J. Physiol. (1984), **346**, *pp.* 379–393
With 10 *text-figures*
Printed in Great Britain

CONTROL OF INTRINSIC RETICULO-RUMINAL MOTILITY IN THE VAGOTOMIZED SHEEP

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(*Received 15 March 1983*)

SUMMARY

1. The intrinsic motility of the reticulo-rumen was studied by electromyography in nineteen sheep subjected to bilateral thoracic vagotomy and maintained by intragastric infusion of a complete liquid diet.

2. The influences of distension, temperature and tactile and chemical stimuli on the intrinsic reticulo-ruminal motility were investigated.

3. The level of electrical discharge in the reticulum and rumen in the first 3 days after vagotomy was increased progressively with distension without giving rise to the large group discharges characteristic of the long-term vagotomized sheep, and was reduced by atropine (0·1–1 mg kg^{-1}) but not by hexamethonium (2 mg kg^{-1}).

4. In the long-term vagotomized animals, the frequency of the large group discharges over the reticulo-rumen varied with the degree of reticulo-ruminal distension. The discharges were absent below a threshold rumen volume; above the threshold they increased progressively with volume until a maximal rate of six to seven regular discharges per minute was established at large ruminal volumes. The discharges were abolished by atropine (0·1–1 mg kg^{-1}) or hexamethonium (2 mg kg^{-1}).

5. With the rumen volume below the threshold, in all areas of the reticulo-rumen localized distension stimulated local discharge only and did not induce large group discharge.

6. Replacement of rumen contents with an equal volume of 0·2 M-acetic, -propionic or -butyric acid buffered to pH 4·0 rapidly abolished the large group discharges over the entire reticulo-rumen.

7. Replacement of rumen contents by an equal volume of 0·9% NaCl at 30 °C immediately abolished the large group discharges; at temperatures between 35 and 43 °C this had no effect.

8. Gentle tactile stimulation increased local discharge in the reticulum and cranial dorsal sac but not in other areas of the rumen and did not affect large group discharge in any region.

9. It is concluded that the intrinsic reticulo-ruminal motility of chronically vagotomized sheep is principally regulated by the degree of reticulo-ruminal distension. Like the C.N.S.-controlled motility of the vagus-intact sheep it is inhibited by high concentrations of volatile fatty acids. Local control mechanisms therefore may interact with central control in the over-all regulation of motility in vagus-intact sheep.

INTRODUCTION

Reticulo-ruminal motility in sheep is controlled from gastric centres in the medulla oblongata by a series of reflexes, principally in the vagus nerves (Titchen, 1968; Leek & Harding, 1975). The major reflexes arise from two types of mechanoreceptors in the reticulo-rumen and abomasum. Slowly adapting mechanoreceptors are present in the muscle layer, and respond to sustained tension (Iggo, 1955; Leek, 1969), while rapidly adapting receptors are present in the epithelium (Harding & Leek, 1972) and give an 'on–off' response to distension and also respond to tactile and chemical stimuli.

Intrinsic reticulo-ruminal motility has been found to develop within 1 to 2 weeks following vagotomy (Ruckebusch, Tsiamitas & Bueno, 1972; Gregory, 1982), such that contractions affect the whole reticulo-rumen nearly simultaneously (Gregory, 1982). This motility is evidently organized through the myenteric plexus. Little is currently known about factors affecting the functioning of the myenteric plexus or of the importance of the plexus in the control of reticulo-ruminal motility in the vagus-intact animal. Studies of the intrinsic motility may therefore yield valuable new information in this respect. In the present study, stimuli believed to influence reticulo-ruminal motility by vagal reflex from reticulo-ruminal receptors have been examined for their effects in the vagotomized animal.

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

METHODS

A total of nineteen sheep of either sex weighing 30–45 kg were used. Reticulo-ruminal motility was recorded by electromyography from chronically implanted nichrome wire electrodes and ruminal pressure from an open-ended catheter on a Polygraph recorder (Grass Model 7D) as previously described (Gregory, 1982) and integrated recordings were made using a Polygraph Integrator (Grass Model 7P 10B). The sheep underwent bilateral thoracic vagotomy and were maintained both before and after vagotomy by intragastric infusion of a complete liquid diet (Ørskov, Grubb, Wenham & Corrigall, 1979) by way of ruminal and abomasal cannulae implanted, together with the electrodes, at a prior operation. The location of electrodes and cannulae is illustrated in Fig. 1. All surgery was performed with conventional aseptic precautions under halothane anaesthesia.

The effects of distension, temperature, tactile stimulation and volatile fatty acids (VFAs) on the intrinsic reticulo-ruminal motility seen after vagotomy were intestigated. The response to distension was studied by manipulation of the rumen volume using a high-speed pump (Watson Marlow, type H.R.) for removal of contents or addition of known volumes of saline solution (0·9% NaCl, w/v) at 39 °C via a tube fixed in the rumen cannula (pump speed 2·5 l min^{-1}). Ruminal motility was recorded for 20 min at each ruminal volume to allow the recording of both initial and steady-state responses. To determine which areas of the reticulo-rumen were sensitive to distension, localized distensions were applied by inflation of balloons placed in various positions within the reticulo-rumen following removal of rumen fluid to, or below, the previously established threshold volume below which large group discharges were not recorded.

The influence of temperature was tested by emptying the rumen and replacing the rumen fluid with an equal volume of saline solution at 30, 35, 39 and 43 °C using the high-speed pump.

The influence of VFAs was tested similarly by replacing the rumen fluid with the same volume of warmed (39 °C) 0·2 M-acetic, -propionic or -butyric acids buffered to pH 4·0 with $NaHCO_3$. After 20 min the contents were emptied and replaced with warmed saline solution.

Tactile stimulation of areas of the reticulo-rumen was applied by gentle manipulation of a test-tube brush or a small partly-inflated balloon inserted via the rumen cannula.

