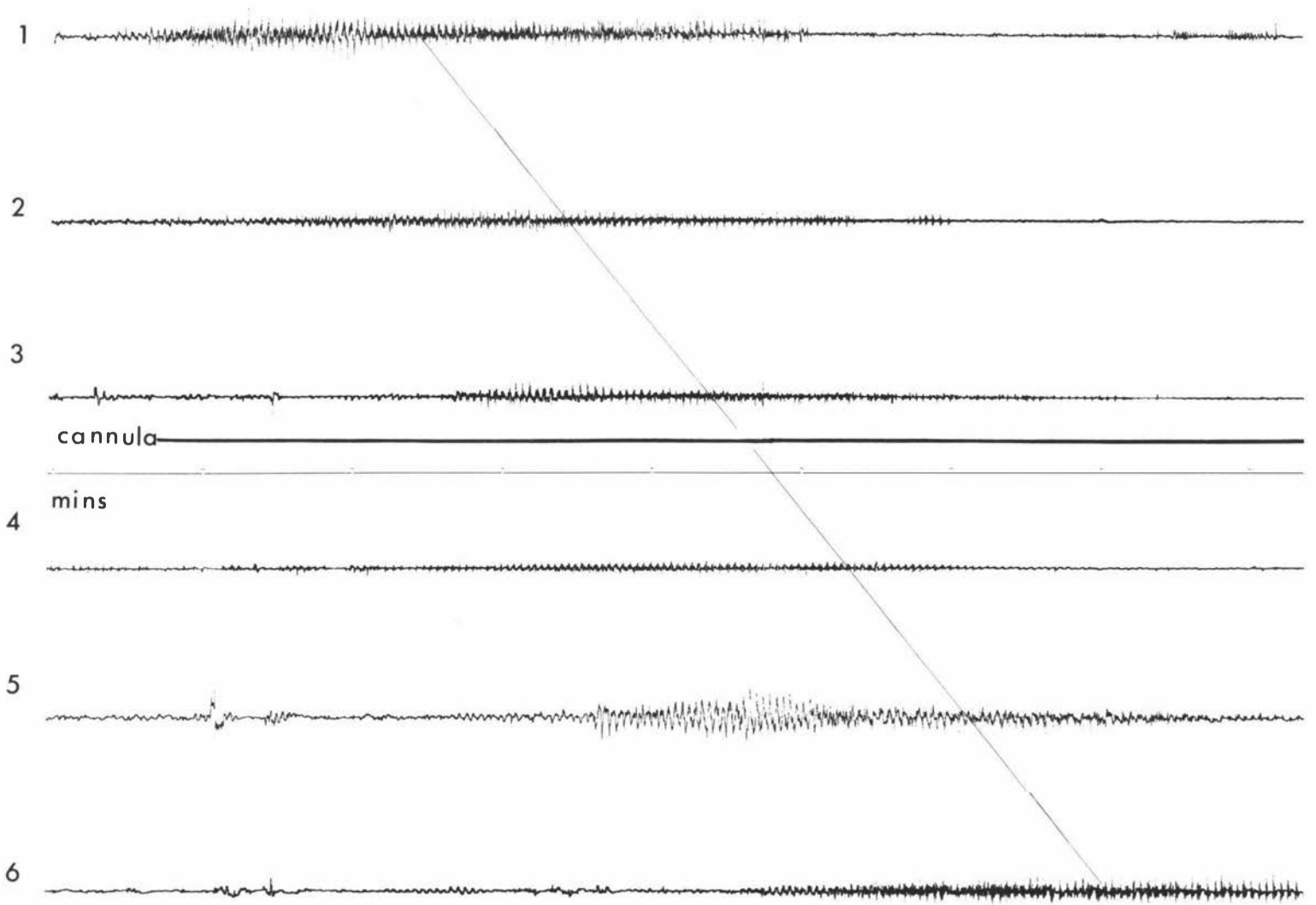

1
2
3
cannula
mins
4
5
6

TABLE XVIII

TIME (SECONDS) FOR AN RSA PHASE OF AN MMC TO MIGRATE BETWEEN SUCCESSIVE ELECTRODES

Electrode Pair	Sheep 30		Sheep 32		Sheep 33		Sheep 34	
	Mean	± S.E.*	Mean	± S.E.	Mean	± S.E.	Mean	± S.E.
1 - 2	56	6	39	5	58	6	38	4
2 - 3	53	7	22	5	57	7	45	5
3 - 4 +	46	7	34	4	31	8	35	5
4 - 5	73	6	56	7	48	7	42	6
5 - 6	87	6	70	8	46	3	40	6

* Mean and standard error (S.E.) of 10 readings at each electrode.

\+ T cannula between electrodes 3 and 4.

Note: The individual readings are not given because there is a large number of them. The readings taken for one sheep are given in Appendix III as an example.

TABLE XIX

THE SPEED OF MIGRATION (cm/second) OF THE RSA PHASE OF AN MCC BETWEEN ELECTRODES

Calculated from time taken between electrodes (Table XVIII) and the distance between electrodes as measured postmortem before stripping the mesentery (Table XIV).

Electrode Pair	Sheep 30		Sheep 32		Sheep 33		Sheep 34	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
1 - 2	0.75	0.48-2.92	0.66	0.36-1.86	0.51	0.29-0.75	0.83	0.56-1.52
2 - 3	0.80	0.47-1.75	0.67	0.26-2.50	0.52	0.14-0.88	0.71	0.46-1.39
3 - 4	0.42	0.23-0.89	0.76	0.44-1.18	0.59	0.17-1.20	0.52	0.33-1.13
4 - 5	0.55	0.37-0.77	0.54	0.32-1.15	0.46	0.20-0.67	0.64	0.30-1.13
5 - 6	0.46	0.37-0.67	0.50	0.29-0.88	0.56	0.39-0.79	0.84	0.39-1.83
Mean Speed 1 - 6	0.60	-	0.63	-	0.53	-	0.70	-

TABLE XX

TIME (SECONDS) FOR THE RSA PHASE OF AN MMC TO PASS AN ELECTRODE

Electrode	Sheep 30	Sheep 32	Sheep 33	Sheep 34
	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.
1	172 ± 16	205 ± 16	149 ± 6	227 ± 15
2	203 13	200 11	159 7	225 12
3	197 6	202 14	151 7	160 18
4	155 5	220 10	189 5	153 13
5	151 8	234 8	191 7	213 18
6	177 8	220 13	206 9	253 21

* Mean and standard error (S.E.) for 10 readings at each electrode.

Note: The individual readings are not given because there is a large number of them. The readings taken for one sheep are given in Appendix III as an example.

phase was also variable. An indication of duration is given by the time an RSA phase takes to pass a given electrode which varied from 149 - 253 seconds (Table XX). The accuracy of such figures is limited because they will depend also on the speed with which an RSA phase is passing an electrode.

Rapid aborad migrating spike potentials: Another pattern of electrical activity, RAMS, was recorded at frequent intervals through the ISA phase (Plate 79). Bursts of spike potentials superimposed on a slow wave would appear and migrate rapidly aborad. The amplitude of these spikes was greater than ISA and they covered a larger segment of the slow wave (Plate 80). The time taken for RAMS to migrate between electrodes is given in Table XXI and their calculated speed of migration is given in Table XXII. It will be seen that RAMS activity migrates at more than 15 times the speed of the RSA phase.

5:3:6 Simultaneous radiological observations and electrical recordings for correlation of digesta movements with myoelectrical activity.

The relationship between the myoelectrical activity and the radiological observations was identical in all animals.

When the only electrical activity recorded was the slow wave, which occurred most consistently during the quiescent phase, often no digesta could be seen in the lumen. If digesta were present they were either static or were being pushed into the region by activity in the region of intestine immediately orad. The amplitude of the slow wave increased as the intestine was distended with digesta.

When the electrical activity recorded was the ISA phase, the pattern of bolus movement seen radiographically was the regional pattern. While there were spike potentials on the slow waves, boluses were passing the electrode; when there were no spike potentials, the lumen was empty.

During the RSA phase, the pattern of bolus movement observed

PLATE 79

Electromyograms from six electrodes on the jejunum with the same distribution as those on Plate 76. ISA is occurring at each electrode but superimposed on this are RAMS. One RAMS is connected by a line indicating its speed of migration across the electrodes.

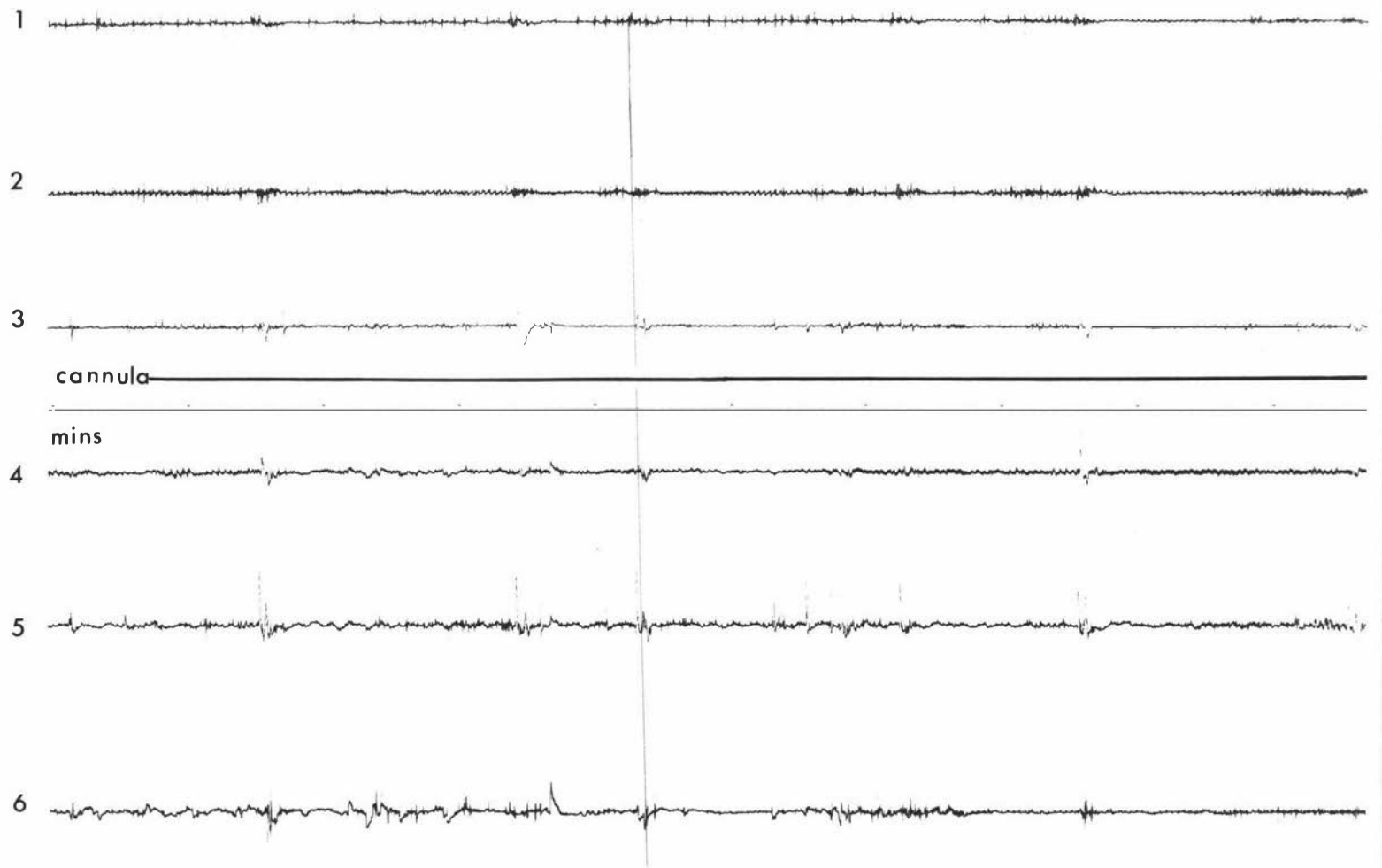

1
2
3
cannula
mins
4
5
6

PLATE 80

Electromyograms from six electrodes on the jejunum with the same distribution as on Plate 76. The paper speed has been increased to 5 mm/second to allow better comparison of the spiking potentials of the ISA phase and RAMS. It will be seen that the spiking potentials of the RAMS are superimposed over a greater proportion of the slow wave. The RAMS at each electrode is connected by the sloping line indicating the speed of migration.

