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REFLEX STIMULATION OF MOVEMENTS OF THE RUMEN IN DECEREBRATE SHEEP

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Rumen contractions occur both independently of, and in association with, contractions of the reticulum (Schalk & Amadon, 1928; Phillipson, 1939). Different directions of successive involvement of the rumen have been described for these contractions (Weiss, 1953). Rumen contractions which occur independently of contractions of the reticulum were termed by Weiss (1953) 'forward-moving ruminal contractions' and described as 'starting at the posterior blind sac'. With the use of the technique of partial exteriorization of the stomach applied to ruminants (Bost, 1958; Titchen, 1958*a*; Reid & Titchen, 1959), it has proved possible to determine that this type of contraction of the rumen starts in the posterior ventral blind sac and successively involves the posterior and then the anterior of the dorsal sac of the rumen and finally its ventral sac (Reid, 1962; Titchen & Reid, 1965). Eructation commonly occurs in association with these contractions. Eructation is a common event in ruminants. In these animals gases, particularly carbon dioxide and methane, are formed in the course of digestion of plant materials in the rumen and reticulum. Gas so produced is continually removed by eructation.

The rumen contractions which regularly and closely succeed the normally diphasic contraction of the reticulum characteristically involve first anterior and later posterior parts of the dorsal sac of the rumen and later also its ventral sac.

Contractions of the reticulum, alone, and with associated rumen contractions have been stimulated in decerebrate preparations of sheep, goats and calves (Iggo, 1956; Titchen, 1958*b*, 1960). The effective stimuli include changes in conditions in the stomach itself. Stretch of the reticulum serves as a potent stimulus to reticulum contractions. If in addition to stretch of the reticulum the reticulo-ruminal fold is stretched, strong

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contractions of the rumen can be elicited. Each rumen contraction stimulated in this manner follows a contraction of the reticulum. Evidence for the reflex character of these responses has been presented (Iggo, 1956; Titchen, 1958*b*, 1960). The experiments described below were concerned mainly with the production in decerebrate preparations of sheep of those contractions of the rumen which occur independently of reticulum contractions in conscious sheep.

METHODS

The sheep used were, in England, Welsh mountain ewe lambs 10–24 kg body weight, in New Zealand, Cheviot ewe lambs 20–25 kg body weight. They were fasted in the laboratory with free access to water for 24–48 hr before the experiment. Previous to this they were on pasture.

Anaesthesia was induced with ethyl chloride. It was maintained with ether rarely for more than 30 min, during which time the dissections and decerebration were carried out. The method of decerebration was similar to that described previously (Comline & Titchen, 1951*a*). The brain stem was transected through, or a few millimetres posterior to, the middle of the superior colliculus. The rumen was exposed for recording with a laparotomy incision about 5 cm long, 2–3 cm behind and parallel to the upper part of the last rib. A circular glass retractor about 2·5 cm internal diameter was used to hold apart the edges of the laparotomy wound throughout the experiment. The ends of the tube were expanded and flattened so that the walls of the retractor were concave outwards and the retractor was thus made self-retaining. The recording thread was attached to a region of the wall of the rumen which lay 5–7 cm behind the posterior border of the retractor when the rumen was inflated to an intrarumen gas pressure of 4–5 cm H_2O: thus records were obtained from corresponding points of the posterior regions of the left lateral wall of the dorsal sac of the rumen in different decerebrate preparations. The pulley which guided the thread to a frontal writing lever was placed anteriorly to the retractor. This arrangement allowed the differential recording on a kymograph paper of two directions of movement of a point of the rumen wall. Movement of the point of attachment in an anterior direction was recorded as a downward deflexion: its displacement in a posterior direction was recorded as an upward deflexion. A rubber balloon inserted into the reticulum and distended with up to 25 ml. of water was used to record reticulum contractions as described previously (Titchen, 1958*b*).

