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# FORESTOMACH MOTILITY IN THE CHRONICALLY VAGOTOMIZED SHEEP

BY P. C. GREGORY

*From the Rowett Research Institute, Bucksburn, Aberdeen AB2 9SB*

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SUMMARY

1. The motility of the reticulo-rumen and omasum in conscious sheep was studied by electromyography from chronically implanted nichrome wire electrodes. The sheep were subjected to vagotomy and were maintained totally by intragastric infusion of liquid nutrients before and after vagotomy. Before vagotomy the motility of the forestomach was essentially similar to that seen in roughage-fed sheep.

2. Bilateral thoracic vagotomy transiently abolished all electrical activity of the reticulo-rumen and omasum, but within 1 day some activity returned. Frequent periods of rhythmic local small group discharges were seen over the reticulo-rumen, while the omasum showed prolonged (1–5 min) bursts of mainly slow wave activity.

3. Within 1–2 weeks of vagotomy strong contractions of the reticulo-rumen were visible by radiography. Electromyographically, they comprised a rhythmic series of some two to five large group discharges recurring approximately once a minute. Each series of activity was separated from the next by a short period of quiescence. The discharges occurred almost simultaneously over the whole reticulo-rumen and so contrasted with the progressive forward or backward spread of activity seen in the intact animal. The bursts of activity in the omasum, lasting 0·5–2 min, were not co-ordinated with the activity of the reticulo-rumen as they are in the intact animal.

4. The activity in the reticulo-rumen and omasum was not affected by bilateral section of the splanchnic nerves and removal of the coeliaco-mesenteric ganglia. Reticulo-rumen but not omasal activity was abolished by atropine (0·1 mg/kg) or hexamethonium (2 mg/kg), while both were stimulated by pentagastrin (3 $\mu$g/kg).

5. Following vagotomy reticulo-rumen motility was no longer influenced by feeding, or by tactile stimulation of the buccal cavity or oesophagus. Severe distension of the abomasum caused a slight acceleration of the motility rhythm compared to the inhibition seen before vagotomy.

6. It is concluded that the reticulo-rumen motility observed after vagotomy is an intrinsic cholinergic motility which is dependent upon the activity of the myenteric plexus. The motility of the omasum after vagotomy is similar to that seen in the intact animal and differs from that of the rumen in that it appears not to depend wholly upon cholinergic control.

## INTRODUCTION

It is well known that the major contractions of the reticulo-rumen are controlled via the vagus nerves from gastric centres in the medulla oblongata (Mangold & Klein, 1927; Hoflund, 1940; Duncan, 1953; Bell & Lawn, 1955; Iggo, 1956; Andersson,

Kitchell & Persson, 1959; Beghelli, Borgatti & Parmeggiani, 1963; Howard, 1968; Harding & Leek, 1971), and that removal of this vagal control results in reticulo-rumen paralysis. This response contrasts markedly with that of the monogastric stomach of man (Grimson, Baylin, Taylor, Hesser & Rundles, 1947; Beattie, 1949) or dog (McCrea, McSwiney & Stopford, 1926) and with that of the abomasum, the ruminant counterpart of the monogastric stomach (Duncan, 1953), which all retain considerable activity after vagotomy although often with considerably modified emptying rates.

However, it has been observed radiographically (Duncan, 1953) and acoustically (Habel, 1956) and confirmed by electromyography (Ruckebusch, Tsiamitas & Bueno, 1972) that over a period of 1–3 weeks following vagotomy the reticulo-rumen regains some form of motility.

The present study was designed to investigate the nature of this reticulo-rumen motility, to see if any further change in the motility pattern occurred in the long term after vagotomy, and to determine whether or not it was due to a resumption of central nervous control. In the studies previously reported the animals lost considerable weight following vagotomy and ill health usually terminated the experiments despite the provision of nutritional support. In order to allow a long-term study and to provide an adequate level of nutrition despite the disruption of propulsive motility which follows vagotomy the sheep were provided with a continuous intragastric infusion of all nutrients (Ørskov, Grubb, Wenham & Corrigall, 1979). The infusion was started at least 2 weeks before vagotomy to avoid any sudden change in the nature of the rumen contents which by itself might alter rumen motility. Stomach motility was recorded by electromyography, as changes in rumen pressure and by X-radiography.

Brief reports of some of these experiments have already been published (Gregory, 1979, 1980).

## METHODS

*Animals.* Twenty-one sheep, Suffolk-Greyface or Suffolk-Blackface crosses, of either sex weighing 30–45 kg were used. All surgery was performed with antiseptic precautions under halothane anaesthesia. Initially the animals were fitted with rumen and abomasal cannulae, and electrodes were implanted into the stomach musculature (Fig. 1). The electrodes were of insulated nichrome wire (120 $\mu$m diameter) bared at the tip where they were sewn into the appropriate muscle site in sets of three about 1 cm apart (Ruckebusch, 1970). Each set was sheathed in portex vinyl tubing for protection and additionally insulated near the implantation site by coating with a quick drying acrylic, M-coat D (Welwyn Strain Measurement Ltd.). They were anchored in position by ligating the sheath to the stomach wall and run subcutaneously for a short distance before exteriorizing. The electrodes were connected to a junction box. Recordings were bipolar, from the two best electrodes of each group of three, and were made on an 8- or 12-channel Polygraph (Grass Model 7D recorder, 7P5 a.c. preamplifier) with a time constant of 0·1 or 0·4 sec. Rumen pressure was recorded via a water-filled, open-ended catheter inserted through the rumen cannula and connected to a Statham P23 1D pressure transducer and thence to the polygraph recorder (7P1F d.c. preamplifier) using a filter at 3 Hz. In some animals prior to vagotomy a balloon was suspended under the lower jaw using a jaw harness. It was connected with pressure tubing to a pressure transducer and jaw movements were recorded on the polygraph using a filter at 3 Hz.

*Animal Maintenance.* The individual sheep were tethered in metabolism cages under continuous lighting and initially allowed free access to water and dry food (chopped dried grass *ad libitum* plus 200 g/day of a mixture of barley (90%) with protein and vitamin supplements (10%)) while recordings were made. They were then introduced to a complete liquid diet; a mixture of volatile fatty acids (65% acetic, 25% propionic, 10% butyric) together with a mixture of minerals (calcium

chloride, calcium phosphate and magnesium chloride), was infused into the rumen, and a casein and vitamin mixture plus trace minerals was infused into the abomasum as described by Ørskov *et al.* (1979). Free access to water was continued. The level of the infusion was adjusted to 430 kJ/kg$^{0.75}$ . day, and 0·5 g N/kg$^{0.75}$ . day for the remainder of the experiment with rumen pH kept at around 6·0–6·5 by infusion of bicarbonate buffer into the rumen. Four to six polypropylene scourers (90 cm diameter) were inserted into the rumen to act as inert roughage.