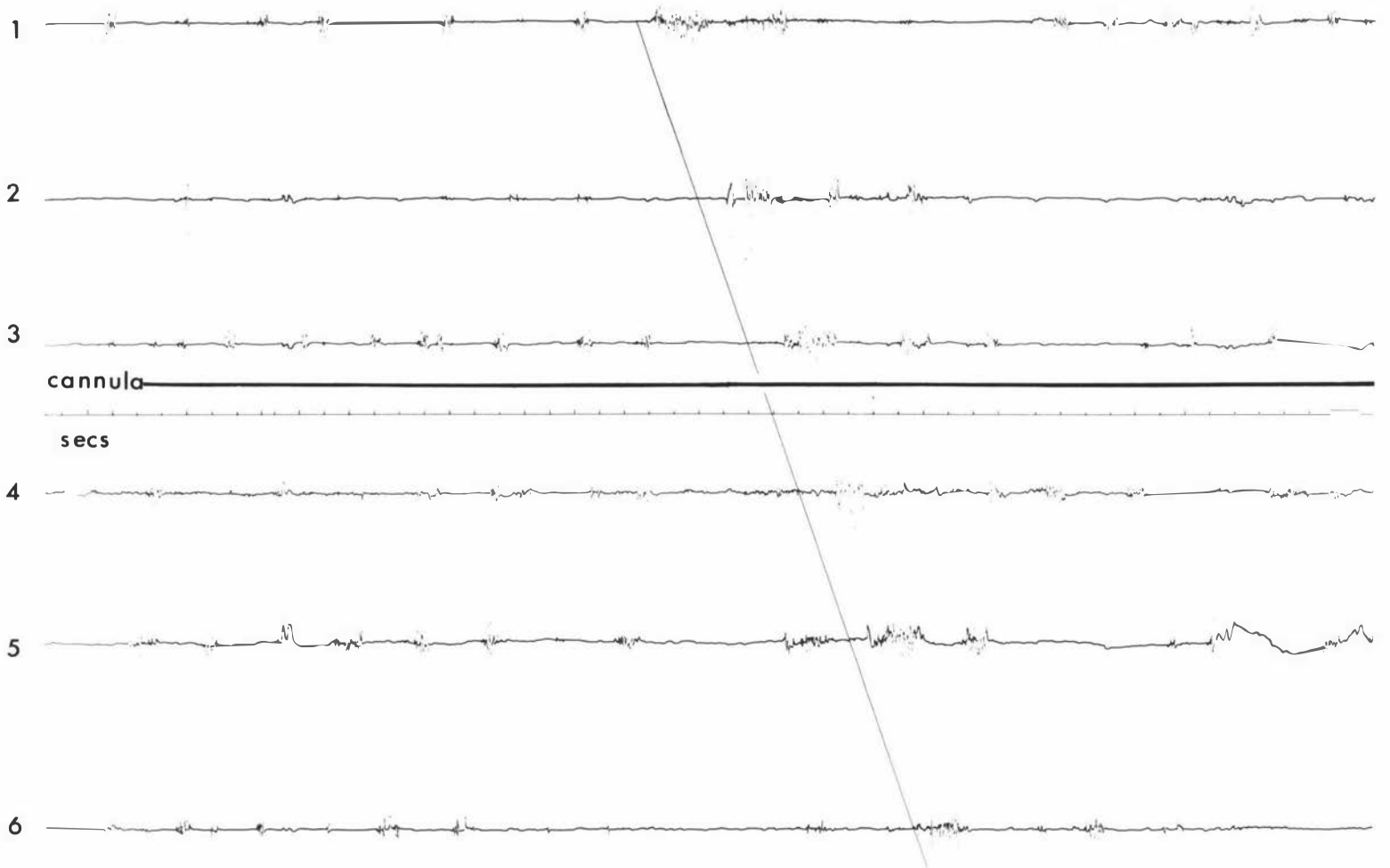

1
2
3
cannula
secs
4
5
6

TABLE XXI

TIME (SECONDS) TAKEN FOR A RAMS TO MIGRATE BETWEEN ELECTRODES

Electrode	Sheep 30	Sheep 32	Sheep 33	Sheep 34
	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.	Mean ± S.E.
1 - 2	3.86 ± 0.09*	2.35 ± 0.06	2.91 ± 0.06	2.81 ± 0.06
2 - 3	3.74 0.10	1.45 0.05	2.79 0.06	2.75 0.06
3 - 4	1.78 0.07	2.39 0.05	1.70 0.07	1.68 0.07
4 - 5	4.63 0.01	2.71 0.06	2.43 0.09	2.44 0.06
5 - 6	4.57 0.13	2.79 0.06	2.49 0.06	2.90 0.07

* The mean and standard error (S.E.) for 30 readings.

Note: The individual readings are not given because there is a large number of them. The readings taken for one sheep are given in Appendix III as an example.

TABLE XXII

THE SPEED OF MIGRATION (cm/second) OF A RAMS BETWEEN SUCCESSIVE ELECTRODES

Calculated from the time taken between electrodes (Table XXI) and the distance between electrodes as measured postmortem before stripping of the mesentery (Table XIV).

Electrode Pair	Sheep 30		Sheep 32		Sheep 33		Sheep 34	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
1 - 2	10.9	9.6-12.3	11.1	9.4-12.4	10.3	9.4-11.5	10.7	9.7-11.9
2 - 3	11.2	10.2-12.7	10.3	8.8-11.5	10.8	10.0-12.0	10.8	9.7-12.1
3 - 4	11.0	9.3-13.0	10.9	9.6-12.4	10.6	9.0-12.9	11.3	9.0-14.6
4 - 5	10.8	9.8-11.6	11.1	10.0-12.5	9.1	7.6-11.0	10.9	9.6-12.3
5 - 6	12.0	11.0-14.1	12.5	11.3-14.0	10.4	9.0-11.3	11.1	9.7-12.2
Mean 1 - 6	11.2	-	11.2	-	10.2	-	11.0	-

The standard error is not given because this would be the same as for the time taken for the wave to migrate between electrodes (Table XXI).

radiologically was the aborad-migrating pattern of bolus movement. As an RSA approached an electrode and spike potentials appeared on every slow wave, the boluses passing the electrode became evenly spaced and moved continuously aborad. As spike potentials covered a greater segment of the slow wave, the boluses became smaller and further apart until, finally, when the RSA reached the electrode, the lumen of the intestine was empty.

With RAMS the pattern of bolus movement was a continuous rapid aborad progression of a long bolus. The bursts of spike potentials crossed the electrode as the trailing edge of the long bolus moved past. No electrical activity appeared to be associated with the passage of the leading edge of the bolus.

5:3:7 Observation of the effects on the myoelectrical activity of the small intestine of removal of digesta or the introduction of digesta.

While the cannula was closed, the RAMS and all three phases of the MMC migrated aborad past the cannula without any detectable modification. When the cannula was open a volume of digesta (10 - 15 ml) was ejected with the arrival of each RAMS. On no occasion in any of the four sheep did a RAMS pass the open cannula, nor were any established aborad of the cannula (Plate 81).

The effect of the open cannula on the migration of the RSA is illustrated in Figures 17, 18, 19 and 20. The volume of digesta ejected as an RSA phase approached depended on how long the cannula had been open: if it had just been opened 15 - 20 ml were ejected but if it had been open for 15 minutes or more as little as 3 - 5 ml were ejected. The frequency at which RSA phases appeared was markedly reduced when the cannula was open. However, on all occasions except one, the RSA phase migrated past the cannula, and as it did so its speed of migration increased (Plate 82); the exception was in sheep 32 during session 2 (Fig. 18). RSA phases started up on the aborad of electrode 3 on two occasions, once in sheep 32 (Fig. 18) and once in sheep 33 (Fig. 19).

PLATE 81

Electromyograms from six electrodes on the jejunum with the same distribution as on Plate 76 (sheep 34). The cannula is open. RAMS are migrating between electrodes 1, 2 and 3 with one of these being indicated by the sloping line. No RAMS appear at electrode 4, 5 and 6.

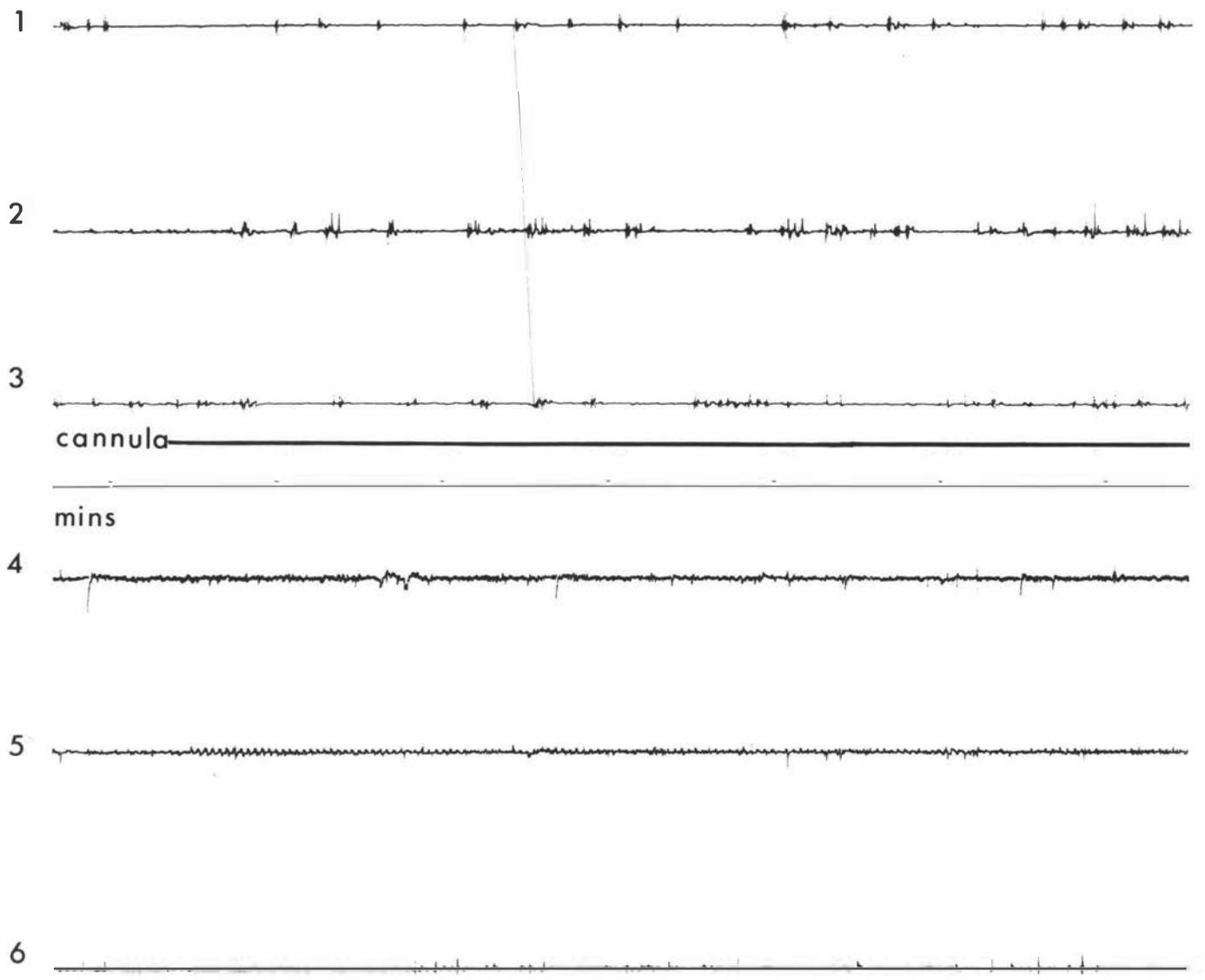

1
2
3
cannula
mins
4
5
6

PLATE 82

Electromyograms from six electrodes on the jejunum with the same distribution as on Plate 76 (sheep 32). The cannula is open. The speed of migration of the RSA phase, as indicated by the sloping line, increases between electrodes 4, 5 and 6.

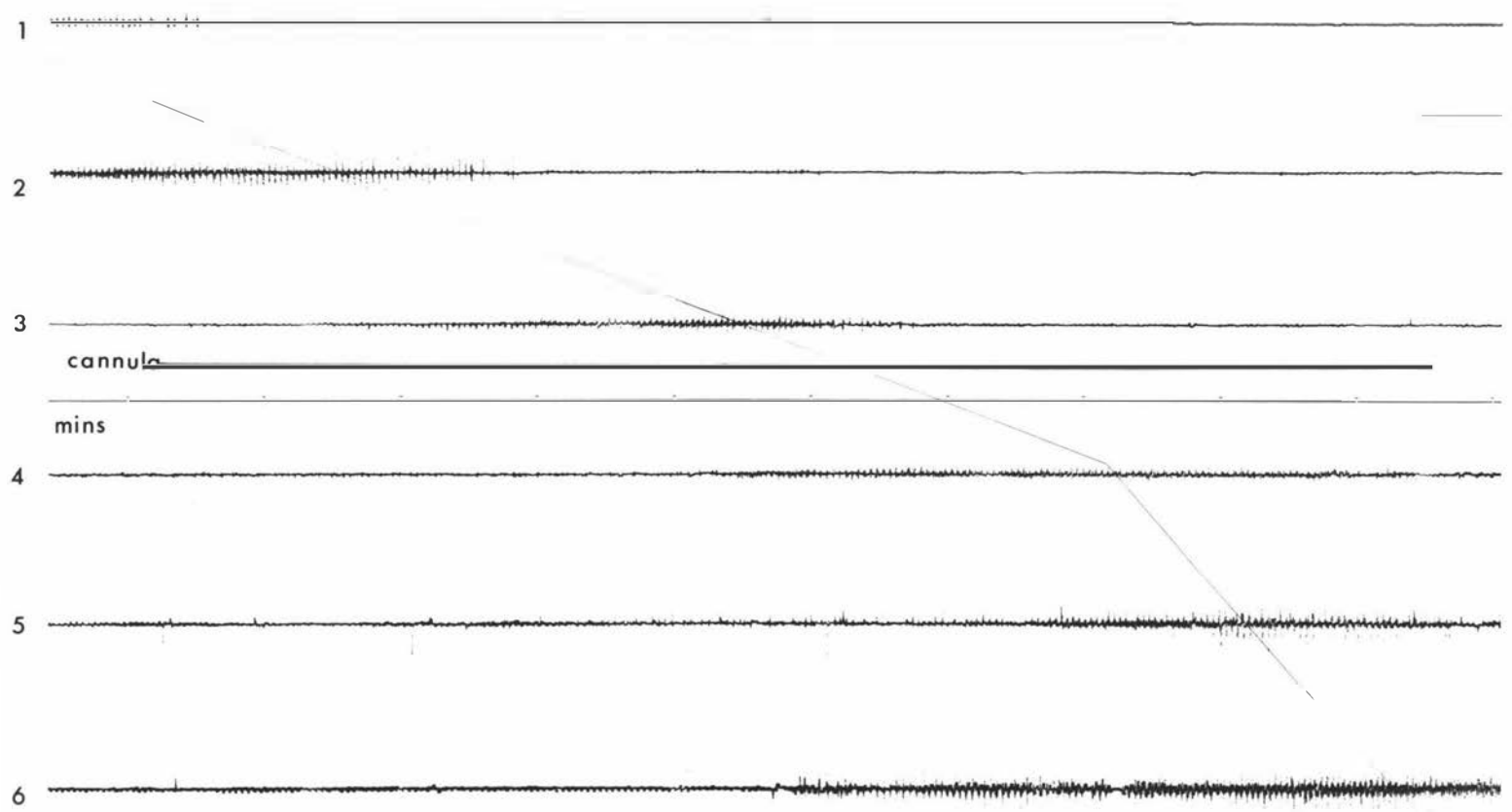

1
2
3
cannula
mins
4
5
6

PLATE 83

Electromyograms from six electrodes on the jejunum with the same distribution as on Plate 76 (sheep 33). The cannula is open. An RSA phase has started aborad of electrode 3.