Records of intrarumen gas pressure and the insufflation of gas into the rumen were made possible by the introduction into the mid-ventral rumen of a glass cannula 12 mm i.d. This cannula was introduced through the same mid-line laparotomy incision used to insert the balloon into the reticulum. A nylon tube 4 mm i.d., was pushed through the cannula into the dorsal gas cap in the rumen. This tube was connected with a water manometer used to record intrarumen gas pressure. The cannula was used for the insufflation of gases into the rumen. The flow of the gases introduced was regulated with a needle valve used in conjunction with a capillary flowmeter. The gases were warmed before their introduction into the rumen by passage through a spiral coil of copper tube kept in a water bath maintained at 40° C. Throughout these experiments the animals lay on their right sides on a table which was tilted so that they were in a standing position although 45–50° from a vertical plane. The preparations were maintained in this position by being supported under the sternum anteriorly, and posteriorly with a sling which passed between the hind legs. The table top was warmed and in addition an infra-red lamp directed on to the left side of the preparation, to keep a rectal temperature of 38–40° C. Nerve stimulation and other procedures undertaken were carried out as described previously (Comline & Titchen, 1951*a*; Titchen, 1958*b*, 1960).

RESULTS

After decerebration either no contractions or an evanescent series of contractions of the reticulum alone, rarely of both reticulum and rumen, were observed, as described previously (Titchen, 1958*b*, 1960). The effects of stimuli were examined after periods of quiescence of the reticulum and rumen of 10–30 min and usually not less than 60 min after ether was last administered. The stimulus whose effects were studied in most detail was the insufflation of gas into the rumen.

Insufflation of gas into the rumen led to rumen distension, increased intrarumen gas pressure, rumen contractions, eructation of gas through the oesophagus and usually a series of contractions of the reticulum together with associated rumen contractions (Fig. 1). The effects were substantially similar with the insufflation of a variety of gases into the rumen at rates up to 300 ml./min whether 5 % CO_2 in O_2, N_2 or, as was most usual, a mixture of CH_4 and CO_2 (40:60) was used. As the intrarumen gas pressure rose to or above 4 cm H_2O characteristic contractions of the rumen occurred. In each such contraction there was movement in a posterior direction of the point of attachment of the recording thread and progressive involvement of more anterior regions of the dorsal sac of the rumen. Points on the anterior dorsal sac of the rumen were involved in the contractions up to 1 sec later than the start of the contraction in points 10–12 cm more posterior: this was judged by the observation of the movement of the rumen wall exposed by the retractor. Contraction of a visible part of the rumen wall was distinguished as a wrinkling beneath the serous surface, approximation of larger blood vessels and, at the height of a contraction, disappearance of blood from smaller blood vessels. The term '*forward-moving wave of contraction*' has been applied in description of these contractions in the subsequent account of the experimental observations. They were recorded on the kymograph paper as upward deflexions. They were usually simple monophasic contractions. Sometimes they were seen as more complex contractions showing two or more peaks of contractions (Fig. 8).

There was with increasing intrarumen pressure, up to 8–12 cm H_2O, a slight increase in the force and a marked increase in the frequency of the forward-moving contractions. Above these pressures the force of the contractions declined. At lower intrarumen gas pressure some, but not all, of the forward-moving waves of contraction were accompanied by eructation. With intrarumen gas pressures of 8–12 cm H_2O it was usual for each such rumen contraction to be accompanied by one if not two eructations. Eructation usually occurred as the contraction involved the mid or anterior regions of the dorsal sac of the rumen: this corresponded with the height of the increase in intrarumen gas pressure due to rumen contraction. Frequently but not invariably eructation was preceded by a contraction of the abdominal muscles which caused a further increase of up to 4 cm in the intrarumen gas pressure. The intrarumen gas pressure at which eructation occurred increased during the course of a period of insufflation of gas into the rumen: thus during the course of an experiment rumen contractions and eructations occurred at progressively higher pressures of gas in the rumen—in some experiments this was as much as 4 cm higher in later stages of the experiment than when the response was first established.