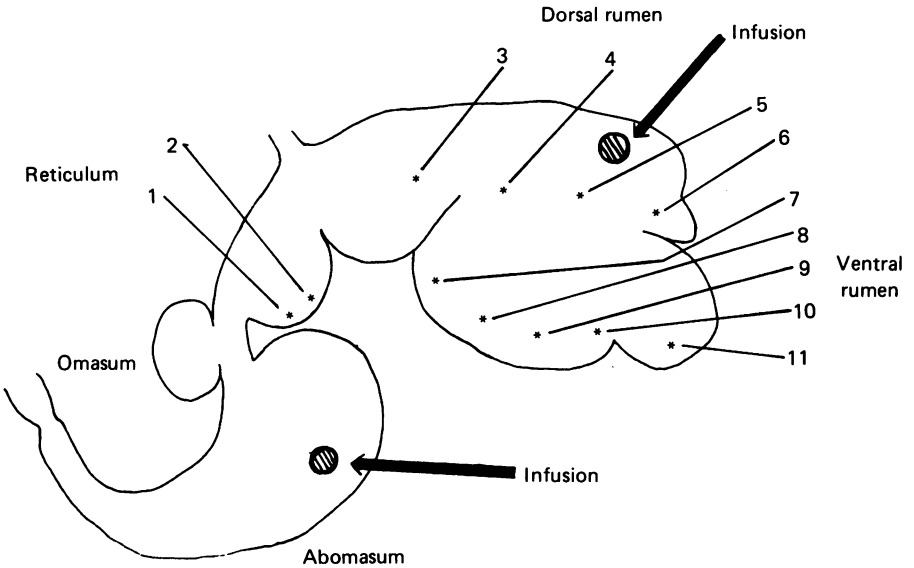

Fig. 1. A diagrammatic representation of a sheep's stomach showing the position of attachment of electrodes and cannulae. Continuous infusion of volatile fatty acids, minerals and buffer were given through the ruminal cannula, and casein and vitamins and trace minerals through the abomasal cannula.

RESULTS

Distension of the reticulo-rumen

1–3 days post-vagotomy. The electrical discharge of the reticulo-rumen in the first 3 days after vagotomy has been described in detail elsewhere (Gregory, 1982) and consists of irregular bursts of activity in the reticulum and regular small group discharges in the rumen. The discharge in both the reticulum and rumen was increased with distension (Fig. 2), giving a continuous discharge in the reticulum and increased duration, and sometimes doubling of the frequency, of the small group discharges in the rumen. There was some adaptation of the response in both the reticulum and rumen over the first 1–2 min, as shown by the integrated records, but thereafter the increased response was maintained over a prolonged distension. Using the integrated records it could be shown (Fig. 3) that there was a progressive increase in both the initial discharge and the steady discharge of the reticulum and rumen with increase in reticulo-ruminal volume. It could also be seen that at the reticulo-ruminal volumes studied the level of the steady discharge did not attain the level of the maximal initial discharge. The discharge of the reticulum and rumen was not present below a threshold ruminal volume (2 l in the individual illustrated). Atropine sulphate (0·1–1 mg kg^{-1}, Sigma) shifted the response curve to the right, increasing the threshold volume (to 4·8 l in this experiment) but did not affect the maximal discharge (Fig. 3). Similar effects were seen on both the initial and steady discharge response. Hexamethonium bromide (2 mg kg^{-1}, Sigma) had no effect on the response to distension.

Long-term vagotomy. The pattern of electrical activity which becomes established in

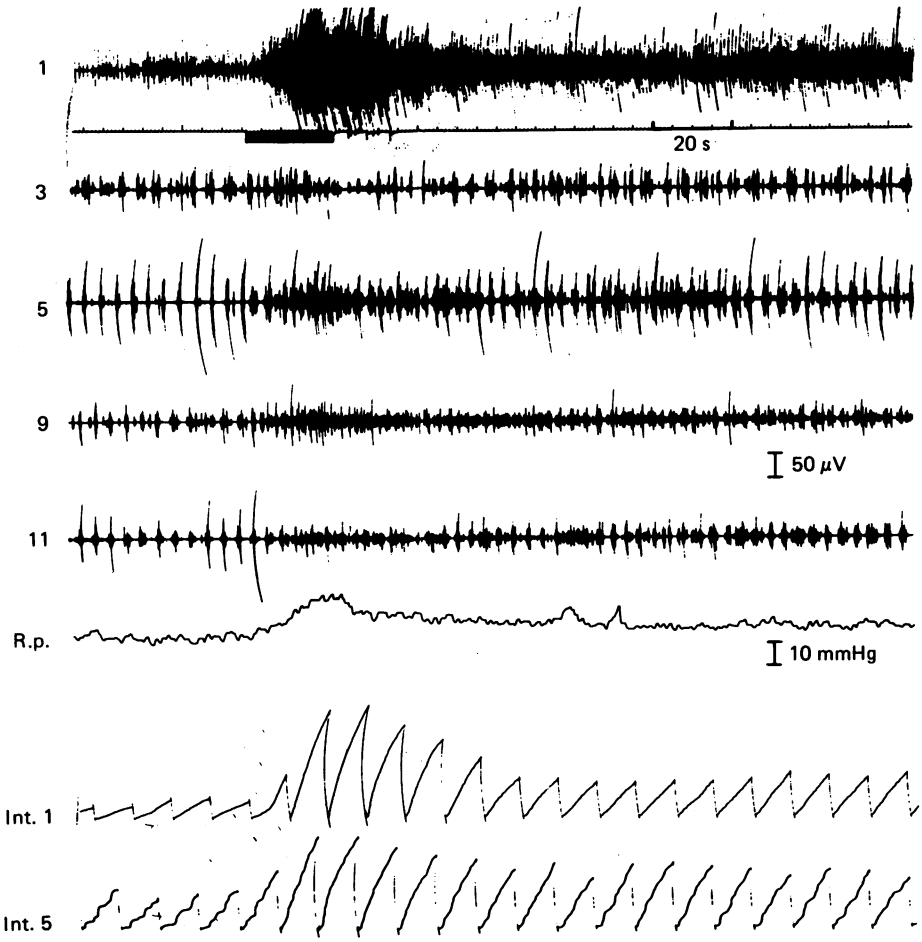

Fig. 2. Influence of rumen volume on the electrical discharge of the reticulo-rumen 2 days after total thoracic vagotomy. Infusion of 1 l warmed (39 °C) 0·9% NaCl into the rumen (filled bar) increases the discharge from the whole reticulo-rumen, shown both as the electromyogram and integrated (10 s) records from the reticulum (int. 1) and mid-dorsal sac (int. 5). Rumen pressure (r.p.) was recorded from an open-tip catheter in the caudo-dorsal blind sac. Numbers refer to electrode position as shown in Fig. 1.