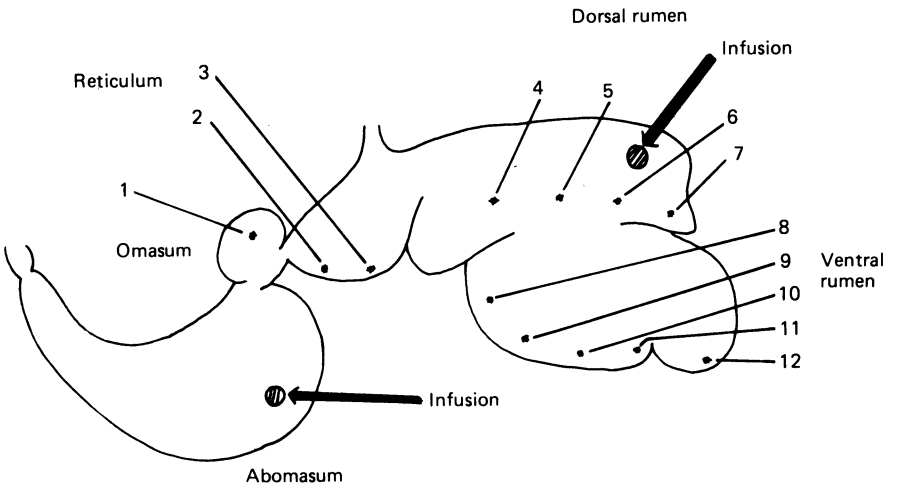


Fig. 1. A diagrammatic representation of a sheep stomach showing the position of attachment of electrodes and cannula to rumen (left side) and of electrodes to reticulum and omasum and cannula to abomasum (right side) in all sheep. Continuous infusion of volatile fatty acids, minerals and buffer were given through the rumen cannula, and casein and vitamins and trace minerals through the abomasal cannula. Rumen electrodes were fixed approximately 10 cm apart, along the floor of the ventral sac, and about 5 cm above the longitudinal groove on the dorsal sac.

In five sheep only control observations were made, recording motility on the dry diet for 3–4 weeks and then on the liquid diet for a further 4–8 weeks. The remaining sixteen sheep were introduced to the liquid diet 1–2 weeks after surgery and then 2–4 weeks later fourteen were subjected to total thoracic vagotomy, one to a partial vagotomy, and one to a sham vagotomy. In these animals rumen contents were first removed and then anaesthesia was induced with halothane and maintained with positive pressure ventilation. The thorax was entered from the left side after the removal of part of the eighth rib. Atropine (0·05 mg/kg) was injected intravenously every 20 min to reduce vagal bradycardia and the main dorsal and ventral branches of the vagus were cut close to the diaphragm together with all the accessory branches, and about 2 cm of each nerve was removed. The anterior and posterior stumps respectively were then reflected and tied together to prevent reinnervation of the forestomachs. In the animal that was partially vagotomized the dorsal branch of the vagus was cut as described and accessory branches removed, but the ventral branch was left intact. For the sham operation the two main branches of the vagus were located and cleared from connective tissue as before, but left intact. After recovery the rumen contents were returned and the sheep were again maintained with the liquid diet.

Two of the fourteen fully vagotomized sheep were further subjected to splanchnicotomy 1 and 2 months following vagotomy. Under halothane anaesthesia the coeliac plexus was located lateral to the adrenal gland by way of a paravertebral incision. All the splanchnic nerves to the plexus were cut, and small sections of each nerve and the coeliac-mesenteric ganglion were removed. A period of 1 week was allowed between nerve section on the two sides of each animal to avoid the severe reduction in blood pressure that could otherwise result. After recovery the animals were maintained for a further 1 and 3 months while recordings were continued.

The influence of distension of the abomasum on reticulo-rumen motility was tested before and

after vagotomy by rapid infusion of warmed 0·9% NaCl, or by inflation of a balloon placed in the antrum via the abomasal cannula. Tactile stimulation of the buccal cavity, oesophagus and abomasum was applied by gentle manipulation of a length of high pressure rubber tubing (1 cm diameter) or portex tubing inserted via the mouth or abomasal cannula respectively. The effects of various drugs on motility were tested by injection or infusion via a temporary jugular catheter.

At the end of the experiment an examination was performed post mortem to confirm the position of the electrodes in the stomach and to check that the vagotomy and splanchnicotomy were both total and permanent.

## RESULTS

### *Motility before vagotomy*

The motility pattern of the sheep fed the dry diet was similar to that reported previously by Ruckebusch (1970), each contraction being associated with a group discharge of spike potentials and slow waves. There was a primary reticulo-rumen cycle rhythm of 0·84 ± 0·08/min (mean ± S.E.M.) at rest associated intermittantly with secondary cycle rumen contractions (Fig. 2*A*). The contractions spread progressively backwards over the reticulo-rumen with a lag of about 10 sec between dorsal and ventral rumen contractions (primary), or forwards over the rumen (secondary). The rate of primary contraction increased during feeding (1·50 ± 0·13/min) and triphasic group discharge of the reticulum was observed during periods of rumination (Fig. 2*B*).

The motility pattern of the same sheep maintained by liquid infusion (Fig. 3*A*) was essentially similar to their resting pattern on the dry diet. At rest the average rate of primary cycle contractions was 0·80 ± 0·07/min, no different from that seen in the animals on the dry diet. However, the force of the contractions was lower, giving an average increase in pressure in the posterior dorsal sac of the rumen of 6 mmHg compared to 15 mmHg when the dry diet was given.

Sheep given the liquid showed frequent short periods of pseudo-rumination (Fig. 3*B*). Triphasic group discharges of the reticulum were associated with regurgitation of rumen fluid in the normal manner but the contraction rhythm was much faster (2·10 ± 0·19/min) than was seen during rumination on the dry diet (1·30 ± 0·07/min). On both diets the contractions of the proximal part of the omasal body were co-ordinated with those of the reticulum (Figs. 2*A* and 3*A*). There was continuous activity of the omasal body for all or part of the interval between two primary cycle contractions but this ceased at the time of the second reticular contraction as previously observed by Bueno & Ruckebusch (1974).

All sheep at times showed low amplitude regular small group discharges (15–30/min) at some rumen electrode sites in addition to the major group discharges associated with the contraction cycles. This activity was seen both in sheep given the dry diet and in those maintained by liquid diet, but was considerably more common in the latter.

### *Motility following vagotomy*

Of the sixteen animals subjected to vagotomy, one died during surgery, and another 4 days after vagotomy from a thoracic infection. The remaining animals were maintained in good health for up to 5 months, before the experiment was terminated, with no significant change in body weight (32·6 ± 3·9 kg), compared to that before vagotomy (34·3 ± 1·0 kg).