Reticulum contractions sometimes occurred after the first few forward-moving waves of rumen contraction (Fig. 1). In some preparations the first reticulum contraction closely followed the first eructation; in others it was not until a number of eructations occurred in a short time that

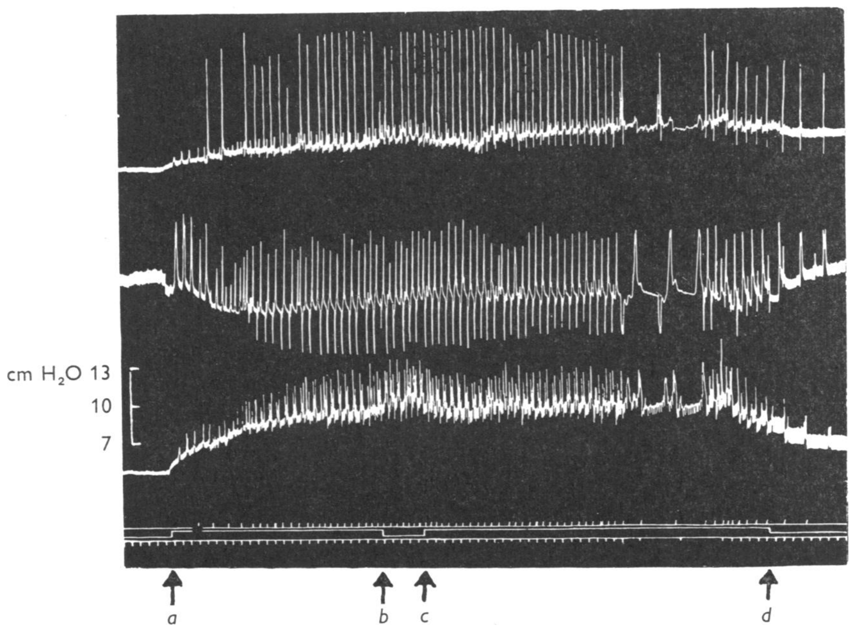

Fig. 1. Decerebrate sheep 15 kg. Effect on the movements of the reticulum and mid-dorsal sac of the rumen of the insufflation of a $CH_4:CO_2$ (40:60) gas mixture into the rumen. Two rates of insufflation used, between *a* and *b*, and *c* and *d* 150 ml./min, and between *b* and *c* 250 ml./min. Records from above downwards: reticulum (balloon water manometer recording system), mid-dorsal rumen (frontal writing lever), intrarumen gas pressure (water manometer recording from open-ended tube in dorsal sac of rumen; calibration to left of record indicates intrarumen pressure in cm H_2O), eructation seen in the neck signalled manually, signal, 30 sec time-marker (during both speeds of rotation of the kymograph drum). The upward deflexion on the rumen record (frontal writing lever) in this and subsequent records was produced by forward-moving waves of rumen contractions: downward deflexions were produced by backward-moving rumen contractions.

reticulum contractions were observed. In preparations in which the insufflation of gas was followed by a series of reticulum contractions there were associated rumen contractions. These progressively increased to a maximum, usually reached by the tenth or so reticulum contraction. In contrast to the rumen contractions with which eructation was commonly associated, and which have been described above, these contractions started in the anterior dorsal rumen. They progressively involved more posterior regions of the dorsal sac of the rumen and accordingly have been referred to as a '*backward-moving waves of contraction*'. With the recording system described these contractions were recorded as downward deflexions on the kymograph paper. In many preparations the characteristic response once established consisted of a forward-moving wave of rumen