the reticulo-rumen muscle 2 weeks after vagotomy has been described (Gregory, 1982). It consists of regular series of large group discharges representing strong contractions which occur almost simultaneously over the whole reticulo-rumen (see Fig. 4). Each series generally comprises two or more discharges and they are separated by quiescent periods. The frequency of the large group discharges varied according to the ruminal volume (Figs. 4 and 5). Below a certain threshold volume (limits, 0·5–3·0 l) the large group discharges were absent throughout the reticulo-rumen, but returned when the rumen volume was raised above the threshold again. There was no consistent relationship between the frequency of the series of contractions and the ruminal volume. In some individuals, as ruminal volume was increased there was an increase in the frequency of the series of contractions, in others there was an increase

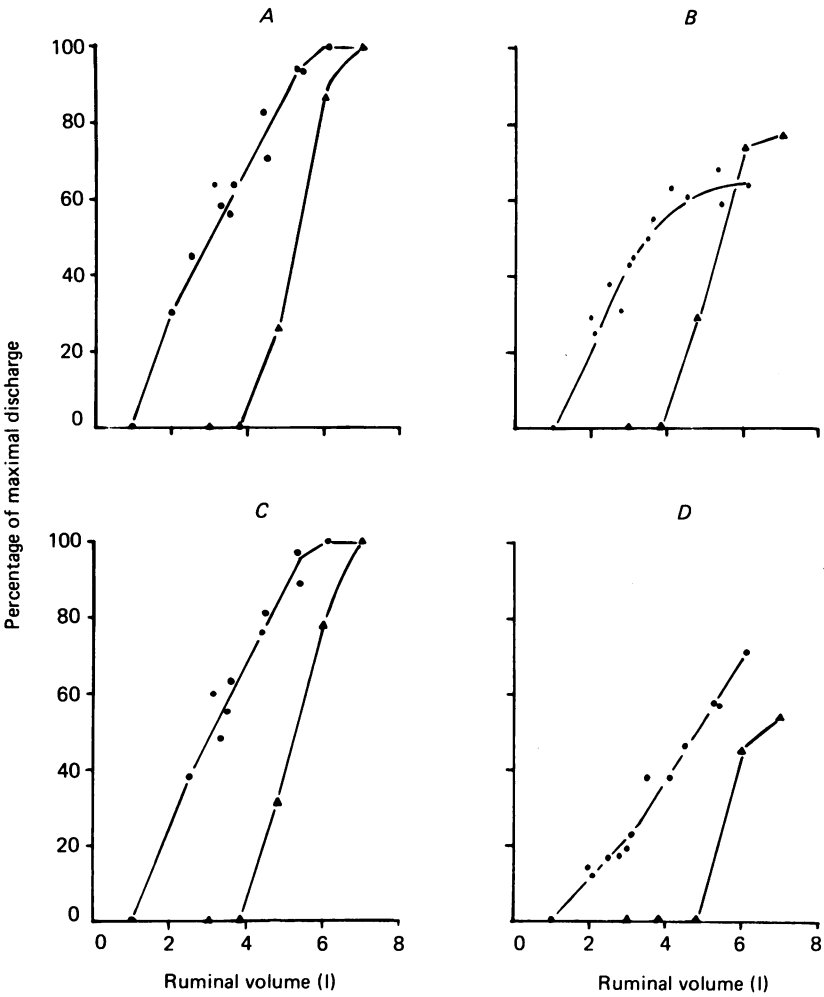

Fig. 3. Influence of atropine (1 mg kg^{-1}) on the change in electrical discharge of the reticulum and rumen with ruminal volume in a sheep 2 days after total thoracic vagotomy. All the curves show the electrical discharge (from integrated records), recorded as a percentage of the maximal discharge, with increasing ruminal volume before (circles) and immediately following atropine injection (triangles). *A* shows the electrical discharge of the reticulum (int. 1) in the initial 1 min after addition of saline solution, *B* shows the steady-state reticular discharge (2–10 min) after saline infusion. *C* shows the initial (1 min) discharge and *D* the steady-state (2–10 min) discharge of the mid dorsal sac (int. 5).

in the number of large group discharges within each series of contractions, or a combination of the two (as in Fig. 4), but in all cases the number of large group discharges increased with ruminal volume (Fig. 5).