The sham-operated sheep showed total loss of reticulo-ruminal electrical activity

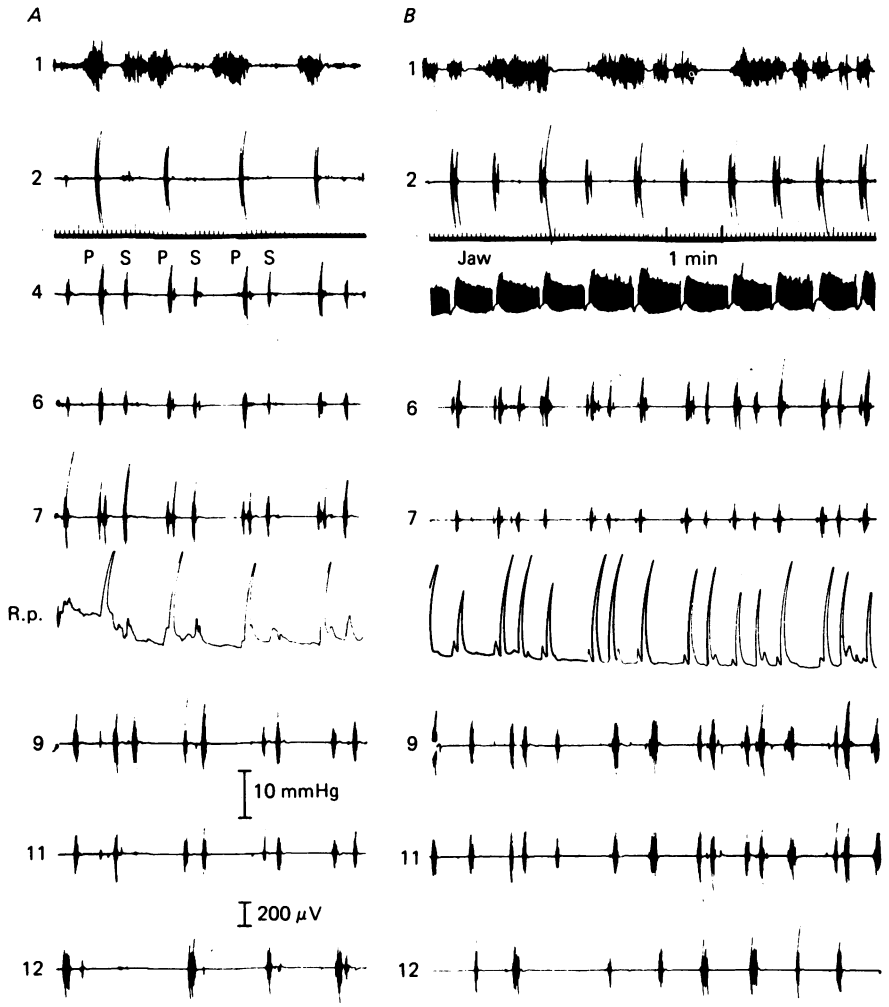


Fig. 2. Motility of omasum and reticulo-rumen in a roughage-fed sheep. Electrode sites are numbered as indicated in Fig. 1. *A* shows the electromyogram from a sheep at rest with primary (P) and secondary (S) cycle contractions, and the more prolonged discharge of the omasum terminating at the time of reticulum discharge. Rumen pressure (r.p.) was recorded from an open-tip catheter in the posterior dorsal sac. *B* shows the electromyogram of the same sheep recorded during rumination. Jaw movements were recorded from a balloon attached under the lower jaw.

immediately after surgery, but within 1 day normal reticulo-rumen motility was regained.

*Partial vagotomy*

The animal subjected to partial (dorsal) vagotomy showed no electrical activity of the forestomach 6 hr after surgery, but within 1 day normal reticulum activity was observed while the rumen showed a regular pattern of low amplitude small group discharges over both dorsal and ventral sacs (Fig. 4*A*) at 12–30/min as observed intermittently in the animals before vagotomy. Over a period of 2 weeks the activity

in both dorsal and ventral sacs of the rumen became grouped into a regular series of three to six large group discharges recurring at about the same 1 min frequency as the reticulum contractions but not co-ordinated with it (Fig. 4*B*). This pattern remained unchanged for a further 2 months until termination of the experiment.

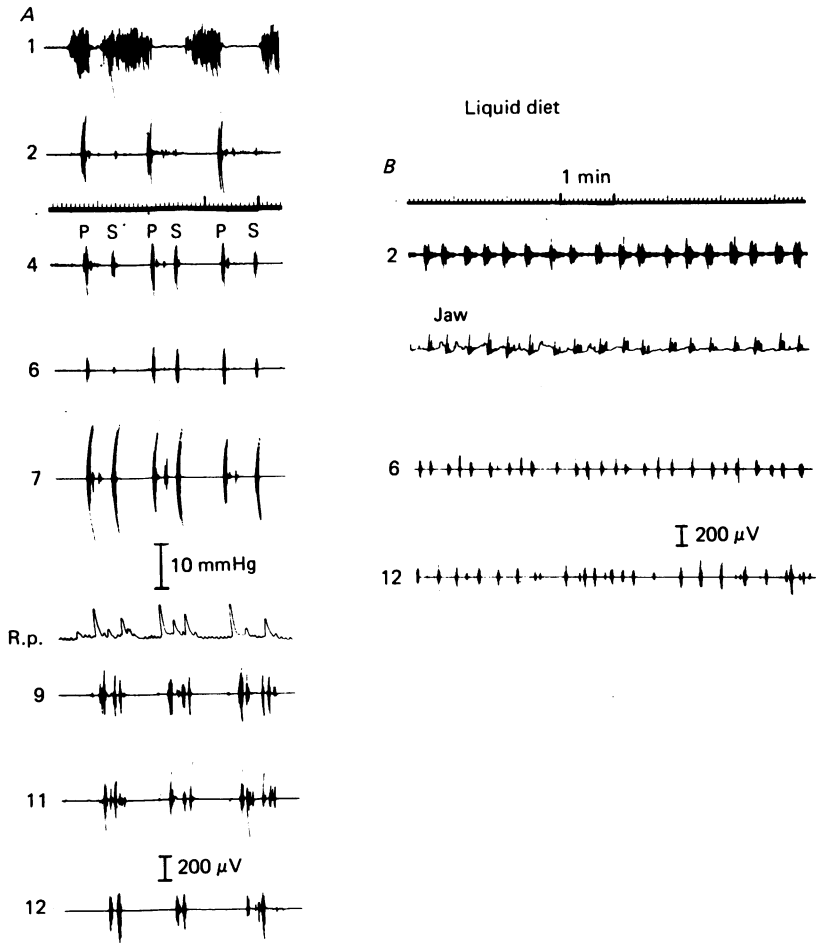


Fig. 3. Motility of omasum and reticulo-rumen in a sheep given the liquid diet. *A* shows a similar pattern to that seen in a roughage-fed sheep at rest, but with smaller increase in rumen pressure with each contraction. *B* shows the electromyogram of a sheep during pseudo-rumination recorded as in Fig. 2*B*.