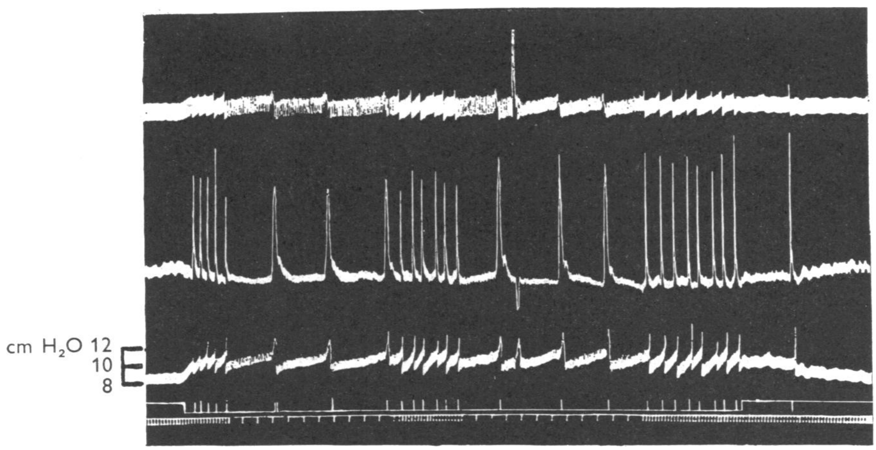

Fig. 2. Decerebrate sheep 12·5 kg. Records as in Fig. 1. Insufflation of CO_2 into rumen at 150 ml./min showing the initiation and maintenance of a series of forward-moving contractions of the mid-dorsal sac of the rumen. One contraction only of the reticulum was recorded. This lone reticulum contraction was succeeded by a backward-moving contraction of the rumen (downward deflexion on the frontal writing lever trace of mid-dorsal rumen activity). Maintained depression of signal indicates period of insufflation of CO_2 into rumen at 150 ml./min; eructuations marked by deflexions of short duration of same signal. Time-marker 30 sec throughout both fast and slow speeds of rotation of the kymograph drum.

contraction with an associated eructation, which was followed after an interval of up to 45 sec by a reticulum contraction with an associated backward-moving wave of rumen contraction succeeded in up to 45 sec by a forward-moving wave of rumen contraction and eructation (Fig. 1). Such responses were maintained essentially unchanged for 60 min or more. At higher rates of insufflation of gas into the rumen in preparations in which there was a regular series of reticulum and backward-moving waves of rumen contraction there were occasionally two or more forward-moving waves of rumen contraction with a corresponding number of eructations between each reticulum and associated rumen contraction (Fig. 1).

In some preparations reticulum contractions and backward-moving waves of rumen contraction were absent or infrequent (Fig. 2). An increase in the rate of insufflation of gas into the rumen was followed by a faster rate of eructation and frequently by one or a number of reticulum and backward-moving waves of rumen contractions interpolated between the forward-moving waves of rumen contractions and eructations (Fig. 3).

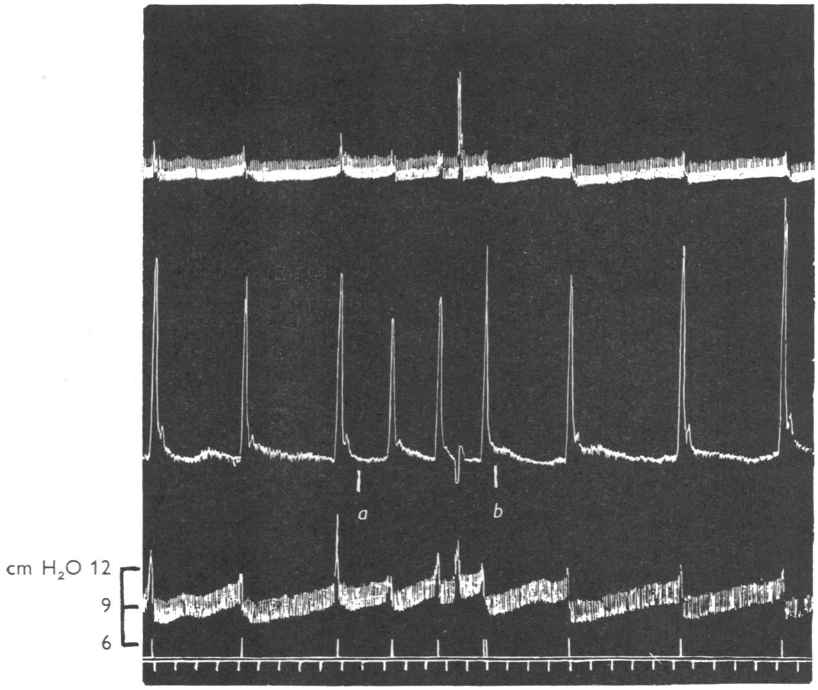

Fig. 3. Decerebrate sheep 14·5 kg. Effect of an increase in the rate of insufflation of CO_2 into the rumen. Before *a* the rate was 150 ml./min. It was increased to 250 ml./min at *a* and maintained at this rate until it was returned to 150 ml./min at *b*. The sequence of the records is as in Fig. 1. Signal indicates each eructation. 30 sec time-marker.