Within each series of contractions the large group discharges occurred at intervals of around 9 s irrespective of ruminal volume (Fig. 6). As the ruminal volume was increased the quiescent period between the series of contractions was reduced. This is illustrated in Fig. 7. The most frequent interval between group discharges was about

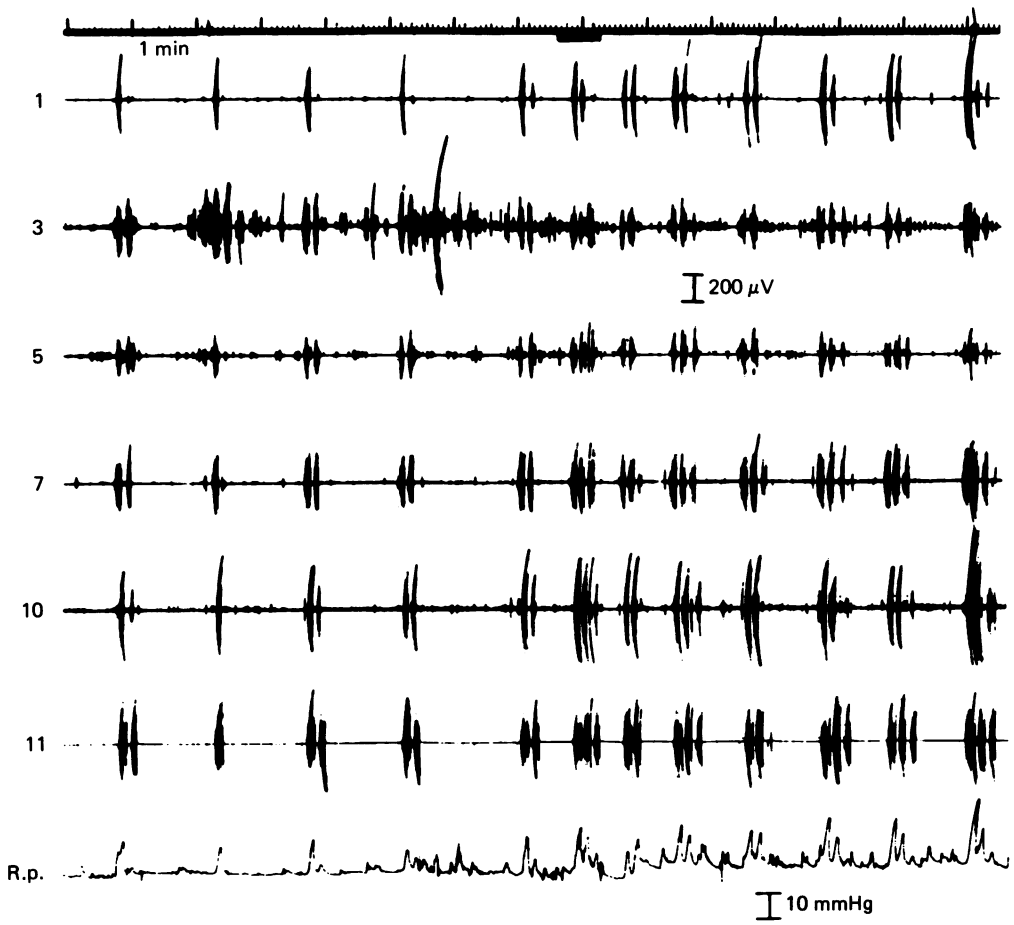

Fig. 4. Influence of reticulo-ruminal distension on electrical discharge in a sheep 3 weeks after total thoracic vagotomy. Rapid infusion of 2·0 l saline solution (filled bar) increases the frequency of large group discharge over the reticulo-rumen.

9 s, i.e. the interval within a series of contractions. The interval between the series, i.e. the quiescent period, shortened from 50–80 s at a rumen volume of 4·5 l (Fig. 7*A*), to 30–40 s at 6·5 l (Fig. 7*C*) and was accompanied by a rise in the proportion of intervals at around 9 s as the number of discharges within a series increased, until at a rumen volume of 7·5 l (Fig. 7*D*) all quiescent periods were abolished. No series of contractions could be distinguished, but rather there was a regular sequence of large group discharges at the maximal rate of 6–7 per minute (see also Fig. 6), i.e. separated by approximately 9 s intervals. The response to distension showed some adaptation in that it declined slightly to a steady response which was established within a few minutes (Figs. 4 and 10*B*). Large group discharges were abolished by atropine (0·1–1 mg kg^{-1}) or hexamethonium (2 mg kg^{-1}) at all levels of rumen volume studied, up to 8 l.

Local distension

With the ruminal volume lowered below the threshold level, local distensions of the reticulum, or of the dorsal or ventral sacs of the rumen failed to elicit large group discharges over the reticulo-rumen. In all experiments the electrical discharge of the area under distension was increased, but no effects were seen elsewhere. The form of the discharge and the response to distension were similar to that described for the first 3 days after vagotomy.

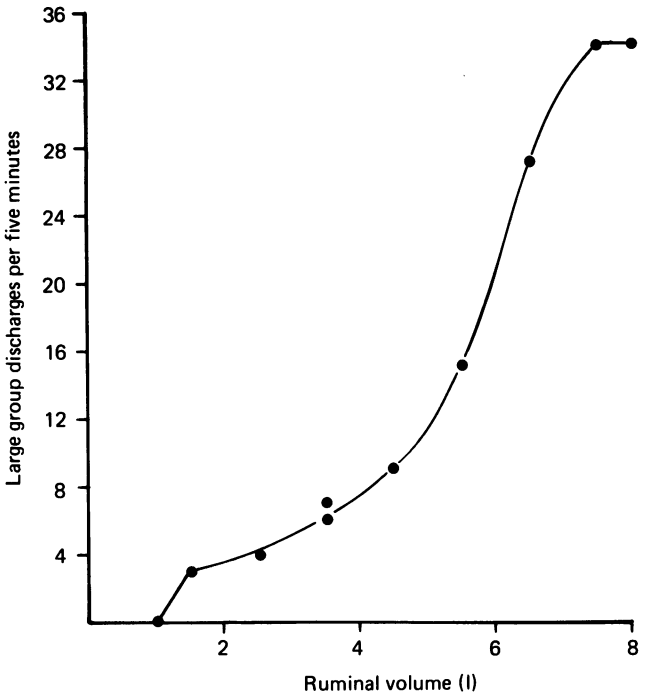

Fig. 5. Influence of rumen volume on the frequency of large group discharge in a sheep 3 weeks after total thoracic vagotomy. The frequency of large group discharges is measured as the mean frequency recorded 2–20 min following saline infusion.