*Total thoracic vagotomy*

*Initial effect.* The remaining twelve sheep that were successfully subjected to total thoracic vagotomy showed similar changes in electrical activity of the forestomach. Immediately after recovery from surgery, and for up to 6 hr thereafter, all electrical activity of the forestomach was generally absent; in one animal in which the rumen was filled with 4 l. of 0·9 % NaCl immediately after surgery electrical activity of the reticulo-rumen and omasum returned after 2–3 hr. In the other animals rumen contents were returned about 6 hr after surgery when the electrical activity had returned. Within 1 day (Fig. 5*A*) the reticulum showed periods of quiescence

interrupted by irregular short bursts of activity (2–10 sec), over a background of continuous low amplitude activity or sometimes regular small group discharges at 35–45/min. The rumen also regained some electrical activity, first in the dorsal sac and then the ventral sac and ventral blind sac. Low amplitude regular small group discharges (slow waves and spikes) occurred in the dorsal sac at a frequency of 14–20/min and in the ventral sac at 12–17/min. However, quite often one or more rumen electrode sites became inactive for up to 2 hr while at other times the activity doubled in frequency for short periods.

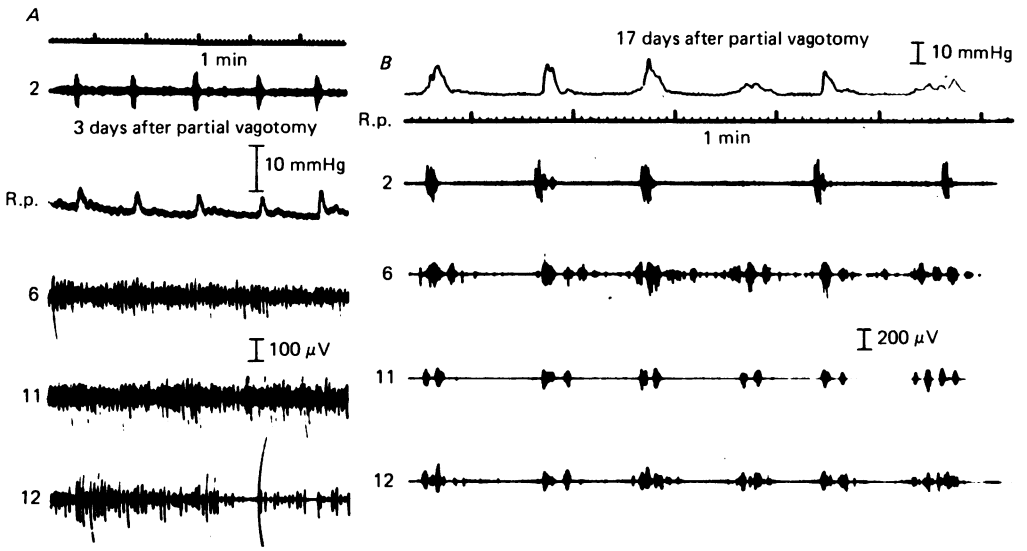


Fig. 4. Motility of reticulo-rumen after partial (dorsal) thoracic vagotomy. *A*, an electromyogram from a sheep 3 days after dorsal vagotomy, showing normal biphasic reticulum contractions, but only regular small group discharges over the rumen. *B*, from the same sheep 17 days after dorsal vagotomy showing a rhythmic series of large group discharges over the rumen at a similar frequency but not co-ordinated with the reticulum discharge.

*Long-term effect.* From 1 to 3 days after vagotomy the electrical discharge from the reticulo-rumen increased in intensity with progressively fewer quiet periods at any site. From 4 to 7 days after vagotomy rhythmic periods of more intense activity (20–60 sec) became apparent separated by quiet or low activity periods. This appeared first in the reticulum and was then generally followed by the dorsal sac (Fig. 5*B*) and finally by the ventral and ventral blind sacs. At first the organization was only localized, as shown by the different activity periods at the two reticular sites, but then gradually became synchronized over the whole reticulo-rumen. This reorganization was marked by the appearance of large group discharges of greater amplitude and duration than those seen in the first few days after vagotomy which generally became less evident and in the ventral sac usually disappeared totally; in the dorsal sac small group discharges often continued together with the large discharges.

Reorganization of activity appeared complete at about 14 days (Fig. 6) and no further change occurred over a period of 5 months. At this time the activity in each

region of the reticulo-rumen generally consisted of some two to five regularly spaced large group discharges (of 3–10 sec duration). These occurred almost simultaneously over the whole reticulo-rumen over a period of 15–70 sec repeated every 1–2 min and caused considerable increase in pressure within the rumen (10–20 mmHg). The discharges were associated with strong contractions as shown by radiography. There was no evidence of any one site of initiation of activity although often the discharge