The form of both types of rumen contractions observed was similar to that seen in sheep in which exteriorizations of the rumen permitted an examination of the sequence of involvement of the different parts of the rumen (Reid, 1962; Titchen & Reid, 1965). Attempts (in decerebrate preparations) to observe directly and record from more than one site of the wall of the rumen have been successful on three occasions. An additional incision of the abdominal wall was required. In these preparations, forward-moving waves of contractions were observed to involve the more posterior before the more anterior regions of the dorsal rumen. The successive involvement of the regions of the dorsal sac by a forward-moving wave of contraction is shown in Fig. 4 in which about 0·3 sec separated the start of the contraction in the two sites, 11 cm apart, chosen for recording. In a number of other preparations, attempts to expose more than one region of the rumen for recording were associated with a failure to obtain any rumen contractions.

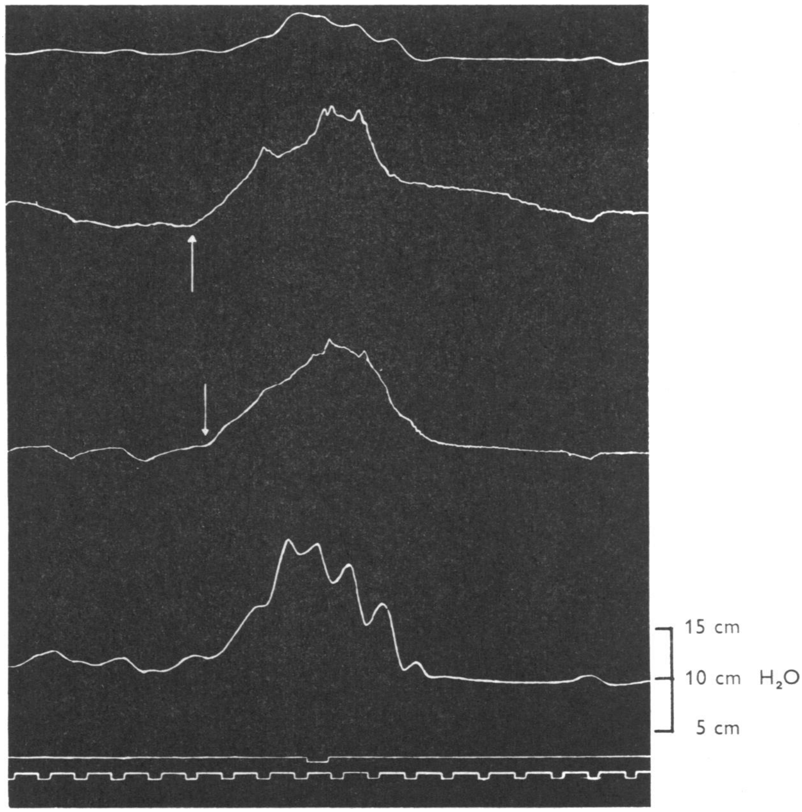

Fig. 4. Decerebrate sheep 24 kg. Successive involvement of two regions of the rumen during one of a series of 'forward-moving' rumen contractions. Records from above downwards: reticulum (balloon water manometer recording system), posterior dorsal sac of rumen, anterior dorsal rumen (both frontal writing lever records with pulley anterior to point of exposure of rumen), intrarumen gas pressure (cm H_2O) from water manometer connected to open-ended tube in gas cap in dorsal rumen, signal (indicates eructation observed in the neck) and time-marker 1 sec. The two points of the dorsal sac of the rumen were 11 cm apart. The start of the contraction (indicated by arrows) was separated by 0·3 sec in the posterior and anterior parts of the dorsal sac of the rumen.