With the ruminal volume just above the threshold level, distension of localized areas of the dorsal sac increased the frequency and amplitude of large group discharges in the area under distension. The response was localized and there was no change in frequency of the large group discharges in other regions of the reticulo-rumen (Fig. 8). Similar experiments with distension of the reticulum or areas of the ventral sac of the rumen resulted in an increased frequency of large group discharges over the entire reticulo-rumen.

Tactile stimulation of the reticulo-rumen

Large group discharges could not be modified or evoked by tactile stimulation in any region, whether the rumen volume was above or below the threshold level. Gentle

stimulation of the reticulum and reticulo-ruminal fold evoked weak continuous discharge of the reticulum or reticulum and cranial dorsal sac respectively. Stimulation of other areas had no effect.

Temperature effect

The replacement of ruminal contents by an equal volume of saline solution at 30 °C immediately abolished the large group discharges, but small group discharges developed instead (Fig. 9). The large group discharges reappeared as the temperature of the rumen fluid rose to 35–36 °C. Replacing the rumen contents at 35 and 43 °C had no influence on the normal pattern of discharge, other than a transient excitatory effect immediately upon filling the rumen (Fig. 10*A*, *B*).

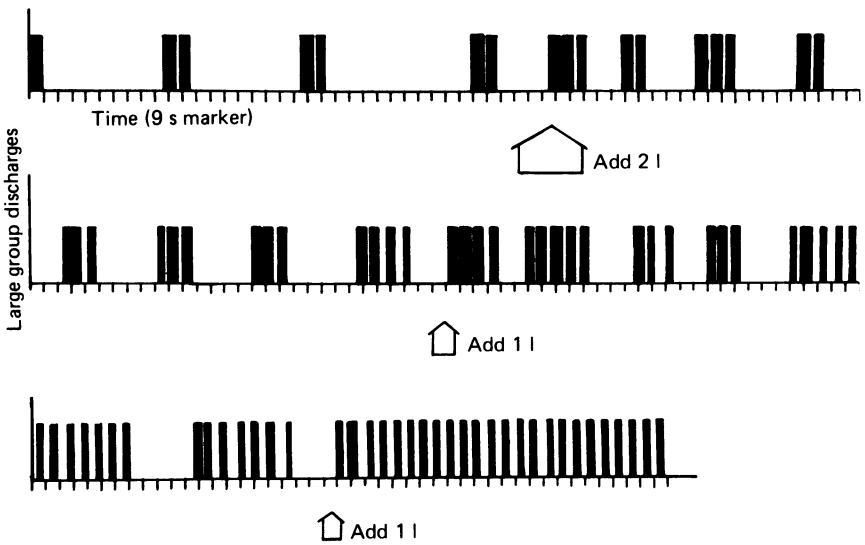

Fig. 6. Diagrammatic representation of the effect of ruminal volume on the frequency of large group discharge. Re-drawn from original trace to show the variation in interval between large group discharges in caudo-ventral blind sac with increase in ruminal volume against a 9 s time marker.

Influence of volatile fatty acids

Replacement of the ruminal contents by an equal volume of warmed (39 °C) 0·2 M-acetic, -propionic or -butyric acids buffered to pH 4·0 rapidly abolished the large group discharges over the whole reticulo-rumen (Fig. 10*C*). Inhibition was most rapid with butyric and propionic acids and was generally complete within 3 min, while complete inhibition of large group discharges with acetic acid took from 7–17 min. There was generally a transient increase in discharge frequency immediately upon filling the rumen with acetic acid, followed by a rapid decrease in frequency of discharges until abolition (Fig. 10*C*). In some experiments all electrical activity was lost, but generally small group discharges started over part or all of the reticulo-rumen, as seen in the reticulum and caudo-ventral blind sac in the experiment

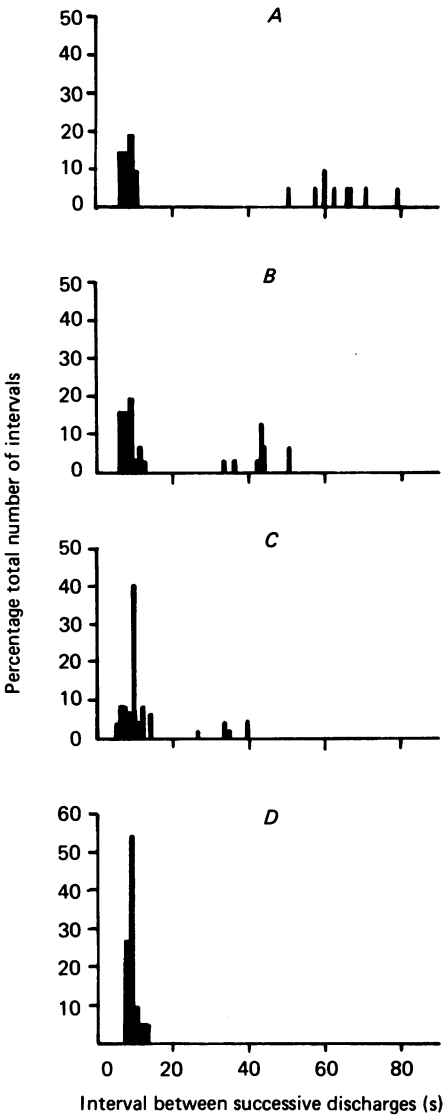

Fig. 7. The influence of ruminal volume on the interval between successive large group discharges. Histograms of the interval between successive large group discharges in the caudo-ventral blind sac are plotted as the proportion of the total number of intervals at different ruminal volumes, recorded 2–20 min after saline infusion. *A*, with rumen volume 4·5 l; *B*, rumen volume 5·5 l; *C*, rumen volume 6·5 l; *D*, rumen volume 7·5 l.

illustrated. After emptying out the rumen and replacing with saline solution the small group discharge persisted for up to 3 h, gradually being replaced by large group discharges. Large group discharges re-started after 27–56 min ($n = 12$). At first these were very weak, and the full-strength control motility pattern was not established until 97–181 min after removing the VFA and replacing with saline solution.