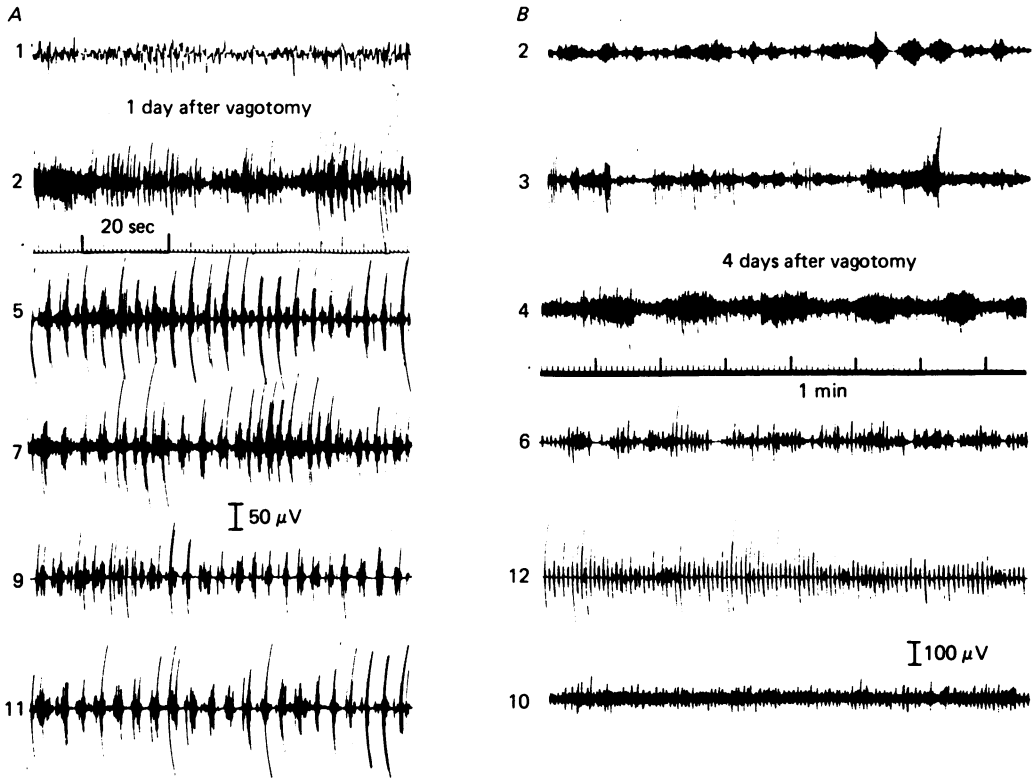


Fig. 5. Motility of omasum and reticulo-rumen after total thoracic vagotomy. *A*, an electromyogram 1 day after vagotomy. The omasum shows 2–3 min continuous discharges. The rumen shows periods of regular small group discharges while the reticulum shows bursts of activity generally over a low amplitude background discharge. *B*, an electromyogram from a sheep 4 days after vagotomy. Strong bursts of local activity occur in the reticulum but are not yet organized over the whole reticulum. The ventral sac shows only regular small group discharge, but in the dorsal sac rhythmic periods of high activity can be observed.

began in the ventral sac or ventral blind sac rapidly followed by the dorsal sacs and reticulum while the discharge continued in the ventral sacs. There was therefore no progressive spread of contraction as is seen in the vagus-intact animal, but rather contractions over the whole reticulo-rumen occurred at one time. Radiography confirmed that the contractions of the ventral sac were generally stronger than those of the dorsal sac.

*Omasum*

Immediately following vagotomy all electrical activity of the omasal body ceased, but within 8 hr activity had returned. This differed from that in the intact animal (proximal region omasal body) in showing longer bursts of activity (2–6 min)

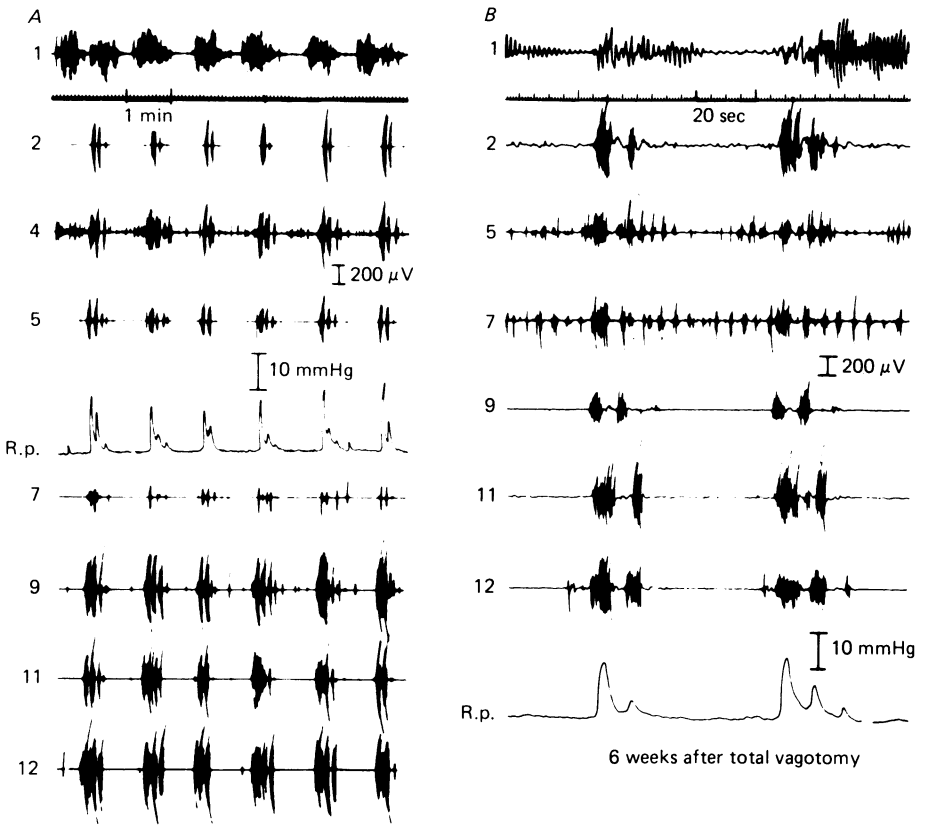


Fig. 6. Motility of the omasum and reticulo-rumen after chronic total thoracic vagotomy. *A*, shows the rhythmic nature of the motility pattern in the reticulo-rumen 14 days after vagotomy. The omasal body shows a phasic discharge of similar rhythm but not co-ordinated with it. *B* is recorded at a faster speed from the same sheep 6 weeks after vagotomy to show the slow waves and spikes associated with each large group discharge. The first series of discharges is generally more synchronous than those following, the degree of synchrony being reflected in the amplitude of discharges and the rumen pressure changes. Regular small discharges persist over parts of the dorsal sac.

separated by similar periods of inactivity. The activity as in the intact sheep was primarily slow wave activity with some low frequency spiking activity. Over the next 7 days activity became generally more condensed to show shorter periods of activity (0·5–2 min) separated by short periods of inactivity (15–60 sec) although occasionally longer bursts (4–6 min) of lower amplitude were seen. The bursts of activity were not related to the activity in the reticulo-rumen.

*Vagotomy with splanchnicotomy*

Two sheep were subjected to resection of the splanchnic nerves and associated ganglia 1 and 2 months after vagotomy. All activity of the forestomach was lost immediately following surgery but within 1 day the long-term post-vagotomy motility pattern was re-established and remained unchanged for a further 1 and 3 months respectively until the end of the experiment.