In some preparations the intensity of the contractions was such as to permit observation of the rumen contractions through the intact abdominal wall. In these it could be seen that the forward-moving waves of contraction of the dorsal sac of the rumen were preceded by a strong contraction of the posterior ventral blind sac of the rumen. Backward-moving waves of rumen contraction were invariably associated with, and closely succeeded, a contraction of the reticulum. After the completion of the contraction of the dorsal sac of the rumen a contraction in the anterior regions of the ventral sac was observed through the abdominal wall. Rarely the posterior ventral blind sac also was seen to be involved in backward-moving waves of contraction of the rumen.

The reflex nature of the forward-moving waves of contraction of the rumen was indicated by the following observations. Forward-moving contractions were obtained after electrical stimulation of the central end of a vagus nerve cut in the neck. It was necessary to establish a background of excitability or to summate the electrical stimulation of afferent fibres in the vagus nerve with a moderate degree of gaseous distension of the rumen to obtain such responses to afferent nerve stimulation. In preparations in which no contractions had been observed in the 30 min previous to stimulation the first contraction usually occurred only after the application of two periods of stimulation separated by an interval of

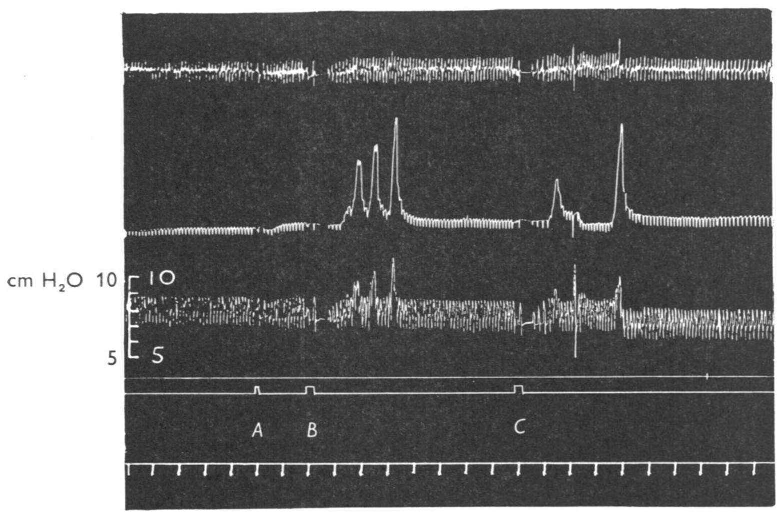

Fig. 5. Decerebrate sheep, 12 kg. Forward-moving contractions of the mid-dorsal sac of the rumen evoked by electrical stimulation of the central end of the left vagus nerve in the neck. Records from above downwards: movements of reticulum, mid-dorsal rumen, intrarumen gas pressure, eructation signal, stimulus signal, 30 sec time-marker. *A* marks stimulation of central end of vagus at 20/sec, 10 V for 5 sec; *B* and *C* stimulation at 20/sec, 10 V for 10 sec. Neon tube stimulator.

60–120 sec. The duration of each period of stimulation was usually 15 sec or less. More prolonged stimulation was followed by gross respiratory movements which obscured the recordings of rumen contractions. Thirty to sixty seconds elapsed between the application of the second period of stimulation and the first contraction of the rumen. Between two and ten contractions of the rumen usually followed stimulation of the central end of the vagus (Fig. 5). Stimulation of the vagus nerve in an afferent sense