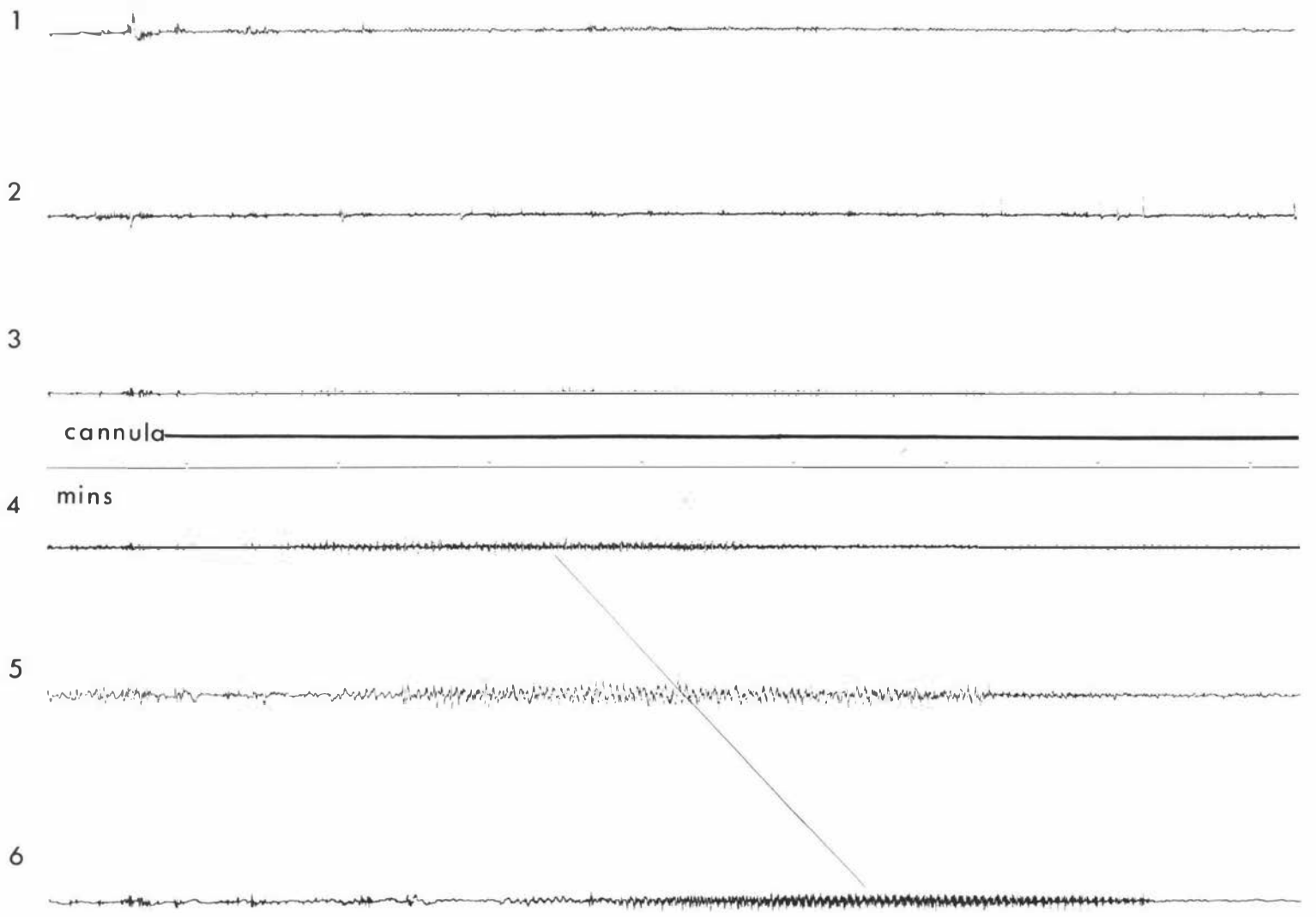

1
2
3
cannula
mins
4
5
6

FIGURE 17

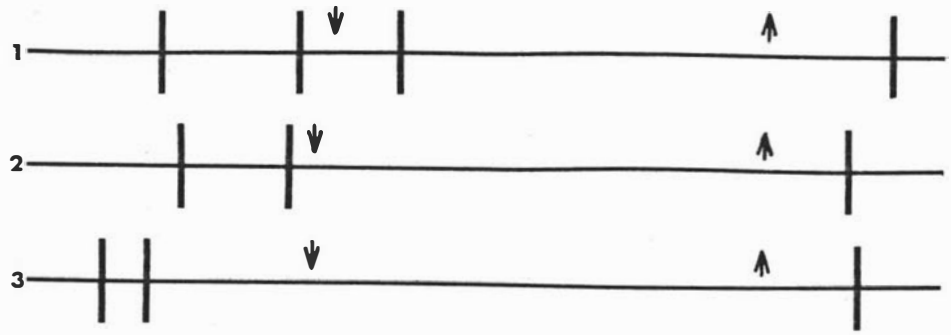
On this figure 3 sessions (1, 2, 3) are shown for this animal for each of 3 different treatments - cannula open, cannula open and balloon inflated aborad to the cannula and 2.2 ml/minute of digesta being introduced aborad of cannula.

The horizontal line represents the position of the cannula; the vertical lines represent RSA phases with that section of the vertical line above the horizontal line being orad of the cannula (electrodes 1, 2 and 3) and that below the horizontal line aborad of the cannula (electrodes 4, 5 and 6); the arrows show the time interval over which the treatment was applied. The time scale at the foot is in minutes.

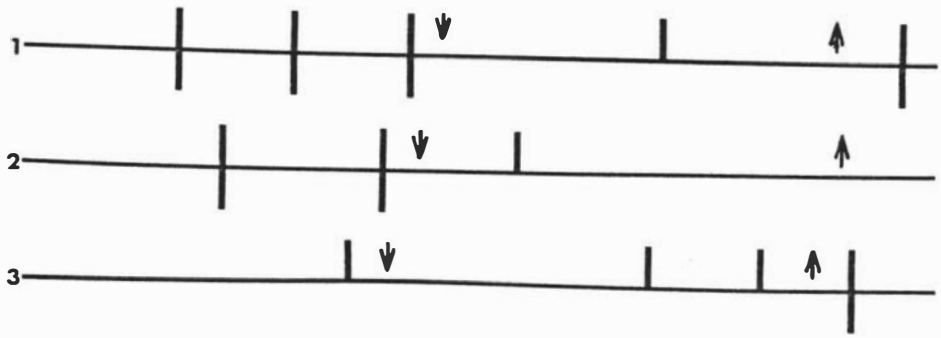
Thus in session 2 with the cannula open there are 2 RSA phases recorded prior to the cannula being opened (both passing from orad to aborad of the point where the cannula is inserted) and no RSA phases recorded while the cannula was open.

SHEEP 30

CANNULA OPEN



CANNULA OPEN BALLOON INFLATED



2.2 ML PER MIN. THROUGH CANNULA

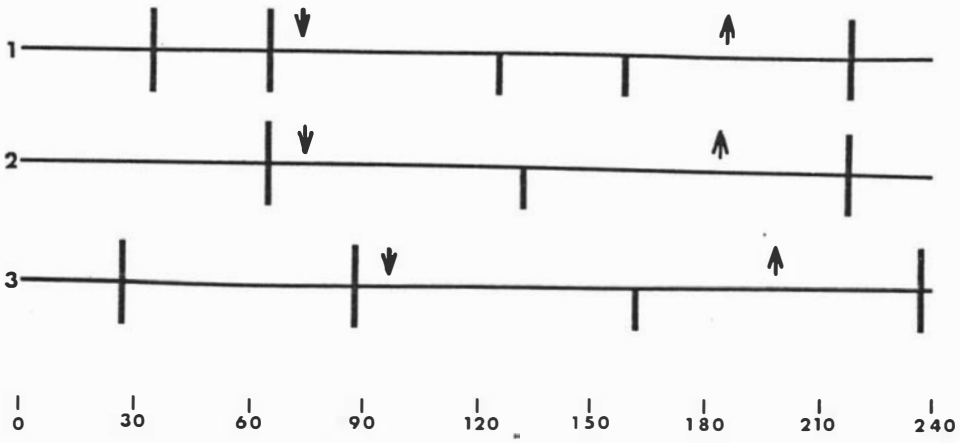


FIGURE 18

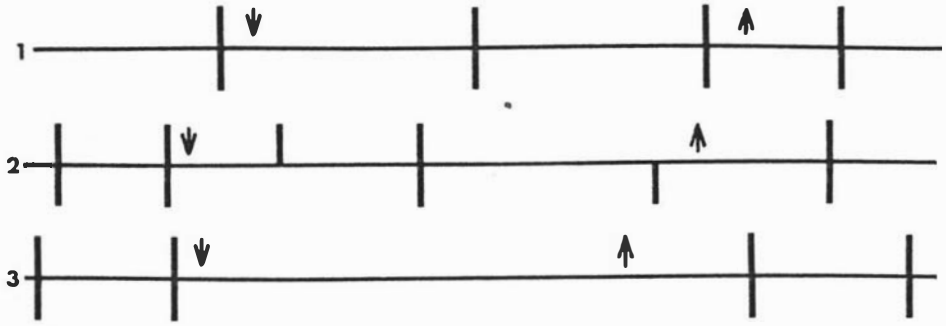
On this figure 3 sessions (1, 2, 3) are shown for this animal for each of 3 different treatments - cannula open, cannula open and balloon inflated aborad to the cannula and 2.2 ml/minute of digesta being introduced aborad of cannula.

The horizontal line represents the position of the cannula; the vertical lines represent RSA phases with that section of the vertical line above the horizontal line being orad of the cannula (electrodes 1, 2 and 3) and that below the horizontal line aborad of the cannula (electrodes 4, 5 and 6); the arrows show the time interval over which the treatment was applied. The time scale at the foot is in minutes.

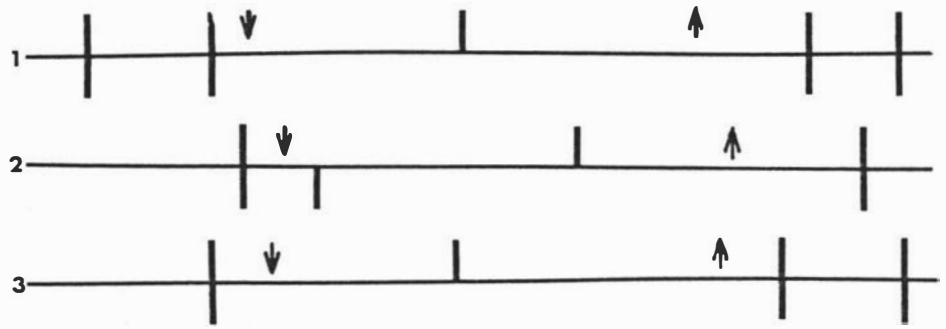
Thus in session 2 with the cannula open there are 2 RSA phases recorded prior to the cannula being opened (both passing from orad to aborad of the point where the cannula is inserted). After the cannula is opened 3 RSA phases are recorded; the first occurs only orad of the site where the cannula is inserted, the second passes from orad to aborad of the cannula site and the third occurs only aborad.