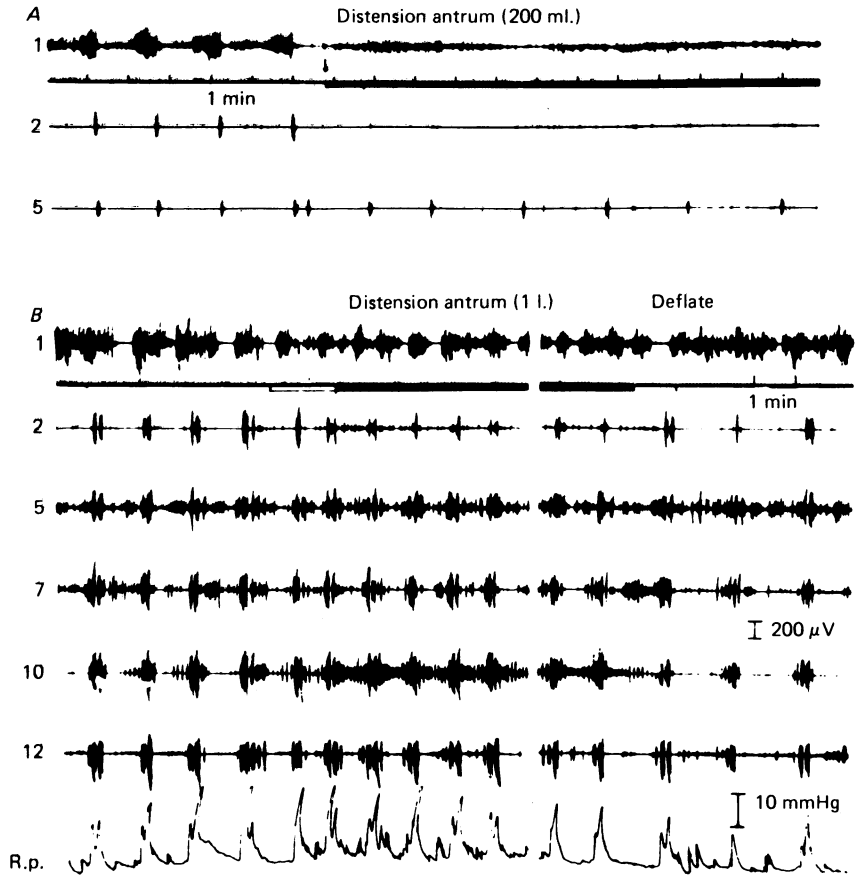


Fig. 7. Influence of abomasal distension on motility of omasum and reticulo-rumen. *A*, an electromyogram from a vagus-intact sheep. Distension of the antrum by an air-filled balloon inhibits primary reticulo-rumen, but not secondary rumen cycle contractions. The omasum discharge is reduced in amplitude but is more prolonged. *B*, from a sheep 3 weeks after total vagotomy. Distension of the antrum now enhances the rate of reticulo-rumen discharge. In this trace five minutes record is omitted (during which time the enhanced reticulo-rumen discharge was maintained), to show the reduction in rate immediately upon deflation of the balloon.

*Tests of completeness of vagotomy*

Some stimuli applied outside the reticulo-rumen are known to influence forestomach motility in intact animals by vagal reflex. These were therefore used to assess the completeness of vagotomy.

The eating of dry food by the intact animal increased the frequency of primary cycle

contractions by an average of 79 % but had no effect on the frequency or amplitude of forestomach contractions after vagotomy. Tactile stimulation of the buccal cavity or the oesophagus stimulated the rate of primary cycle contractions by an average of 65 % in the intact animal but had no effect on the motility seen after vagotomy.

In the intact sheep distension of the abomasum by rapid infusion of 600–900 ml. of warm 0·9 NaCl or by inflation of a balloon in the antrum with 200–500 ml. air abolished primary cycle contractions (Fig. 7) with little effect on secondary rumen

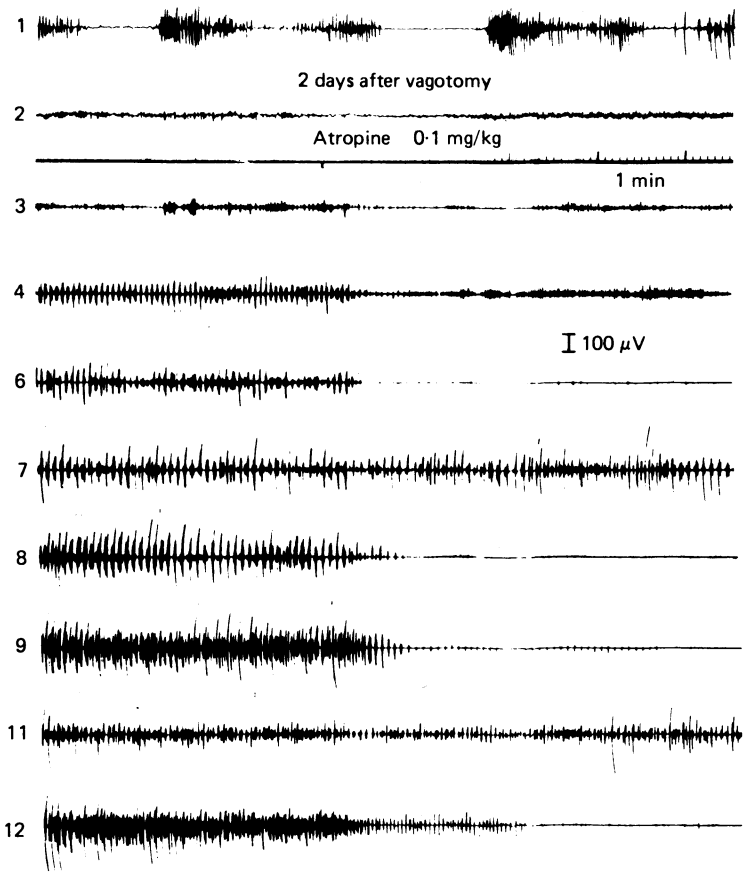


Fig. 8. Influence of atropine sulphate on discharge of omasum and reticulo-rumen 2 days after total vagotomy. The omasum discharge is unaltered. The reticulo-rumen discharge is generally abolished, but some rumen electrodes show only slight or no inhibition.

contractions. In sheep vagotomized for more than 14 days little effect was observed with infusion of 600 ml. 0·9 % NaCl or inflation of a balloon in the antrum with up to 500 ml. air, but inflation with 1 l. air, or rapid infusion of 1 l. warm 0·9 % NaCl caused an increase of 20–35 % in the frequency of the reticulo-rumen discharges (Fig. 7 *B*). There was no consistent effect on the amplitude of reticulo-rumen contractions or on the number of group discharges within one group. The omasum showed an increased frequency of discharge but at a lower amplitude.

*The action of drugs*

Tests were made to determine the nature of the motility seen after vagotomy.

*1–3 days post-vagotomy.* In the first few days after vagotomy atropine sulphate (0·1–0·2 mg/kg; Sigma) generally abolished the electrical activity of the reticulo-rumen (Fig. 8) although at some rumen sites small group discharges continued even after atropine, 1 mg/kg. Hexamethonium bromide (2 mg/kg; Sigma) had no effect