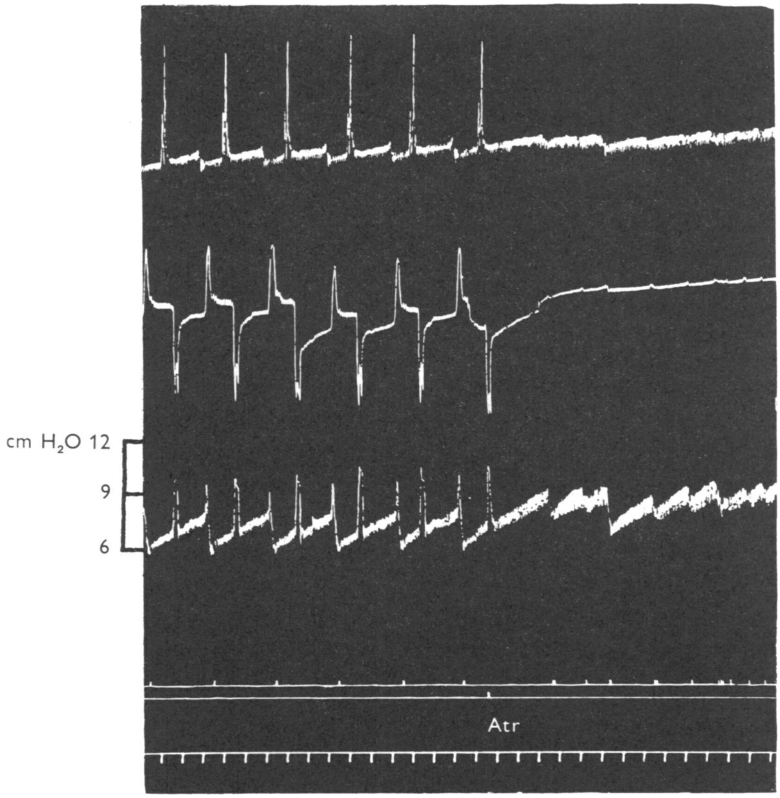

Fig. 6. Decerebrate sheep, 16·2 kg. Atropine (0·1 mg/kg) injected intravenously (at Atr) indicated by signal, resulted in cessation of reticulum and mid-dorsal rumen contractions, but not of eructation. CO_2 insufflated at a rate of 150 ml./min throughout trace. Sequence of records as in Fig. 1. 30 sec time trace.

never proved effective with intraruminal gas pressures of less than 2 cm H_2O. This form of response to stimulation of the vagus in an afferent sense was abolished by cutting the other vagus nerve or by administering atropine (0·1–0·2 mg/kg intravenously).

Similarly, the response of the rumen to its gaseous distension ceased when both vagus nerves were cut in the neck, or after the intravenous injection of atropine (Fig. 6).

Stimulation of the vagus nerve in an efferent sense produced forward-moving waves or backward-moving waves of rumen contraction according to the frequency of the stimulation. In both decerebrate preparations and in sheep under chloralose anaesthesia stimulation at frequencies up to 6/sec of the peripheral end of a vagus nerve cut in the neck caused forward-moving waves of rumen contractions. At frequencies of stimulation of or above 20/sec strong reticulum contractions and backward-moving waves of rumen contraction were produced. At intermediate frequencies the response of the rumen was variable. Strong cardio-inhibitory effects were