SHEEP 32

CANNULA OPEN



CANNULA OPEN BALLOON INFLATED



2.2 ML PER MIN. THROUGH CANNULA

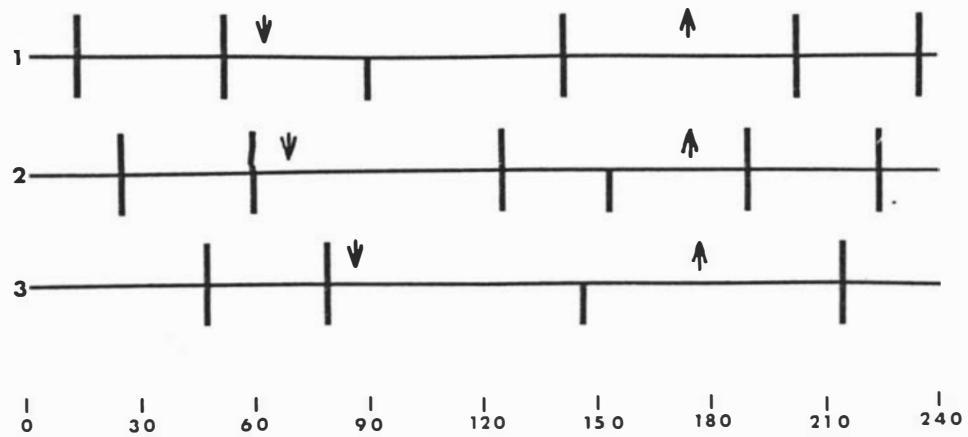


FIGURE 19

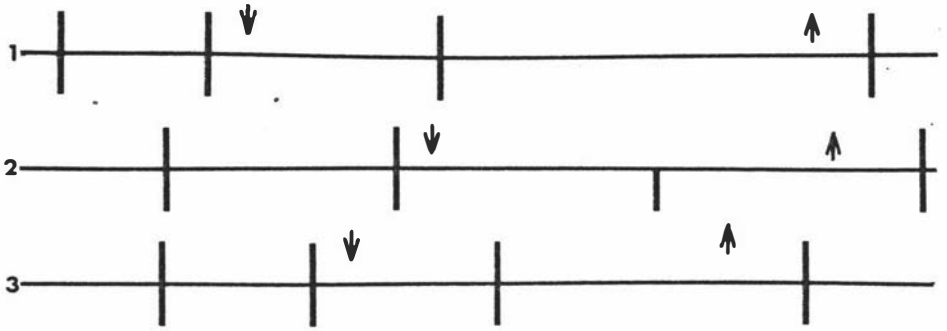
On this figure 3 sessions (1, 2, 3) are shown for this animal for each of 3 different treatments - cannula open, cannula open and balloon inflated aborad to the cannula and 2.2 ml/minute of digesta being introduced aborad of cannula.

The horizontal line represents the position of the cannula; the vertical lines represent RSA phases with that section of the vertical line above the horizontal line being orad of the cannula (electrodes 1, 2 and 3) and that below the horizontal line aborad of the cannula (electrodes 4, 5 and 6); the arrows show the time interval over which the treatment was applied. The time scale at the foot is in minutes.

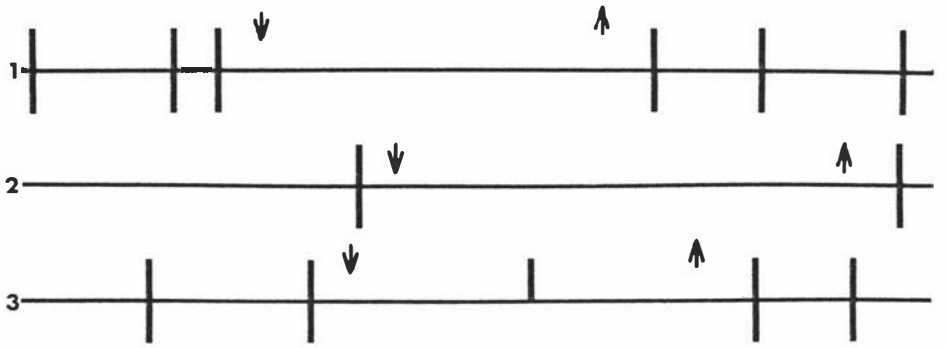
Thus in session 2 with the cannula open there are 2 RSA phases recorded prior to the cannula being opened (both passing orad to aborad of the point where the cannula is inserted). After the cannula is opened one RSA phase is recorded occuring only aborad of the site where the cannula is inserted.

SHEEP 33

CANNULA OPEN



CANNULA OPEN BALLOON INFLATED



2.2 ML PER MIN. THROUGH CANNULA

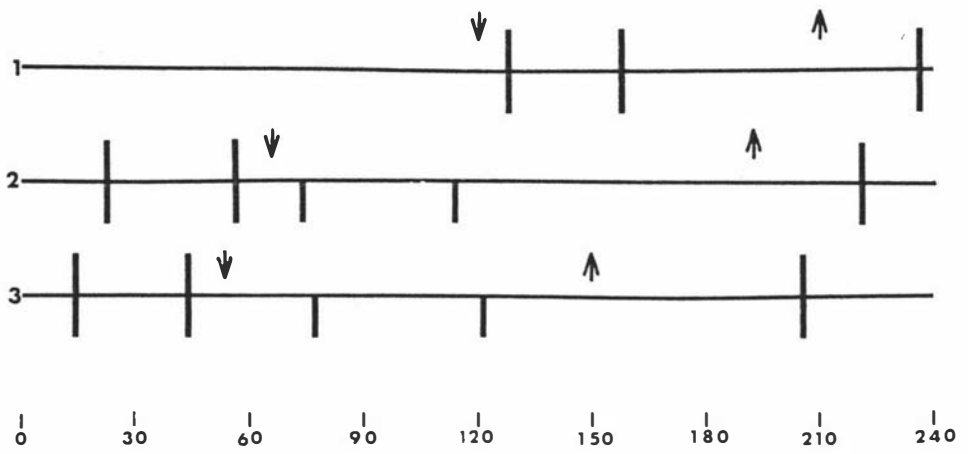


FIGURE 20

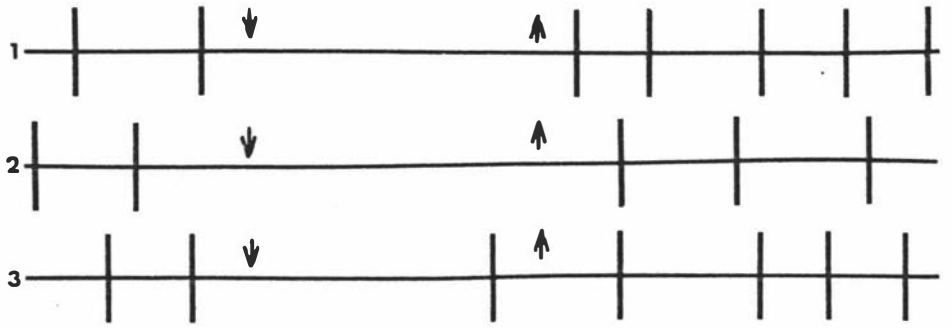
On this figure 3 sessions (1, 2, 3) are shown for this animal for each of 3 different treatments - cannula open, cannula open and balloon inflated aborad to the cannula and 2.2 ml/minute of digesta being introduced aborad of cannula.

The horizontal line represents the position of the cannula; the vertical lines represent RSA phases with that section of the vertical line above the horizontal line being orad of the cannula (electrodes 1, 2 and 3) and that below the horizontal line aborad of the cannula (electrodes 4, 5 and 6); the arrows show the time interval over which the treatment was applied. The time scale at the foot is in minutes.

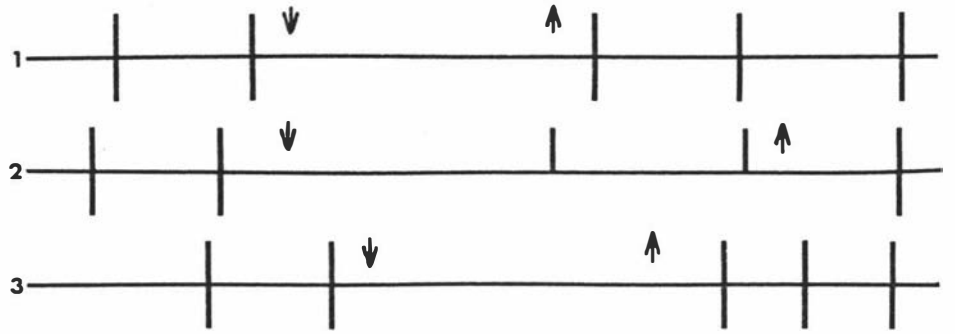
Thus in session 2 with the cannula open there are 2 RSA phases recorded prior to the cannula being opened (both passing orad to aborad of the site where the cannula is inserted). No RSA phase occur during the time the cannula is open.

SHEEP 34

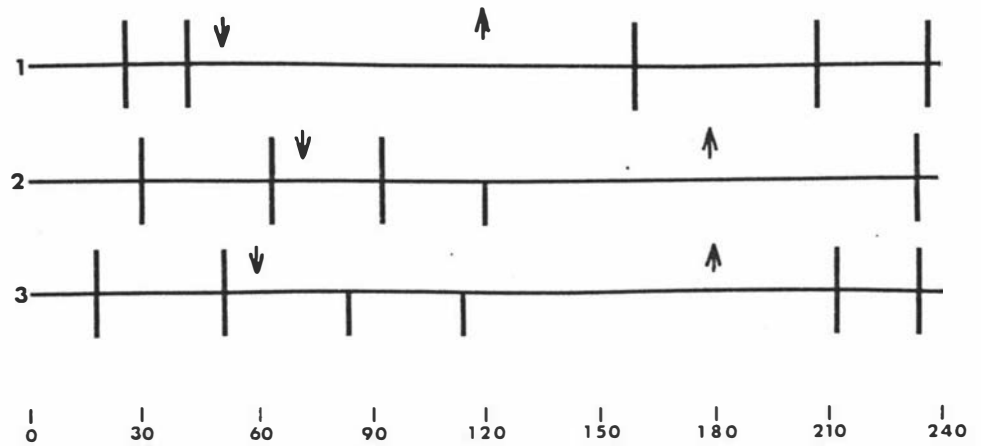
CANNULA OPEN



CANNULA OPEN BALLOON INFLATED



2.2 ML PER MIN. THROUGH CANNULA



With the cannula open and the aborad intestine sealed off by inflating a balloon in that part of the intestine encased in mesh, the volume of digesta ejected by the RAMS did not alter. As before, no RAMS passed the cannula. The volume of digesta ejected through the cannula as an RSA phase approached again depended on how long the cannula had been open, but it was approximately twice that delivered from the open cannula without the balloon. The effect on the RSA is illustrated in Figures 17, 18, 19 and 20. Under these conditions the RSA stopped at the cannula (Plate 84) except for one occasion when it started up independently aborad to the cannula (Fig. 18).

When digesta was infused into the intestine aborad to the cannula it had little or no effect on the volume of digesta delivered through the cannula by either type of activity. The major effect was to increase the number of RSA phases that were initiated aborad of the cannula (Plate 85). It also appeared that the frequency of RSA phases occurring from and orad of the cannula was reduced (Figs. 17, 18, 19 and 20).

5:4 DISCUSSION

Both methods of recording the activity of the small intestine had their limitations. To observe the movement of digesta radiographically it had to be made radio-opaque by the introduction of barium sulphate and this may have influenced the results. Barium sulphate has a high specific gravity and therefore tends to sink rapidly to the lowest point if not kept in suspension by some form of agitation. The problem is unavoidable because the radio-opacity of a substance depends on its being dense and of high atomic number. However as far as could be determined electromyographically, the addition of barium sulphate to the digesta did not alter the motility patterns. A further limitation was the inability to make continuous observations over extended periods because of the restricted capacity of the apparatus, the possibility of radiation damage to the animal and the radiation hazard to the observer. Intermittent observation meant that some significant event could be missed. Measurements taken from a radiograph are not accurate because of distortion of the image consequent on the geometry of its formation. Accurate assessments of

PLATE 84

Electromyograms from six electrodes on the jejunum with the same distribution as on Plate 76 (sheep 32). The cannula is open and the aborad intestine sealed by an inflated balloon. The RSA phase migrates across electrodes 1, 2 and 3 but does not appear at electrodes 4, 5 or 6.