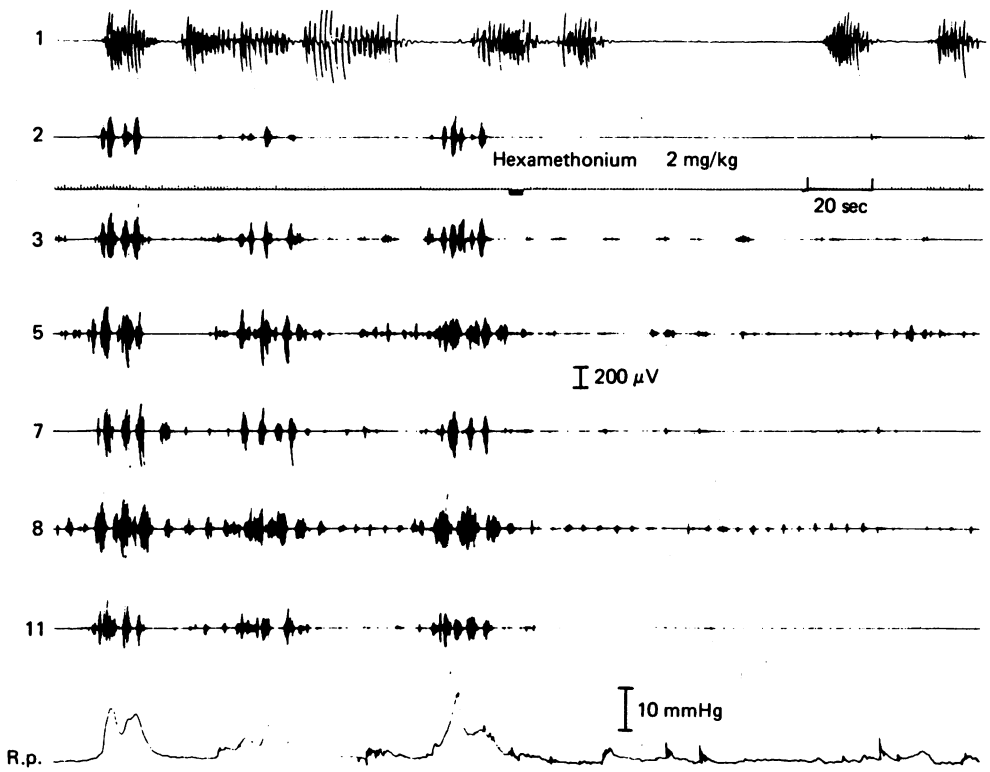


Fig. 9. Influence of hexamethonium bromide on motility of omasum and reticulo-rumen 3 weeks after total vagotomy. All large group discharges over the reticulo-rumen are abolished for 30 min but the small group discharges and the omasal discharge are unaltered.

at this time. Eserine (0·1 mg/kg; Sigma) caused a gradual increase in amplitude and duration of the small group discharge over the whole reticulo-rumen for 3–10 min but did not alter the frequency of the discharge or cause the appearance of large group discharges.

*Long-term post-vagotomy.* At 4–6 days after vagotomy hexamethonium (2 mg/kg) abolished the discharge in the reticulum but had no effect on the small group discharge in the rumen. By 14 days afterwards either atropine (0·1 mg/kg) or hexamethonium (2 mg/kg) abolished the large group discharges now present for 5–7 min or about 30 min (Fig. 9) respectively. The electrical activity was usually totally inhibited for this period but sometimes low amplitude small group discharges were observed at some

rumen electrodes especially after hexamethonium. Eserine (0·1 mg/kg) at 14 days post-vagotomy reduced or abolished the quiescent period between activity sequences so that a continuous series of large group discharges occurred over the whole reticulo-rumen at 5–7/min. The animals often showed considerable respiratory distress following eserine injection when it became necessary to administer atropine to relieve the condition.

*Omasum*

In the intact animal atropine (0·1–0·2 mg/kg) produced a transient inhibition (1–2 min) followed by periods (2–4 min) of continuous activity, at reduced amplitude, separated by equally long quiescent periods. Normal activity recommenced at the same time as biphasic reticulum contractions reappeared (10–15 min). In contrast, at all times after vagotomy similar doses of atropine had no distinct effect on the activity of the omasum, while hexamethonium (2 mg/kg) similarly had no effect.

*Pentagastrin*

Pentagastrin (3 $\mu$g/kg; Peptavlon, I.C.I.) inhibited all reticulo-rumen contractions for 2–7 min and primary cycle contractions for 7–10 min in intact sheep (Fig. 10*A*). In contrast the activity of the omasal body was stimulated showing a continuous burst of activity for 3–4 min followed by increased activity suppressed only at the resumption of biphasic reticulum contractions. At 3 weeks after vagotomy pentagastrin induced a sustained (40 sec) electrical discharge of the whole reticulo-rumen (Fig. 10*B*) followed generally by an increase in the frequence of the grouped discharge for up to 7 min. The omasal body was stimulated as in the intact animal showing a continuous discharge for 3–5 min, with a higher proportion of spiking activity.

*General anaesthesia*

In the intact animal general anaesthesia with sodium pentobarbitone (Nembutal, 20 mg/kg; Abbott Ltd.) totally abolished reticulo-rumen contractions for 30 min; normal activity was not re-established until 60–90 min after injection. The omasum retained activity although this was of reduced amplitude but of more prolonged bursts (1–2 min) until normal reticulum activity returned. In animals at least 2 weeks after vagotomy sodium thiopentone (15 mg/kg, Pentothal, Abbott Ltd.) totally inhibited reticulo-rumen contractions for 1–1½ min and reduced the amplitude of the contractions for up to 5 min after injection. There was no effect on the activity of the omasal body.

## DISCUSSION

The provision of a liquid diet successfully overcame the maintenance problems encountered by previous workers with vagotomized sheep (Mangold & Klein, 1927; Hoflund, 1940; Duncan, 1953; Ruckebusch *et al.* 1972) and the sheep showed little or no change in body weight even 5 months after vagotomy. There was little effect of the liquid diet itself on the resting motility rhythm of the forestomach other than an increased occurrence of the regular small group discharges which are observed at all rumen electrode sites for a few days after vagotomy. These discharges have been reported by Ruckebusch (1970) to be present for 1 week after surgical implantation