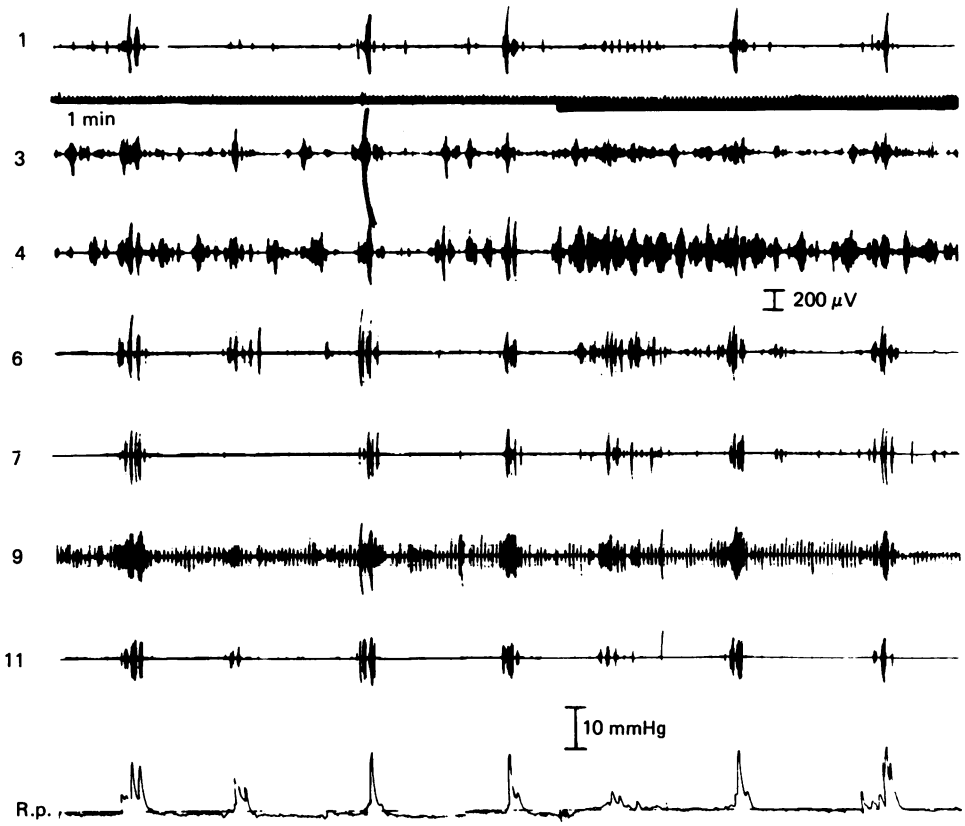

Fig. 8. Influence of local distension on over-all reticulo-ruminal discharge. Distension of the mid-dorsal sac (400 ml balloon) at a ruminal volume of 2·5 l (above the threshold level) increases the frequency of large group discharges in the mid-dorsal sac but not elsewhere.

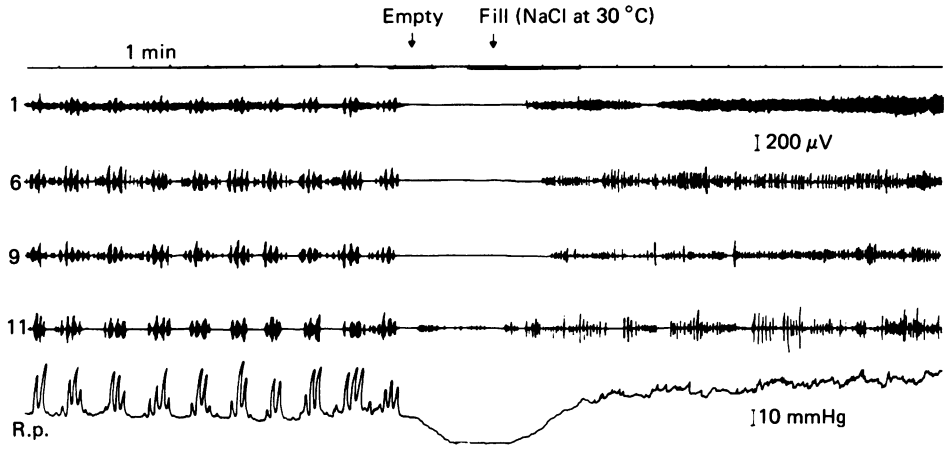

Fig. 9. Influence of temperature on reticulo-ruminal discharge. Emptying of the rumen and replacing with an equal volume (7·5 l) of saline solution at 30 °C where indicated caused an immediate loss of large group discharge, and occurrence of small group discharge over the whole reticulo-rumen. In this animal, maximal discharge rate was established at a rumen volume of 9·0 l.

DISCUSSION

No studies of neuronal activity within the myenteric plexus of the sheep's reticulo-rumen have yet been made, but the properties of such neurones in other animal tissues have been studied and it is interesting to consider the results reported here in the light of those findings. In the myenteric plexus of the cat's small intestine there are neurones that produce a regular discharge approximately every 6 s (Wood, 1974). The discharge from these neurones is abolished at 30 °C. Neurones with similar properties to these, discharging every 9 s instead, might be important in the production of the large group discharge in the sheep's reticulo-rumen. Indeed Leek (1969) observed that the afferent discharge in some gastric vagal fibres was phasic (every 4–10 s) and coincided with local intrinsic contractions of the sheep rumen. Further studies showed there to be three populations of mechano-sensitive neurones in the cat small intestine (Mayer & Wood, 1975) one of which resembled the slowly adapting mechanoreceptors located in the muscle layer of the reticulo-rumen of sheep (Leek, 1969) and goat (Iggo, 1955). These receptors have little or no discharge at low levels of reticulo-ruminal distension, but their level of discharge increases with the level of distension, and is sustained during prolonged distension (Iggo, 1955; Leek, 1969). They are believed to play a major role in the vago-vagal reflex control of reticulo-ruminal motility. In view of the responses of the vagotomized reticulo-rumen to distension it seems that similar receptors also connect with the myenteric plexus.