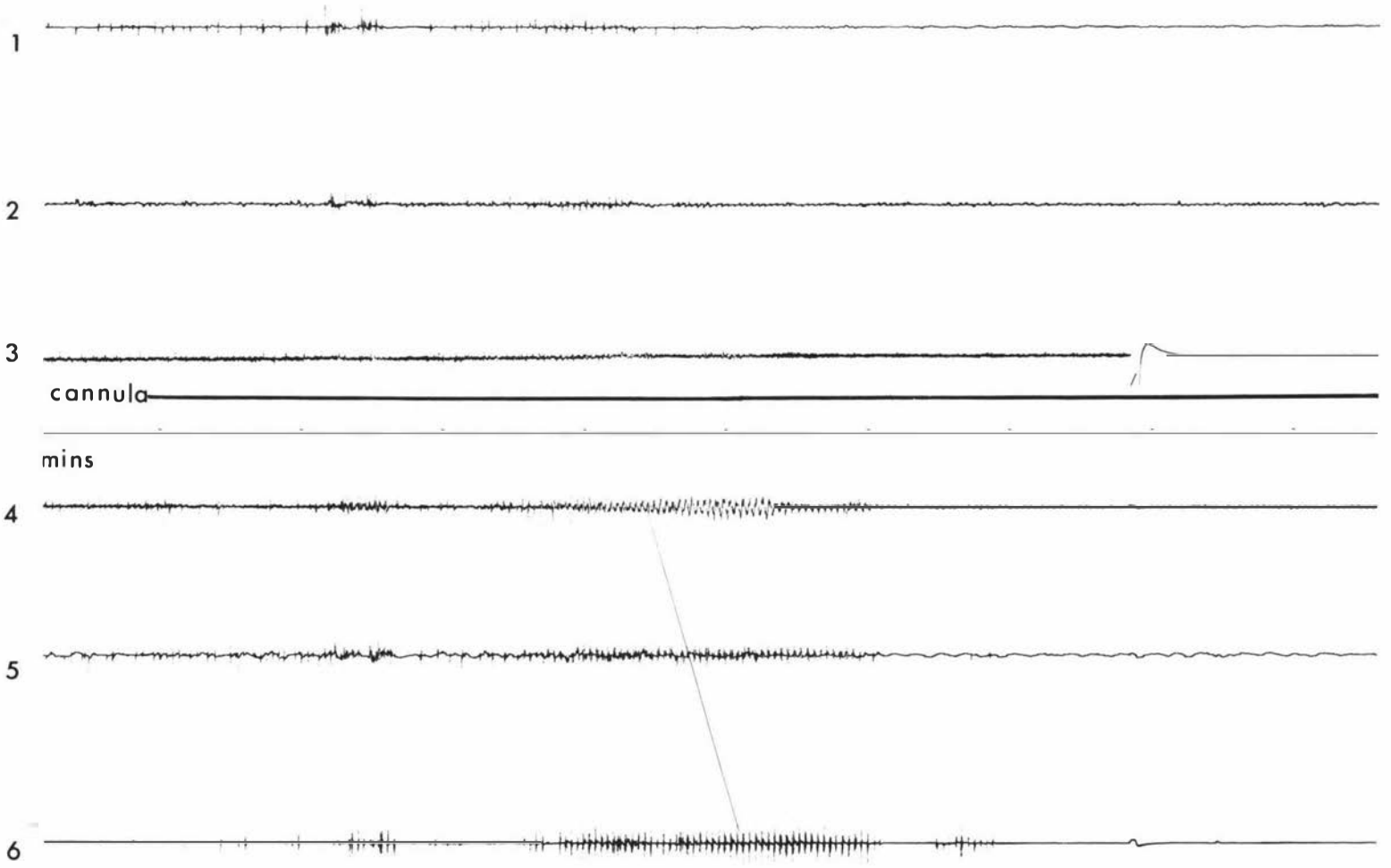
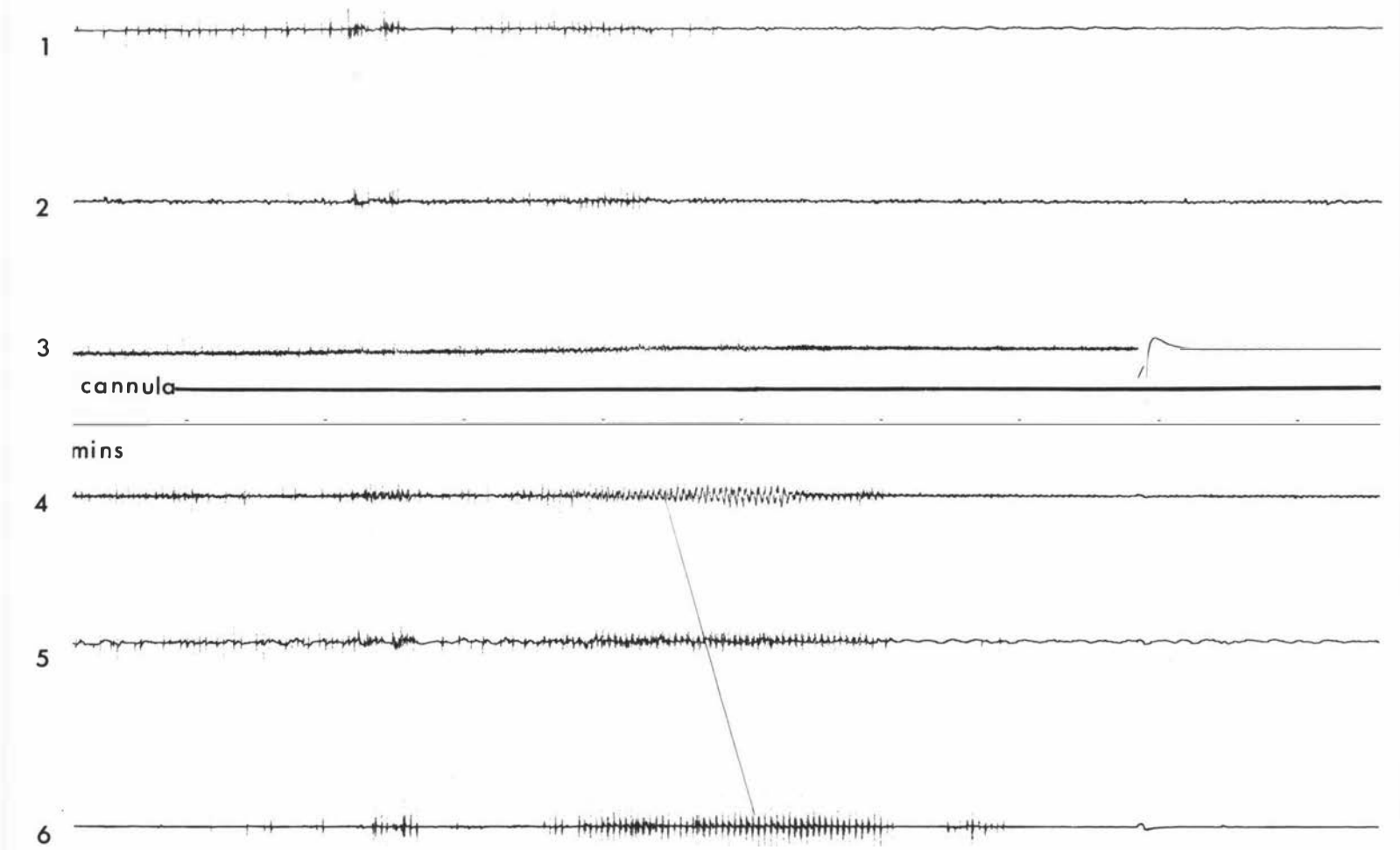

1
2
3
cannula
mins
4
5
6

PLATE 85

Electromyograms from six electrodes on the jejunum with the same distribution as on Plate 76 (sheep 34). The cannula is open and digesta are being introduced to aborad jejunum at a rate of 2.2 ml/ minute. No RSA phase at electrodes 1, 2 and 3. However, RSA has started aborad of electrode 3 and is being recorded by electrodes 4, 5 and 6.


1
2
3
cannula
mins
4
5
6

lengths could not be made because the small intestine was not in intimate contact with the x-ray film so there always was some degree of magnification and because it was not possible to determine the exact orientation of the gut relative to the film. Even with a number of radio-opaque markers spaced at measured distances along the gut, on many occasions it was difficult to decide whether a bolus had passed the marker or was passing along a superimposed loop of small intestine.

The apparatus used for recording the electrical activity of the intestinal wall was not ideal for the purpose as the frequency response was too low to allow the optimum information to be recorded. Also it would have been desirable to record from many more sites simultaneously but only 6 recording channels were available. The spacing of electrodes used often made it difficult to decide whether or not a series of events was propagated between electrodes and whether the recording from one particular site gave a good indication of activity in the region as a whole. The electrodes themselves appeared to function well.

In spite of these limitations, the deficiencies of one system tended to be compensated for by the advantages of the other, and combining radiological observation of the movement of digesta with recording of the myoelectrical activity of the wall of the small intestine allowed a better appreciation of the patterns of activity than either method on its own. The combination proved adequate for correlating the pattern of bolus movement with the pattern of electrical activity.

The use of a number of breeds of sheep housed and managed in two different ways tended to reduce the possibility of the observations made being breed or management specific. Individual animal variation was a minor feature: all animals exhibited the same basic patterns of electrical activity and digesta movement.

Most experiments were carried out in animals that had some surgical modifications which could mean that the patterns of activity observed did not give a true indication of what happens in the normal animal.

The most frequently used modification was the implantation of a catheter in the duodenal bulb: no change in motility or digesta flow could be seen after insertion of the catheters. The insertion of T cannulae in the jejunum and encompassing the intestine with mesh did not have any detectable effect on the passage of digesta or electrical activity except that a small amount of digesta pooled round the shoe of the cannula. The insertion of re-entrant cannulae at any point aborad of the ascending duodenum did, however cause interference with normal function. This will be discussed later.

The electrical events recorded closely resemble those that have been previously reported from the sheep (Ruckebusch, 1970; Bueno et al., 1977; Ruckebusch and Bueno, 1977). Over the aborad duodenum and jejunum a slow wave occurred which had a frequency of 19.8 - 21.8/ minute and migrated aborad at 8 - 12 cm/second. Superimposed on this slow wave were various patterns of spiking activity which also migrated aborad forming the MMC and the RAMS. The MMC comprised three distinct phases, the quiescent phase, the ISA phase and the RSA phase. The speed of migration of the RSA phase was variable with a mean of 0.63 cm/second over the jejunum. The RAMS spread much faster, passing aborad over the duodenum and proximal jejunum at 8 - 12 cm/second.

Radiological observation showed that digesta passed through the pylorus and pooled in the duodenal bulb and ascending part of the duodenum. Contraction of the duodenal bulb and ascending duodenum initiated a rapid aborad progression of a large bolus which continued well down into the jejunum, closely resembling the peristaltic rush described in the dog by Alvarez (1914). No direct correlation between individual contractions of the pyloric antrum and of the duodenal bulb as reported in the dog (Bedi and Code, 1972) could be established, which is in agreement with previous observations by Ruckebusch and Bueno (1977). However, there was some inter-relationship. Abomasal antral activity ceased for a brief period (30 seconds or less) after a bolus had started to move rapidly through the duodenum, and for much longer periods (15 - 20 minutes) when an RSA phase became established in the duodenum. These observations suggest an inhibitory influence of intestinal distension on antral motility as proposed by Ruckbusch (1975). The pattern of digesta movement observed most commonly in the

jejunum following fragmentation of the original bolus did not resemble any of the patterns described previously, but those seen in the ileum closely resemble the descriptions given for the cat (Cannon, 1902) and the dog (Code et al., 1968).

There has been considerable debate as to the mechanism of control of the muscular activity of the small intestine. Many experiments designed to demonstrate the control, particularly of RSA phase, have given conflicting results. A most significant observation, reported by Aeberhard et al. (1980) is that the RSA phase occurs on sections of small intestine that have been totally detached from any extrinsic nerve supply. It has been demonstrated that the pattern of contraction of the small intestine can be influenced by some hormones such as insulin and motilin (Wingate et al., 1976; Bueno et al., 1977) but the role these play has not been established: in any case there appears to be differences between species (Borody et al., 1981).

An hypothesis for the control of intestinal motility has been proposed by Code et al. (1968). It combines three concepts: (1) the maximum frequency at which contractions can occur is the frequency of the slow wave and this has a decreasing gradient from duodenum to ileum (Alvarez, 1914; Douglas and Mann, 1939; Douglas, 1948, 1949): (2) the wavelength of the slow wave defines the physiological segment of the small intestine and this also decreases in size towards the terminal ileum: (3) whether or not a contraction occurs on a particular slow wave depends on the excitability of the muscle fibres, which may be influenced by the extrinsic nerve supply or hormones. The regional patterns of digesta movement seen in the small intestine of sheep can be explained on the basis of this hypothesis.

The site of origin of the slow wave is reported by Ruckebusch and Bueno (1977) to be approximately 20 cm aborad of the pylorus. This arrangement allows digesta to collect in the duodenal bulb and ascending part of the duodenum until the volume is sufficient to initiate a contraction. The strong simultaneous contraction of the first part of the duodenum will propel the digesta as a bolus beyond the point of origin of the slow wave. The leading edge of the bolus will then provide a stimulus for a contraction which occurs 90^{o} to 180^{o} orad on

the slow wave (Farrar and Zfass, 1967). It follows that if the bolus is of a critical length, it will provide a continuous stimulus for the propagation of a contraction, so explaining the rapid continuous aborad movement of boluses through the duodenum and orad jejunum. If this hypothesis is correct, the bolus length would have to be ¼ to ½ the length of the wavelength of the slow wave on the duodenum (Fig. 21). From its velocity and frequency, the slow wave wavelength can be calculated to be approximately 30 cm, so that the critical length of the bolus would be between 7.5 cm and 15 cm. Measurements taken from radiographic cine-films (5:3:3), which showed that the continuous moving boluses were 9 cm - 12 cm long. The hypothesis is further substantiated by the demonstration that (a) removal of the bolus stopped the migrating contraction and (b) that a continuously aborad moving contraction could be initiated by introducing the volume of digesta needed to form a bolus of the correct length (5:3:3).

The pattern of break up of the continuously aborad-moving bolus in the jejunum can also be explained by the slow wave being the functioning physiological segment of the small intestine. The length of this physiological segment decreases as it moves aborad, and it has been shown that one or more of the slow waves disappears (Code et al., 1968). In the jejunum, as the length of the slow wave shortens, the size of the bolus is decreased by the contraction in effect advancing along the bolus and nipping some digesta off the trailing edge (Fig. 21). The dropping of one slow wave completely will further add to the fragmentation of the original bolus.