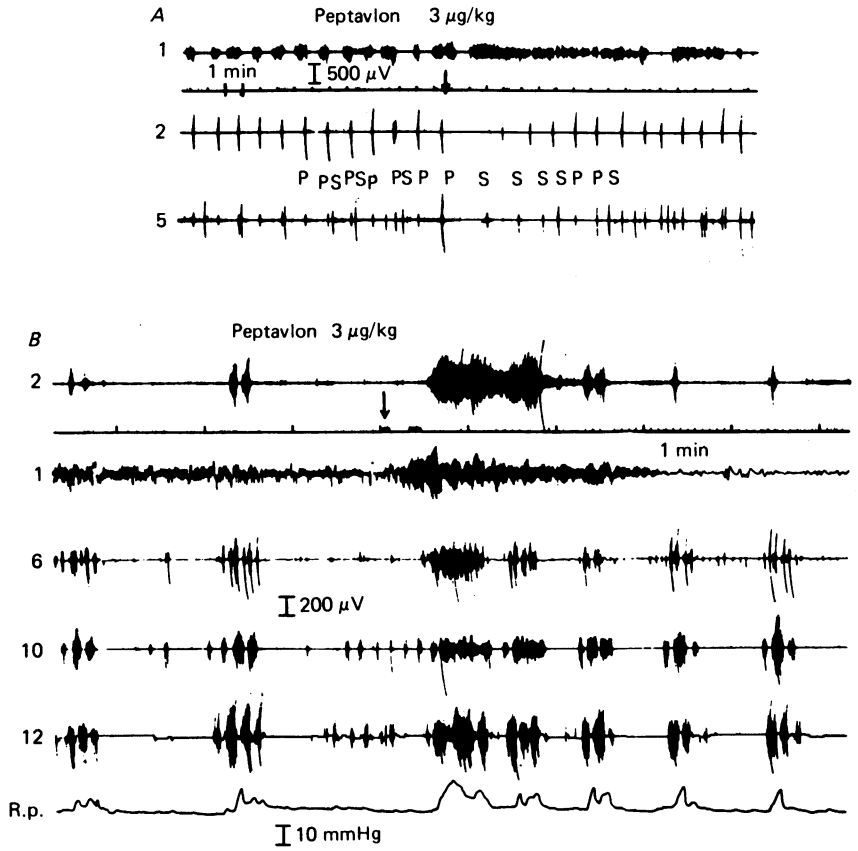


Fig. 10. Influence of Peptavlon on motility of omasum and reticulo-rumen. *A*, an electromyogram from a vagus-intact sheep. Peptavlon inhibits primary, but not secondary cycle contractions for up to 7 min, and causes prolonged omasal discharge for 3–4 min. *B*, an electromyogram from a sheep 3 weeks after total vagotomy. Prior to Peptavlon injection the omasum showed continuous low amplitude discharges for 3–5 min separated by similar periods of quiescence. Peptavlon induced a higher level of omasal discharge for a further 3–4 min, a continuous reticulum discharge for 1–2 min, and rumen discharge for ½–1 min. The rate of the large group discharges over the whole reticulo-rumen was enhanced for up to 5 min.

of electrodes, or after denervation of areas of the rumen or isolation of small strips of rumen wall. This suggests that such discharges are due to local muscle activity which is independent of vagal control or is inhibited by vagal discharge. The occurrence of such activity in sheep prior to vagotomy might be a result of a low afferent input to the gastric centres, due to the liquid diet, leading to a weaker efferent discharge.

Following the initial paralysis of the forestomach, movements have been reported as resuming some 2–3 weeks after vagotomy (Duncan 1953, Habel 1956, Ruckesbusch *et al.* 1972). It might be argued that this motility could result from re-establishment of central nervous control, perhaps due to incomplete vagotomy or reinnervation of the forestomach by regeneration of vagal fibres.

In the present study a number of observations indicate that the forestomach

motility seen after vagotomy is not under central nervous control and must be regarded as intrinsic motility.

(1) In each animal examination post mortem showed that vagotomy was complete.

(2) The animal in which only the dorsal thoracic vagus plus accessory branches were cut showed no sign of recovering a normal rumen motility even 2 months after surgery despite an intact vagal supply to the reticulum.

(3) The study confirms previous reports (Duncan, 1953; Titchen, 1958) that the splanchnic nerves do not initiate the motility observed.

(4) The approximate synchrony of contractions over the whole reticulo-rumen in the vagotomized sheep contrasts markedly with the spreading contractions in intact sheep.

(5) A number of stimuli which accelerate forestomach contractions in intact sheep by way of a vagal reflex, including feeding (Phillipson, 1939; Leek, 1969*a*) and stimulation of oesophagus and buccal cavity (Ash & Kay, 1959) have no effect on motility after vagotomy.

(6) Finally, although contractions of the omasal body continue normally after vagotomy they are no longer co-ordinated with the motility of the reticulo-rumen as in intact sheep (Bueno & Ruckebusch, 1974).

It is evident therefore that the motility of the vagotomized reticulo-rumen is not derived from the central nervous system. It does however appear to be of neurogenic rather than myogenic origin, since it is abolished by atropine or hexamethonium and enhanced by eserine, and must therefore be derived from the intrinsic neural network of the forestomach, the myenteric plexus (Habel, 1956).

The intrinsic motility does differ from that seen in the abomasum (Duncan, 1953), omasum (Bueno & Rucksbusch, 1974) and human stomach (Grimson *et al.* 1947, Beattie, 1949) in that it takes 1–2 weeks following vagotomy to become fully established. It seems likely that some reorganization within the myenteric plexus may take place during this period. It is unlikely that the delay is due to development of hypersensitivity to transmitter release from the plexus since esterine injection 1–3 days post-vagotomy increased the over-all electrical discharge but did not induce the motility pattern seen 14 days after vagotomy. The nature of the initial activity before development of the large group discharges is uncertain. Generally atropine (0·1 mg/kg) inhibited activity in both reticulum and rumen, but often some activity remained and occasionally the small group discharge at some rumen sites was totally unaffected even by large doses of atropine (1 mg/kg). The possibility of some myogenic activity cannot therefore be discounted. The complete lack of effect of hexamethonium in these first few days after vagotomy indicates that such activity evidently involves little synaptic transmission and as in the intact animal these discharges probably represent local muscle contractions.

Whereas the motility of the vagotomized reticulo-rumen contrasts markedly with that seen in the intact animal, vagotomy has little effect on the motility pattern of the omasum other than removing co-ordination with the motility of the reticulo-rumen. The present study therefore confirms the conclusions of Bueno & Ruckebusch (1974) that the motility of the omasum is principally intrinsic with mainly inhibitory influences from the gastric centres. The lack of effect of atropine and hexamethonium suggests that this motility is at least partly non-cholinergic and perhaps myogenic in nature.

In the intact animal abomasal distension inhibits reticulo-rumen motility via reflexes carried by vagus or splanchnic nerves (Titchen, 1958). Following vagotomy more severe abomasal distension is necessary for any effect on reticulo-rumen motility to appear and this effect is excitatory rather than inhibitory. It is possible that abomasal distension releases sufficient gastrin to bring about the stimulatory response. Alternatively the response may depend on neural links by way of the myenteric plexus, or represent a response to pressure on the rumen from the distended abomasum or from back-flow of abomasal contents to the rumen.

It is known that pentagastrin inhibits reticulo-rumen motility in intact sheep (Ruckebusch, 1971) while stimulating the contractions of the omasal body. On the other hand after vagotomy pentagastrin stimulated the motility of both the reticulo-rumen and the omasum. This lends support to the view that pentagastrin in some way circumvents the blood–brain barrier and exerts its inhibitory effect through a direct central action (Chapman, Grovum & Newhook, 1979).

In conclusion the present study demonstrates that, like the abomasum and the monogastric stomach, the sheep forestomach possesses an inherent capacity for intrinsic motility once the central influences have been removed by vagotomy. It seems possible that even in the intact animal the motility observed may depend on the interplay of central and local control mechanisms.

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