In the vagotomized sheep the increase in motility was greatest in the initial 1–2 min after distension. If rapidly adapting receptors were also involved in the response they should adapt within seconds rather than minutes (Mayer & Wood, 1975; Leek & Harding, 1975) and so perhaps the reduction in responses is due rather to accommodation of the musculature of the reticulo-rumen, an effect previously observed to influence the vagal afferent discharge during sustained reticulo-ruminal stretch (Leek, 1969).

It is necessary to consider if other factors might also influence the response of the vagotomized reticulo-rumen to distension. The cell bodies of the gastric vagal afferent neurones are located in the nodose ganglion (Falempin, Mei & Rousseau, 1978; Falempin & Rousseau, 1979) and therefore activation of myenteric plexus neurones by an axon reflex mechanism through peripheral branches of afferent vagal fibres cannot be a factor in this preparation. In the newly vagotomized sheep, atropine (0·1–1 mg kg^{-1}) reduced but did not abolish the enhanced electrical discharge following distension while hexamethonium (2 mg kg^{-1}) had no effect. This suggests that a direct myogenic response to stretch, or even release of a stored transmitter substance other than acetylcholine (Bulbring & Crema, 1959), might occur at the high level of distension necessary to produce discharge in the presence of atropine. Such effects do not appear to be involved in the production of the large group discharges, which were abolished both by atropine and hexamethonium. Muscle stretch is also known to lower the resting membrane potential (Bulbring, 1955) rendering the muscle more excitable and this may be an important factor in the responses observed with distension. In many smooth muscle tissues there are regular fluctuations of resting membrane potential, and hence of muscle excitability, which are seen as minute rhythms (Bulbring, 1962) or slow waves (Holman, 1968). In the sheep's reticulo-rumen

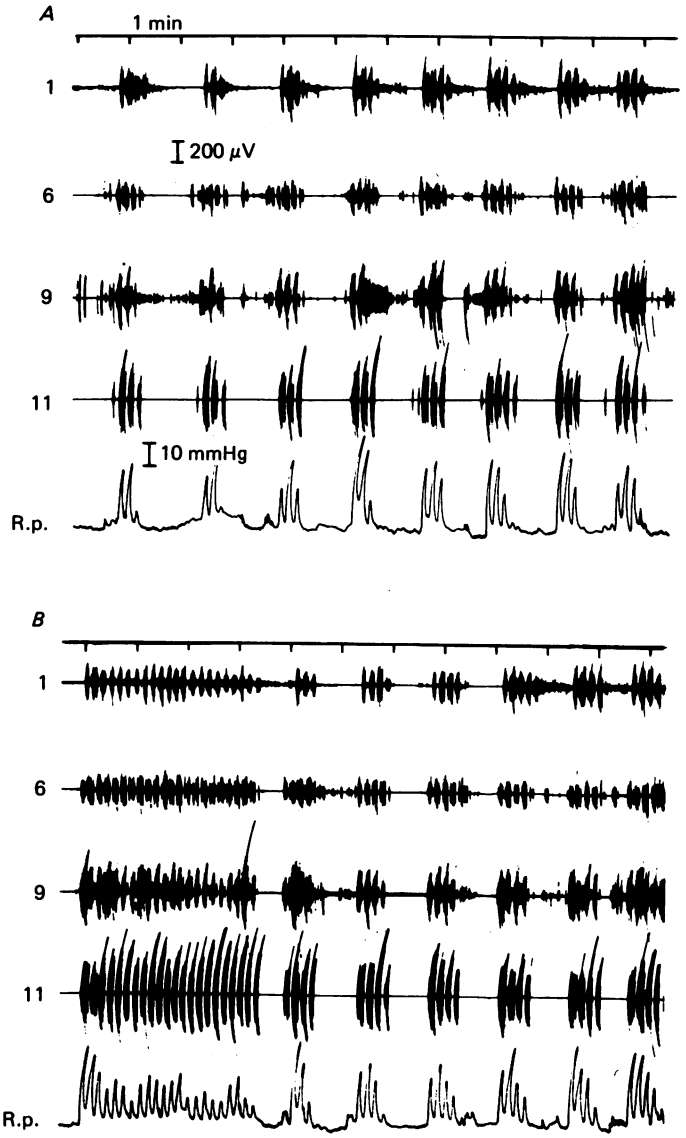

Fig. 10. Influence of acetic acid on reticulo-ruminal discharge. *A*, control electromyogram from a sheep 6 weeks after total thoracic vagotomy. *B*, electromyogram from the same sheep immediately after emptying of rumen fluid and rapid replacement with an equal volume (6·5 l) of saline solution at 39 °C by high-speed pump (2·5 l min^{-1}). *C*, electromyogram from the same sheep immediately after emptying of rumen fluid and replacement with an equal volume (6·5 l) of buffered acetic acid (0·2 M, pH 4·0) at 39 °C as before.

slow waves have been reported (Ruckebusch, 1970) but not described. In the present study slow waves were only observed with great difficulty. They were of low amplitude and appeared only in conjunction with the small and large group discharges, and were not seen in the absence of a spike discharge. The difficulty in recording the slow electrical rhythms in the reticulo-rumen might be due to the poor