The regional patterns of movement seen in the more aborad jejunum and ileum can be explained similarly by the relationship between bolus length and slow wave wavelength. In the jejunum, once the boluses have become considerably shorter than the length of the slow wave the stimulus resulting from the presence of a bolus causes a contraction some distance orad of the bolus. This contraction is not maintained because the slow wave moves aborad of the bolus onto a section of empty intestine, so the stimulus is not maintained. The next slow wave to pass over the bolus results in a second contraction which migrates aborad for a short distance then also fades out and so on

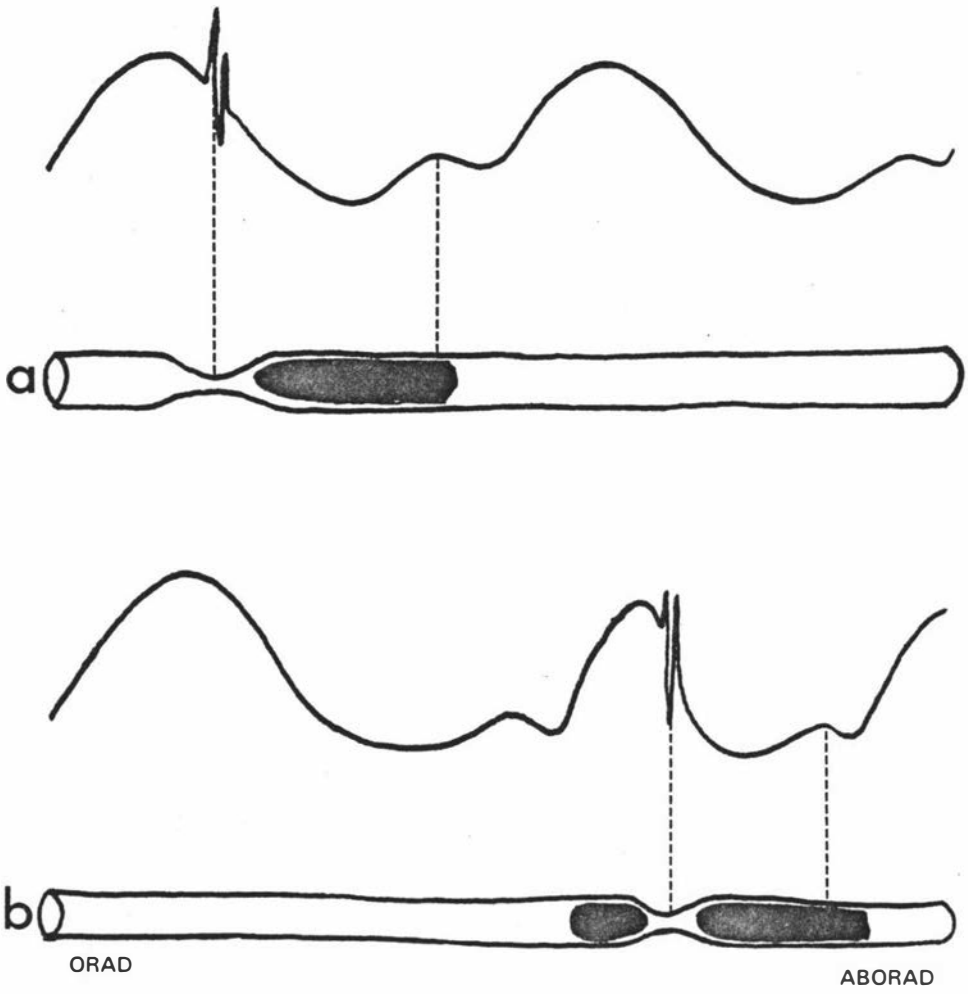
FIGURE 21

This diagram illustrates the relationship between the wavelength of the slow wave and the propulsion of a bolus by a RAMS.

The point on the aborad migrating slow wave which causes the intestine to be susceptible to stimulation is joined to the influenced section of the intestine, at the leading edge of the bolus, by a broken line. The stimulus provided by the leading edge of the bolus moving along the intestine reflexly evokes an aborad-moving intestinal contraction behind it. The part on the slow wave carrying the spike potential, indicating the reflex muscular activity, is connected to the contracting region of the intestinal wall by a second broken line. These two points are separated by half the wavelength of a slow wave.

(a) If the length of the bolus is slightly greater than half the wavelength of the slow wave the leading edge of the bolus will stimulate a contraction half a wavelength behind it. This contraction will propel the bolus aborad and as it moves it will provide a continuous stimulation to maintain the contraction. The result is that the bolus is propelled aborad at the velocity of the migrating slow wave.

(b) If the bolus is substantially greater in length than half the wavelength of the slow wave, (as happens, for instance, as the wavelength of the slow wave decreases in the more aborad jejunum) the contraction half a wavelength behind the bolus, chops off a part of its orad section which is left behind, to be propelled by the next contraction. This phenomenon will occur continually as the bolus passes aborad in the small intestine because of the progressive decrease in wavelength of the slow wave.


a
b
ORAD
ABORAD

(Fig. 22). This pattern of activity results in the stop-start movement of the boluses in this region. Sometimes the stimulus for contraction resulting from one bolus evokes a contraction over a more orad bolus, causing it to be split into two parts which then amalgamate with adjacent boluses. Should the amalgamation of boluses proceed to the point where a bolus of critical length is formed, this bolus will continue some distance aborad in a single continuous movement.

In the ileum these processes continue. The further shortening of the length of the slow wave results in the boluses being shorter and closer together. As the slow wave passes over these boluses, the stimulus evokes contractions which often occur over a more orad bolus, splitting it, and pushing the resulting segments into the orad and aborad boluses. The next slow wave may cause the newly amalgamated boluses to migrate a short distance aborad and the following slow wave may again cause division and amalgamation (Fig. 23).

To explain the caudally migrating rhythmic contractions (RSA) by this hypothesis is more complex. Digesta are propelled through the small intestine by a series of contractions of the wall which tend to occur at a set frequency controlled by the slow wave frequency. If the relationship between the flow of digesta into the small intestine and the frequency of the slow wave becomes correctly adjusted, boluses will take on a length and spacing directly related to the wavelength of the slow wave. When this happens, contractions will occur with every slow wave so that an RSA phase starts up. As the RSA becomes established, the length of intestine contracting with each slow wave increases, thus decreasing the size of the boluses and increasing the distance between them. This continues till the lumen is empty (Fig. 24).

The importance of the rate of passage of digesta into the small intestine as a factor affecting the establishment of the RSA phase was demonstrated by other observations. When the flow of digesta through the pylorus was increased by distending the abomasum the RSA phase was abolished until this flow rate returned to normal. Altering of the volume of digesta in the small intestine by addition or subtraction of

FIGURE 22

This diagram illustrates the relationship between the wavelength of the slow wave and the propulsion of boluses by ISA in the jejunum. The point on the aborad migrating slow wave which causes the intestine to be susceptible to stimulation is joined to the influenced section of the intestine at the leading edge of the bolus by a broken line. The portion of the slow wave carrying the spike potential indicating muscular activity is connected to the contracting region of the intestinal wall by another broken line. The dotted line connects the same slow wave as it migrates caudally across the same section of intestine illustrated in a, b and c.

(a) Neither the orad nor aborad bolus are in a section of the intestine which is susceptible to stimulation. The central bolus stimulates a contraction which migrates aborad with the slow wave.

(b) The area of contraction has migrated with the slow wave and causes the central bolus to move a short distance aborad. However there is now nothing in the susceptible region of the gut to maintain the contraction, so it is not continued.

(c) As the slow waves move aborad the intestine over the orad bolus becomes susceptible to stimulation and the sequence of events such as occurred with central bolus in (a) and (b) repeats itself. The intestine over the aborad bolus has also become susceptible to stimulation so a contraction occurs half a wavelength orad which is the region in which the central bolus now lies. This bolus is divided by the contraction the orad part moving orad and the aborad part amalgamating with the aborad bolus.

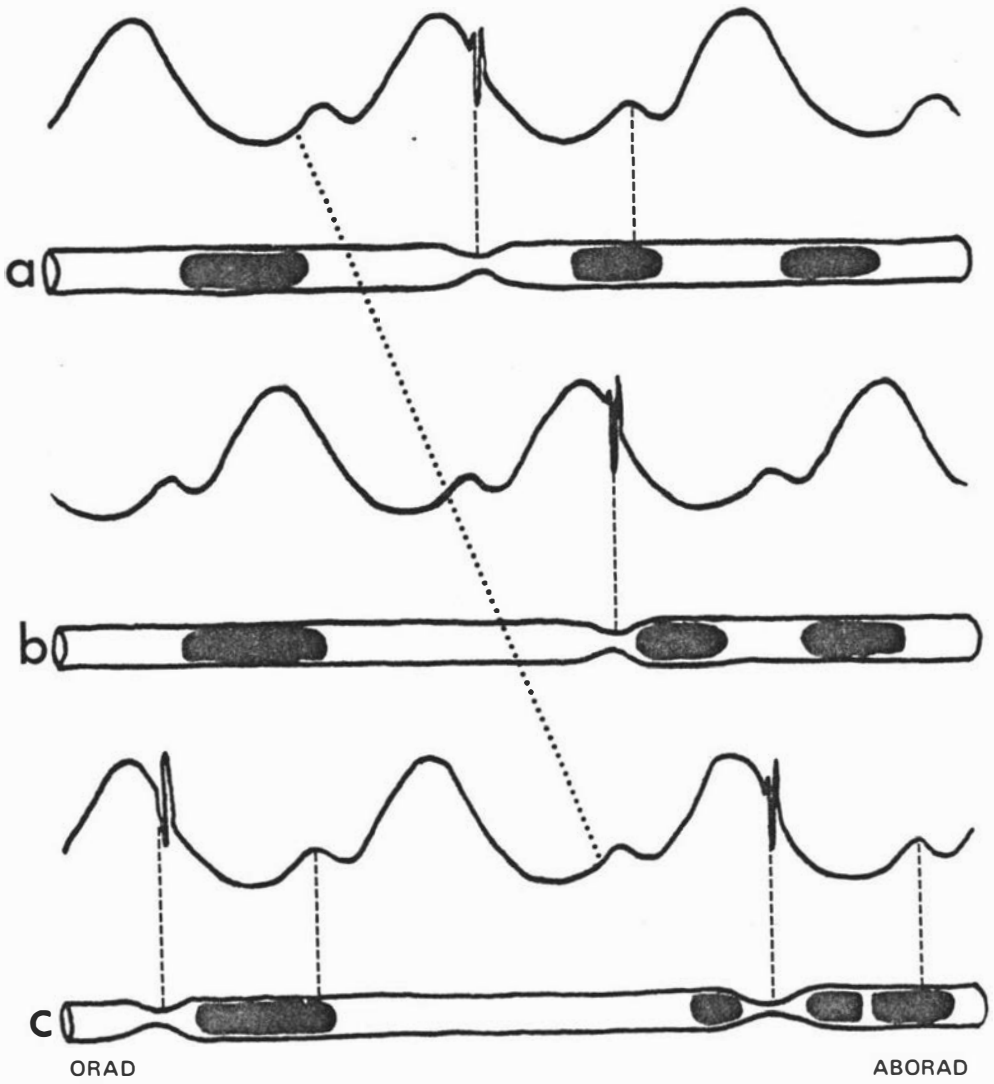

a
b
c
ORAD
ABORAD

FIGURE 23

This diagram illustrates the relationship between the wavelength of the slow wave and the propulsion of boluses by ISA in the ileum.

The point on the aborad migrating slow wave which causes the intestine to be susceptible to stimulation is joined to the influenced section at the leading edge of the bolus of intestine by a broken line. The part on the slow wave carrying the spike potential, indicating muscular activity, is connected to the contracting area of intestine by a broken line. The dotted line connects the same slow wave as it migrates caudally across the same section of intestine illustrated in a, b, c and d.

(a) Equal sized boluses equally spaced approximately half a wavelength apart. One bolus acts as a stimulation for a contraction which divides the immediately orad bolus.

(b) The parts of divided boluses have amalgamated with the bolus orad or aborad.

(c) These boluses are propelled a short distance aborad but are not of sufficient length to sustain the contraction so it fades out leaving the boluses equally spaced.

(d) The boluses stop moving briefly but the next slow wave advances over them evoking a contraction which may either cause a bolus to move a short distance as is occurring with the orad bolus or may cause a division of a bolus as is occurring with the two more aborad boluses.

The sequence of events depicted in (a) then repeats itself.

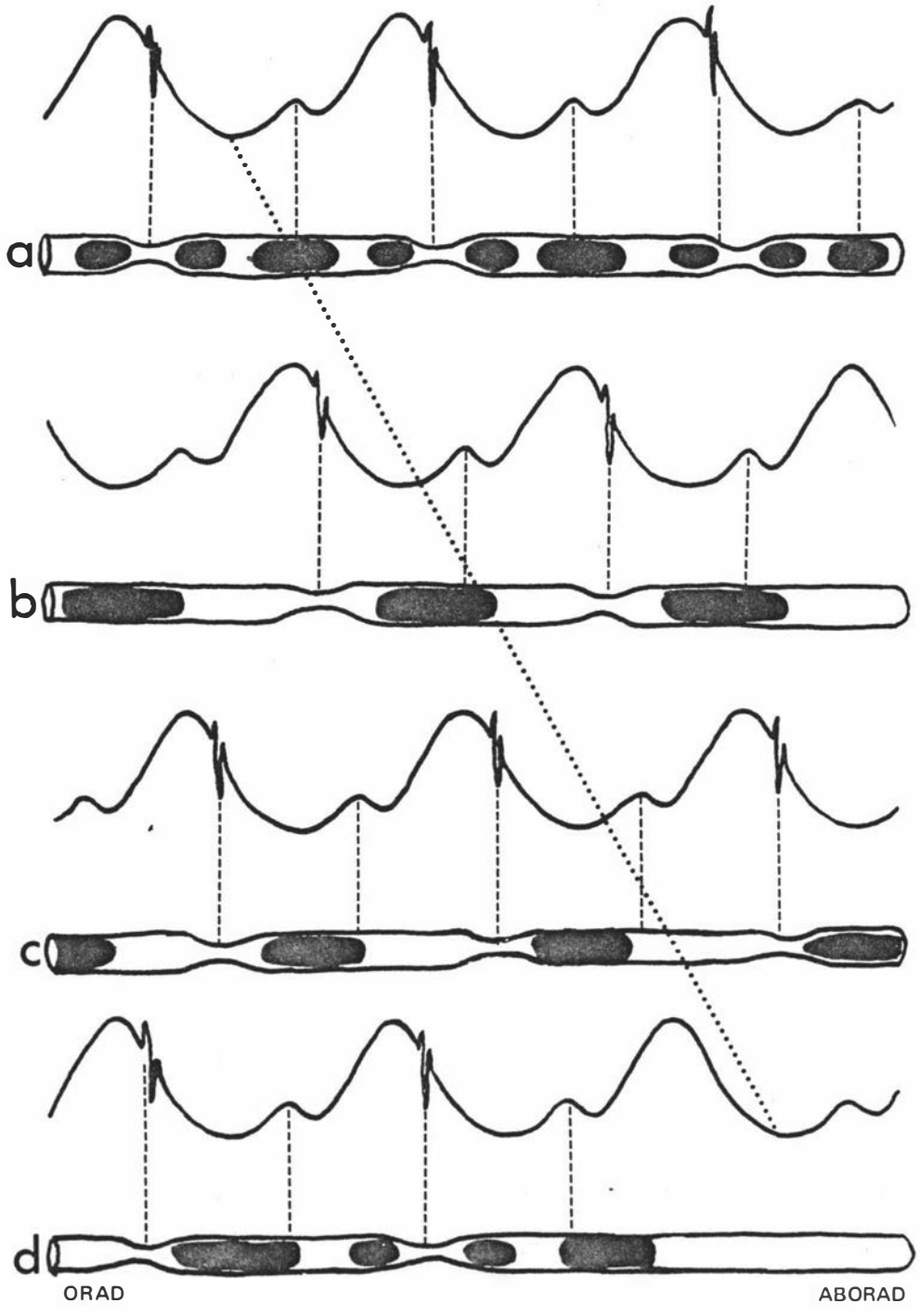

a
b
c
d
ORAD
ABORAD

FIGURE 24

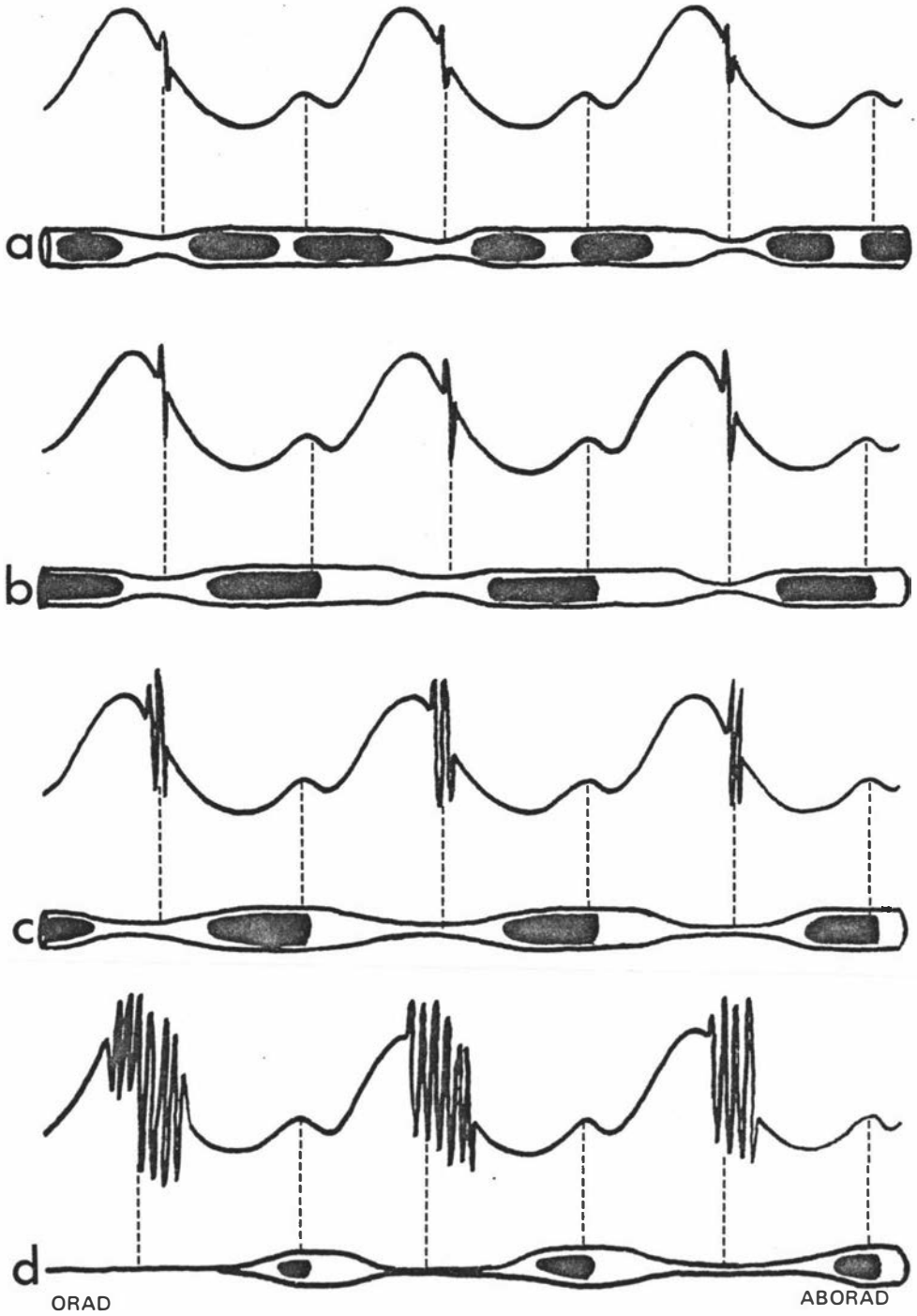
This diagram illustrates the relationship between the wavelength of the slow wave and the propulsion of boluses by RSA. The point of the aborad migrating slow wave which causes the intestine to be susceptible to stimulation is joined to the influenced section of intestine by a broken line. The part on the slow wave carrying the spike potential, indicating muscular activity, is joined to the contracting area of intestine by a broken line.

(a) A sufficient number of boluses are present within the intestine to cause spike potentials on every slow wave.

(b) Should the amount of digesta in the intestine allow it, the boluses get evenly spaced and equal in size.

(c) The spike potentials start to occupy a greater proportion of the slow wave and a greater length of the intestine is contracted so the boluses get smaller and further apart but remain equally spaced.

(d) This trend continues with a greater and greater length of the intestine contracting between the boluses until eventually no digesta remains in the lumen.


a
b
c
d
ORAD
ABORAD

digesta through a T cannula also had a marked influence on the occurrence of the RSA phase, both manipulations inhibiting it. The changes in the pattern of small intestine activity reported with weaning (Ruckebusch and Bueno, 1973) could be a reflection of the change in flow rates through the pylorus imposed by the different feeding regimes.

The variation in the pattern of activity seen in different species can also be explained on the basis of the hypothesis that has been advanced. The different feeding habits and anatomy of the alimentary tract, result in different ranges of flow rate through the pylorus and the different wavelengths of the slow waves relative to the flow rate impose different patterns of activity. In the ruminant the stomach function results in a relatively constant flow of digesta through the pylorus so the repetitive sequence of MMC occurs at frequent, evenly-spaced intervals. If the stomach function is disturbed by imposing a 3 times per day feeding routine on an unweaned animal, the cycle of activity of the small intestine is disrupted because the flow rate through the pylorus no longer remains constant. In simple-stomached animals such as the dog, whose feeding habits are to gorge once per day, the MMC only occurs after some hours of fasting because immediately after feeding the flow rate of digesta into the small intestine is too great to allow the slow wave to establish a regular sequence of contractions. This relationship of flow rate, slow wave and function is further supported by the findings of Ruckebusch and Bueno (1976). They showed, in pigs, that changes in the feeding regime which would result in variation in the passage of digesta through the pylorus also changed the activity of the small intestine.

The results of this have supported the general hypothesis of Code et al. (1968). There is little doubt that the major factor controlling the pattern of muscular activity in the small intestine is the relationship between the rate of passage of digesta through the pylorus and the site of origin and frequency of the slow wave. It would appear that extrinsic control, neural or hormonal, plays only a minor role and probably operates by altering the sensitivity of the small intestine to stimulation or by altering the frequency or speed of propagation of the slow wave.

The effects on the passage of digesta resulting from the insertion of re-entrant cannula in various sites along the small intestine can also be explained on the basis of the proposed hypothesis. If the cannula is placed in the duodenum orad of the site of origin of the slow wave (Ruckebusch and Bueno, 1977) but far enough aborad of the pylorus so that contraction of the duodenal bulb and duodenum orad of the cannula will propel through the cannula a volume of digesta great enough to initiate a continuously aborad moving bolus, there is little effect on the passage of digesta. If however, a re-entrant cannula is placed aborad of the point of origin of the slow wave there is a pronounced effect on digesta movement. The cannula disrupts the boluses so that the relationship between slow-wave wavelength and bolus length become disorganised with the result that the aborad propulsion of digesta is markedly impaired. Also RSA phases do not appear to cross a re-entrant cannula, adding to the delay of passage time of digesta through the small intestine. The possible consequence of this slowing of the passage time has been reported by MacRae and Wilson (1977).

These dramatic effects on digesta flow caused by the insertion of a re-entrant cannula in certain sites indicate that any data on passage or absorption obtained from animals prepared with re-entrant cannulae must be interpreted with great care.

Chapter VI

GENERAL CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

The co-ordinated muscular activity of the sheep's alimentary tract performs a variety of functions in different regions. The oesophagus transports material efficiently with rapidly migrating rings of contraction. Contractions of the reticulo-rumen delay the aborad progression of digesta to allow fermentation, eliminate the gas resulting from fermentation, and mix digesta and sort it to progress through the reticulo-omasal orifice. Movement of the walls of the abomasum effectively mixes secretions with digesta and pumps them through the pylorus, while the patterns of activity in the small intestine mix the digesta and propel it in a general aborad direction at a pace which allows absorption of nutrients. The movements of the caecum and orad colon again delay the aborad progression of digesta, functioning as a secondary fermentation site. Slow continuous passage through the spiral colon permits the absorption of water forming the digesta into the hard dry pellets which are stored in the aborad colon and rectum before excretion.

Although the muscular activity of the various regions of the alimentary tract appears different and has different effects, the form of the action is basically the same. It is a ring of contraction which migrates a variable distance along the muscular tube that forms the tract from pharynx to anus. This ring of contraction is generally preceded by a ring of relaxation and is commonly referred to as peristalsis. In some regions there may also be tonic contractions, replacing or superimposed on peristalsis, increasing the tension in the wall and applying increased pressure to the contents.

The sequences of contractions of the reticulo-rumen, as determined radiographically, did not differ to any significant extent from those previously described but a number of details of the movement, especially of the folds and pillars, were revealed. The ability to observe the form and sequence of these contractions lead to the conclusion that they could be explained by waves of peristalsis passing

caudally and cranially as was originally suggested by Wester (1926). The rather bizarre track they take appears to be a result of how the reticulo-rumen develops from the primordial digestive tube and the organisation of the different muscle layers in this section of the tract.

That the sequence of events should vary with the degree of fasting is not surprising as it has been well-established that the major stimulus for peristalsis is distension. The difference between contraction sequences in the replete and fasted state can be partly explained by the peristalsis migrating over increasing distances with increasing distension. Distension of the caudal ventral blind sac by gas displaced from the dorsal rumen may provide the stimulus for a cranially moving contraction which can eliminate the gas by eructation through the cardia. Conditions in the aborad regions of the tract especially in the abomasum, also influence the form and frequency of the contraction sequences. The regular rhythmic nature of these sequences is controlled extrinsically from the brain stem and is modified basically by vago-vagal reflexes.

The suggestion that the sequential contraction of the various structures that make up the reticulo-rumen complex can be explained on the basis of peristaltic and antiperistaltic waves requires further investigation. The path of propagation of the migrating waves of contraction could be established by recording the electrical activity from a large number of electrodes closely spaced across the rumen, simultaneously with recordings from small strain gauges. Much further information could be obtained radiographically using the new large field image intensifiers and with a system of obtaining a good dorso-ventral or ventro-dorsal image. It is possible that some of the evolving methods of depicting movement using images formed by ultrasound will provide yet another tool to investigate the pattern of rumen movement: the ultra sound systems presently available give clear images of movement of the individual flaps of the heart valves and can show abnormality of these movements (Feigenbaum, 1976).

The demonstrated regular pattern of flow of digesta within the rumen

gives an indication of how the digesta is either held up for further breakdown or is passed out through the reticulo-omasal orifice. The fate of a particular piece of digesta appears to depend on whether it sinks in the rumen contents that surround it. The further it sinks the closer it comes to being passed out, but if it floats, it will be held up and cycled in a particular region either till the density of the surrounding digesta changes or the density of the piece of digesta increases.