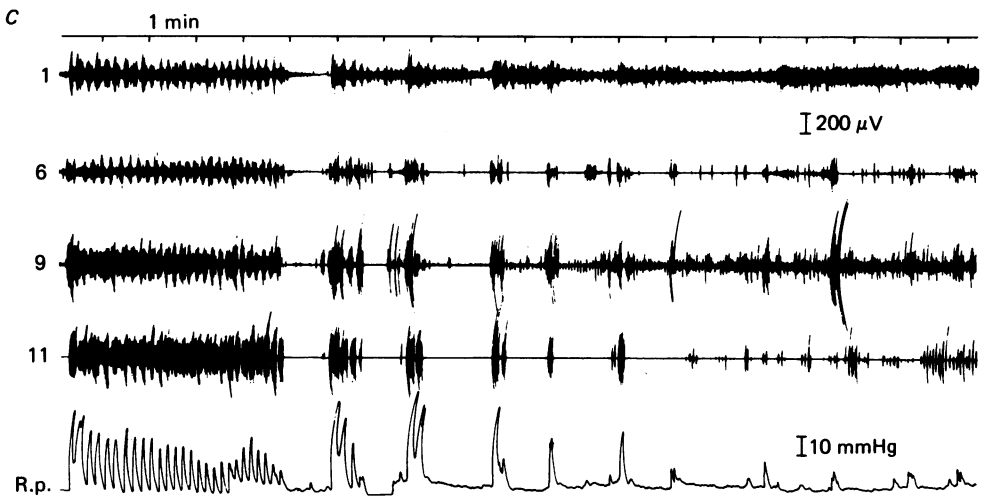

Fig. 10*C*. For legend see facing page.

definition of the longitudinal muscle layer, the layer from which such rhythms originate (Bortoff, 1961). The approximate one minute rhythm of the series of discharges at normal level of ruminal volume suggests that the excitability of the muscle might vary to some extent according to a minute rhythm (Bulbring, 1962). Nevertheless the importance of such rhythms on reticulo-ruminal motility cannot yet be defined, and the involvement of myenteric plexus neurones with properties similar to slowly adapting vagal mechanoreceptor units remains the most convincing mechanism for the response of the chronically vagotomized sheep to distension.

The frequency of large group discharges depends on the level of reticulo-rumen distension (measured as ruminal volume). There was little evidence that this response derived from the effects of distension on a 'pace-maker region', rather it is likely that all areas of the reticulo-rumen respond directly. There was an increase in the over-all reticulo-ruminal discharge frequency following distension in the ventral sac or reticulum with ruminal volume above the threshold level, but this could be the result of general reticulo-ruminal distension from displacement of rumen fluid following inflation of the balloon. When the balloon was inflated in the dorsal sac (above the level of the rumen fluid) only a local increase in discharge frequency occurred. The failure to induce large group discharge in any region by local distension at rumen volumes below the threshold level suggests that distension produced in this manner did not sufficiently stimulate the myenteric plexus neurones. Perhaps a more intense stimulation is needed, or stimulation over a wider area.

In the vagus-intact sheep, rapidly adapting mechanoreceptors have been described in the reticulo-rumen epithelium which respond to tactile stimuli, VFAs, acid, alkali and high and low osmolarity (Harding & Leek, 1972). The inhibition of reticulo-rumen motility in vagus-intact sheep by VFAs (Ash, 1959) is considered to be mediated through vago-vagal reflex by way of excitation of these receptors (Upton, Ryan & Leek, 1976). In the present study, evidence for the involvement of similar receptors in the control of the intrinsic motility of the vagotomized reticulo-rumen is

ambiguous. Tactile stimulation which induced rumination in vagus-intact sheep (Ash & Kay, 1959) caused a slight increase in the electrical discharge of the reticulum and cranial dorsal sac. It had no effect in other areas of the rumen, perhaps because such stimulation might only affect a localized area and a response would be difficult to detect unless the stimulus was applied very close to the electrode. However, in all areas there was no influence on the large group discharge. On the other hand, acetic, propionic or butyric acid (0·2 M, pH 4·0) abolished the large group discharge over the entire reticulo-rumen. This inhibition of motility could occur via excitation of the same VFA-sensitive receptors believed to mediate the response in the vagus-intact animal (Harding & Leek, 1972), by some other VFA-sensitive neurones, which have a direct link to the myenteric plexus, or by some other mechanism. Further experiments are being performed to determine if the motility of the vagotomized and vagus-intact sheep are inhibited at the same VFA concentrations and thus whether the inhibition is likely to be through the same mechanism.

It is interesting to note that intrinsic contractions have also been recorded *in vitro* from strips of reticular and ruminal muscle (Dussardier & Navarro, 1953; Duncan, 1954; Sanford, 1958; Bowen, 1962). The pattern of contractions of the ruminal strips has been described, and consists of a rhythmic series of contractions, each period of activity separated by a quiescent period (Dussardier & Navarro, 1953; Duncan, 1954), which bears obvious similarity to the pattern observed in the present study in the chronically vagotomized reticulo-rumen. One of the features of the latter is that well-defined, strong reticulo-ruminal contractions (large group discharges) do not occur until 1–2 weeks after vagotomy (Ruckebusch *et al.* 1972; Gregory, 1982). There is at present little evidence concerning the neurogenic or myogenic nature of the *in vitro* motility, which prevents further comparisons being drawn with the motility of the chronically vagotomized reticulo-rumen, but the reasons for the delay in appearance of the motility in the vagotomized sheep become even more confusing. Because of the delay in the appearance of this intrinsic motility, the local regulatory mechanisms described in this paper cannot yet be evaluated for their importance in the control of motility in the vagus-intact sheep. Nevertheless the present experiments show that there is the potential for considerable local control of motility. The results suggest that there could be a dual innervation of slowly adapting mechanoreceptors and possibly of VFA-sensitive receptors by the vagus nerves and myenteric plexus neurones, and this could allow interplay of central and local mechanisms in the over-all regulation of reticulo-ruminal motility in the vagus-intact sheep. Further experiments will be needed to clarify the possible role of local control mechanisms.

The author wishes to thank Dr R. N. B. Kay for his help throughout and for his review of this manuscript, Dr F. White and Mr C. A. Simpson for assistance with the surgical preparation of the animals, and Mr E. D. Goodall and Mr S. Miller for their assistance.

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