It is suggested that rumination comes into play when the reticulo-rumen system becomes overloaded; it also provides an additional sorting and breaking down mechanism. If new ingesta introduced into the reticulo-rumen by eating is not broken down fast enough the density of material in the rumen may decrease until the stage is reached when the digesta passed over the cranial pillar is inadequately processed. This digesta will be made up of large pieces which will provide a tactile stimulation of the reticular fold region as they are tipped back and forth across the reticulo-ruminal fold.

Such tactile stimulation has been shown to be the main stimulus for rumination (Ash and Kay, 1959; Iggo and Leek, 1970; Leek, 1971). The ruminating process separates the liquid from the solid phase in the mouth and the liquid phase is likely to be passed through the reticulo-omasal orifice rapidly. The solid phase is mechanically broken down by chewing (Reid et al., 1979) and is returned to the rumen saturated with saliva. This hypothesis readily explains the results of much previous research. However, further work is required to substantiate it. For example the density of digesta in various regions could be measured and the change that occurs with rumination established; likewise the changes in digesta density that occur with various diets and their relationship to the time spent ruminating seem worth examining.

Little additional comment can be made on the function of the omasum from the observations made in the study reported here. The pattern in which the barium sulphate was detained in the omasum suggests there is little space between leaves and that they are separated only by a

thin film of fluid. The flow of digesta from the omasum to abomasum appeared to result from its being flushed out by abomasal contents at each ventral displacement associated with reticular contractions rather than by some positive movement of the omasum. It is unlikely that conventional radiographic techniques will provide much additional information on the function of the omasum.

The mechanical functions of the abomasum in mixing digesta with abomasal secretions and pumping it through the pylorus is again achieved by migrating rings of contraction. The contractions pass over a tapering tube so the volume of digesta that can be contained between consecutive rings of contraction decreases. The result is that the liquid digesta are forcibly pushed past the movement of the contraction causing very efficient mixing. The integration of pyloric contractions with the abomasal contractions propels a variable volume of digesta into the duodenum. The frequency of these migrating rings of contraction is controlled intrinsically by the slow wave; it remains remarkably consistent within breeds and is unaltered by distension. The effect of distension of the abomasum is similar to the effect of distension elsewhere in the alimentary tract, it causes inhibition orad to the distended region and excitement aborad. Distension of the abomasum inhibits the contractions of the reticulorumen perhaps, in part, by mechanically displacing digesta from the reticulum and stimulates increased activity of the duodenum. It may also stimulate contractions of the abomasum itself. Those animals in which distension of the abomasum was caused by swallowing of a large volume of air when bottle-feeding showed a series of rapidly migrating contractions occurring round the lesser curvature. These displaced the gas cap to the pyloric antrum from where it is passed into the small intestine. The stimulus for these contractions is most likely to be the gross distension resulting from the large gas cap as they were only seen when this was present. Radiological examination provided a clear picture of the contractions of the abomasal walls and their influence on digesta. It would seem worthwhile to study further in this way the entry and exit of digesta and to look for evidence of selection leading to differential passage of solid and fluid fractions.

The patterns of activity described in the small intestine are made up

from basic migrating rings of contraction and the differences between patterns are only differences in frequency of occurrence and distance migrated. There has been considerable debate as to how the patterns of peristalsis are initiated and controlled but recent evidence indicates the control is independent of an extrinsic nerve supply. This being the case, some explanation has to be put forward for the different types of activity seen over the same section of the small intestine. There has been some evidence produced (Wingate et al., 1976) to suggest that the control is hormonal, at least, in part. However, the observations made here strongly suggest that the pattern of activity results mainly from an interaction between the flow rate of digesta and distension of the intestine on one hand and the frequency, velocity and wavelength of the slow wave on the other, as has been suggested by Code et al. (1968). It may well be that the hormones affect the motility patterns by altering the sensitivity or degree of response to the stimulation of distension. Indirect evidence has already been produced indicating the influence of digesta flow on the pattern of small intestinal activity such as the change following weaning (Ruckebusch and Bueno, 1973) and the change with altered feeding regimes (Ruckebusch and Bueno, 1976). The effects of the insertion of cannulae into the intestine provide further evidence of the importance of digesta flow in determining intestinal activity. The disruption of digesta flow by the insertion of re-entrant cannulae in certain regions was marked; the cause is suggested as being the intereference with the size and spacing of boluses of digesta and their relationship with the slow wave. The altered pattern of digesta flow resulting from transections, reversed segments and removed segments (Douglas, 1949; Hiatt et al., 1966; Aeberhard et al., 1980) can also be explained on this basis. The transection results in a sudden step in the gradient of slow wave frequency, and in reversed segments the slow wave will be moving against the flow. Further proof of this proposed hypothesis could be obtained by passing various rates of flow of digesta through comparatively long segments of small intestine in vitro so that there is no influence from extrinsic nerve supply or hormones, and observing the form of activity that develops.

The effects of cannulation on intestinal function have serious impli-

cations for nutrition research since they must now bring to question many results that have been derived from cannulated animals, especially where re-entrant cannulae have been used. In some cases, as was found with caecal cannulation (MacRae et al., 1973), accommodation may occur, but there was no evidence of accommodation to the gross effects observed in the experiments carried out in this study. The possible interference to stomach function caused by anchoring the stomach wall to the abdominal wall in the long-accepted techniques of rumen cannulation and abomasal cannulation also warrant further study.

There remains much to be learnt about alimentary tract function and the part played by alimentary tract motility. The interactions of diet, intake level, meal pattern with sites of digestion, of the rate of passage of digesta with the stimulation of receptors (including chemoreceptors), and of the physics of digesta movement with the differential passage of digesta components all deserve further investigation, as do the regulatory systems controlling both function and motility. Many of the features and inter-relationships will be similar in both ruminants and animals with a simple stomach. In other respects, however, because of the adaption of the ruminant alimentary tract to the herbivorous diet new situations have arisen with different stimuli, different effectors and different effects. The results of this thesis support the view that alimentary tract function should be studied in the light of motility. Future work should therefore combine the study of alimentary tract motility and digesta movement with studies of other activities such as digestion, absorption, microbial populations and mucosal adaptations. In this way could be built up a sound, comprehensive picture of the alimentary tract the function of which is basic to the economy of the animal.

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Appendix 1

ANAESTHESIA

All surgical procedures were carried out under general anaesthesia, the same technique being used in all sheep.

Food was removed from the animals twenty-four hours before and water twelve hours before induction of anaesthesia. No premedication was given. Anaesthesia was induced using a 5% solution of thiopentone sodium (Intraval sodium May and Baker) at a dose rate of 20 mg/kg injected rapidly into the jugular vein. An endotracheal tube was then inserted and the anaesthesia maintained with 2% halothane (Fluothane I.C.I.) in oxygen. The anaesthetic apparatus used was a semi-closed to and fro system through a Water's soda-lime cannister. The halothane percentage was controlled by an out of circuit vaporiser (Fluotec mark 3 Cyprine Ltd.). Following surgery the sheep were observed closely until they were able to remain in sternal recumbency unaided ensuring that there was no regurgitation and aspiration of digesta.

Appendix 2

The Estimation of the Volume of Gas in the Abomasal Gas Cap.

Because a radiograph compresses three dimensions into two, it is not possible to measure a volume from a radiograph taken in one plane: at least two radiographs, in planes at 90^{o} to each other, are required. With the X-ray apparatus available, it was not feasible to get standing dorso-ventral or ventro-dorsal radiographs which would have allowed measurement of the volume of gas in the abomasum. However, a computer programme was drawn up which allowed an estimate of the volume in the gas cap to be derived (Boyne, A.W., Macpherson, G., Wenham, G. 1975). This programme made the following basic assumptions. If the height of the gas cap was greater than half its cranio-caudal dimension, its shape for the purposes of the calculation was considered to be a cylinder capped by a dome. If the height was less than half the cranio-caudal dimension, its shape was considered to be a dome. A factor of 1.36 times was included in the programme for radiographic magnification. This factor was determined as follows. Strips of lead 5 cm long were placed on both flanks of the animal over the region of the abomasal gas cap. Taking care to make sure that they were at right angles to the direction of the X-ray beam, a radiograph was taken and the lengths of the shadows of the lead strips measured. The longest shadow, that of the lead strip furthest from the film, measured 7.9 cm so that it had been magnified 1.58 times. The shortest shadow, that of the lead strip nearest the film, measured 5.70 cm so that it had been magnified 1.14 times. If it is assumed that the abomasal gas cap lies close to midline, then its magnification would be 1.36 times. This factor of magnification was added into the computer programme.

To test the results obtained with this method a known volume of air was introduced to the abomasum of Sheep number 1 and 21 on 3 occasions just before the radiograph was taken. The correlation with the calculated volume was only moderately good (Table XXIII).

TABLE XXIII

THE ESTIMATION OF THE VOLUME OF GAS IN THE ABOMASAL GAS CAP.

Sheep Number	Volume of Air Introduced Ml	Calculated Volume (Ml) of air
21	150	154
21	200	246
21	400	451
1	150	144
1	200	271
1	400	346

Boyne, A.W., Macpherson, G., and Wenham, G. (1975)

Personal communication. Rowett Research Institute, Scotland.

Appendix 3

DETAILS OF MYOELECTRICAL OBSERVATIONS ON SHEEP 30 AND 34

From such results mean and standard error of the following were calculated :

1. slow wave frequency; (Table XVII)

2. time for the RSA phase of MMC to migrate between electrodes; (Table XVIII)

3. time for RSA phase of MMC to pass on electrode; (Table XIX)

4. time for a RAMS to migrate between electrodes; (Table XXI)

SHEEP 34

Electrode	Session	Reading of slow wave frequency									
1	1	23	23	23	23	21	21	23	24	23	22
	2	23	23	23	24	23	21	22	23	21	23
	3	23	24	23	22	23	21	24	22	23	22
2	1	21	22	22	22	22	21	23	23	23	22
	2	21	22	22	23	21	22	22	23	22	21
	3	23	23	22	23	23	23	21	22	22	22
3	1	22	21	22	23	23	21	23	23	22	20
	2	22	21	22	22	23	22	21	24	22	21
	3	23	23	22	22	23	23	22	21	21	20
4	1	20	21	21	21	20	20	23	23	22	20
	2	20	21	21	21	21	21	22	22	21	21
	3	23	23	22	20	20	21	21	20	20	21
5	1	21	20	21	22	20	21	23	23	22	20
	2	21	22	23	23	23	21	21	22	22	22
	3	23	22	21	21	19	19	20	22	22	21
6	1	21	22	22	22	21	21	23	23	22	19
	2	21	22	22	22	22	21	23	23	22	23
	3	23	23	22	19	23	23	20	20	21	21

SHEEP 34

Between Electrodes	Session	Time (seconds) for the R.S.A. Phase of M.M.C. to migrate between electrodes.			
1 - 2	1	53	24	21	
	2	31	33	37	
	3	27	57	45	55
2 - 3	1	66	28	70	
	2	39	33	40	
	3	23	68	44	40
3 - 4	1	22	17	55	
	2	22	33	55	
	3	16	45	33	49
4 - 5	1	36	24	89	
	2	43	43	46	
	3	27	34	49	32
5 - 6	1	22	36	84	
	2	53	45	52	
	3	18	27	28	30

SHEEP 34

Electrode	Session	Time (seconds) for R.S.A. phase of M.M.C. to pass on electrode.			
1	1	164	136	200	
	2	104	245	103	
	3	251	180	142	191
2	1	207	251	224	
	2	180	262	229	
	3	160	158	147	202
3	1	191	206	180	
	2	213	224	199	
	3	196	202	153	202
4	1	153	158	164	
	2	144	144	120	
	3	158	185	153	169
5	1	141	153	153	
	2	87	158	144	
	3	191	164	153	164
6	1	181	170	224	
	2	200	158	164	
	3	164	153	153	202

SHEEP 34

Between Electrodes	Session	Time (seconds) for a RAMS to migrate between electrodes									
1-2	1	2.9	2.9	2.9	3.1	3.1	2.9	2.8	2.7	3.2	3.3
	2	3	3	2.2	2.2	2.2	2.2	2.2	3.3	3	2.2
	3	3	2.8	2.7	3.1	2.6	3.2	2.8	2.9	3.2	2.8
2-3	1	2.6	2.4	2.6	2.8	2.9	2.3	2.7	2.6	2.6	2.4
	2	2	3	2.2	1.8	2.2	2	2.2	2.8	2.3	3.3
	3	2.6	3	2.8	2.5	3.1	2.7	2.7	2.9	2.6	3.0
3-4	1	1.7	1.7	1.7	1.4	1.3	2.0	2.0	1.7	1.7	1.6
	2	3	2	1.7	1.7	1.7	1.7	1.7	1.1	1.4	2.7
	3	2	1.4	1.7	1.7	1.5	1.4	1.7	1.9	1.7	2
4-5	1	2.4	2.4	2.4	2.6	2.7	2.2	2.6	2.3	2.3	2.8
	2	2.2	2.2	2.2	3.4	2.2	2.3	2.4	2.4	2.6	2.3
	3	2.2	2.4	2.0	2.8	2.4	2.3	2.3	2.7	2.9	2.3
5-6	1	2.9	3	3	3.2	2.8	2.7	2.9	2.7	3.2	3.4
	2	2.6	3	2.2	2.2	2.2	2.2	3.2	2.1	2.2	2.6
	3	2.5	2.2	2.7	2.3	2.3	2.7	2.9	2.5	2.5	2.3