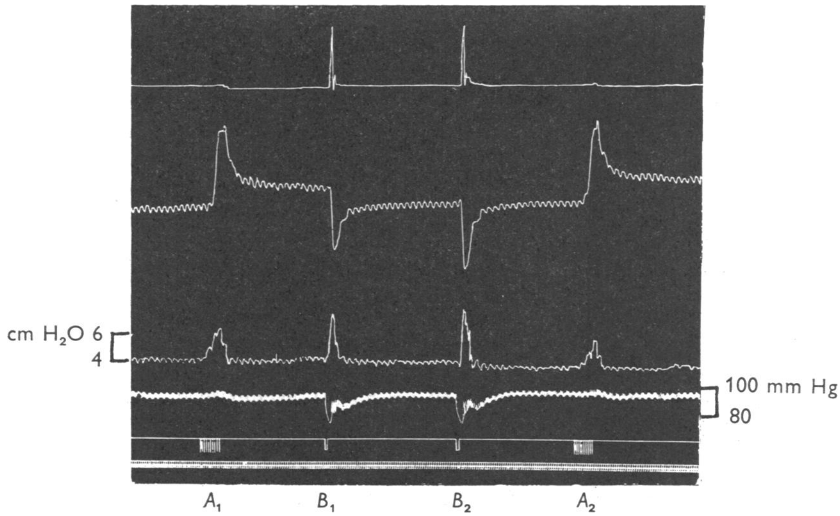

Fig. 7. Decerebrate sheep 14·5 kg. Forward-moving and backward-moving contractions of the rumen produced by stimulation of the peripheral end of the left vagus nerve cut in the neck. Records from above downwards: reticulum, mid-dorsal rumen, intrarumen gas pressure, carotid arterial blood pressure, signal and 1 sec time-marker. Signal indicates, at A_1 and A_2, 10 shocks delivered at rate of 1/sec, 6 V; at B_1 and B_2 stimulation at 20/sec 6 V. Reticulum contractions, marked bradycardia and backward-moving rumen contractions obtained with higher frequencies of stimulation., Forward-moving rumen contractions with but little effect on the reticulum or on heart rate were obtained with slower frequencies of stimulation. Time: 1 sec.

observed with the higher frequencies of stimulation; the cardio-inhibitory and reticulum responses to low frequency stimulation were weak, if at all detectable. The two different types of responses are shown in Fig. 7. Both types of response appeared equally sensitive to atropine and to hexamethonium salts, injected intravenously.

Inhibition

In previous experiments on decerebrate preparations in which the reflex stimulation of reticulum contractions and backward-moving waves of rumen contractions was examined, inhibition proved a considerable experimental difficulty. This was also the case in the present experiments: it limited the amount of experimental analysis possible. Insufflation of gases into the rumen at rates in excess of 300 ml./min tended to become inhibitory. Inhibition was manifest first as a decrease in the force of forward-moving waves of rumen contractions which were usually at the same time increased in frequency. This response was seen at intrarumen gas pressures of 12 cm H_2O or more. Judged from the distension of the oesophagus in the neck there was a greater volume of gas removed from the rumen in each eructation as well as an increased frequency of eructation. At such pressures there was also commonly an increase in the frequency of reticulum contractions or, if reticulum contractions had not previously been present, their first appearance. Backward-moving contraction waves of the rumen were associated with the reticulum contractions.

At higher intrarumen gas pressures (14 cm H_2O or more) a progressive reduction in the force of both reticulum and rumen contractions occurred. Initially, as the intrarumen gas pressure rose to these levels eructation became associated with reticulum, as well as with forward-moving waves of rumen contractions. As the pressure increased the contractions of the abdominal muscles associated with eructation became stronger and finally became the only contractions of abdominal structures associated with eructation. Movements of the reticulum and rumen disappeared completely.

In preparations in which more extensive dissection had been undertaken it was frequently observed that the intrarumen gas pressure at which eructation first occurred was 14 cm H_2O or more. In such preparations rumen contractions did not occur and only an evanescent series of reticulum contractions was seen.

Distension of the reticulum during a period of insufflation of gas into the rumen had different effects on the two types of rumen contractions. Backward-moving rumen contractions frequently first appeared after distension of the reticulum. Forward-moving contractions of the rumen were inhibited by this stimulus; their force was reduced or they disappeared. Eructation occurred at a higher threshold measured in terms of intrarumen gas pressure.

In the experiment in which the record shown as Fig. 8 was obtained backward-moving rumen contractions were not observed until after distension of the reticulum. The forward-moving rumen contractions stimulated by gaseous distension of the rumen regularly occurred in two different phases before distension of the reticulum. Eructation was associated with the larger of the rumen contractions. During distension of the reticulum there were no clear differences in the height of the forward-moving rumen contractions; each rumen contraction became more prolonged. Eructation occurred with each forward-moving rumen contraction.

The effect of distension of the reticulum was apparent not only during the actual period of distension but also as an after-effect. Thus in Fig. 8 although both reticulum and backward-moving rumen contractions disappeared on reduction of the volume of the fluid in the reticulum balloon there was a gradual return of more forceful forward-moving rumen contraction, which in addition increased in complexity and had clearly

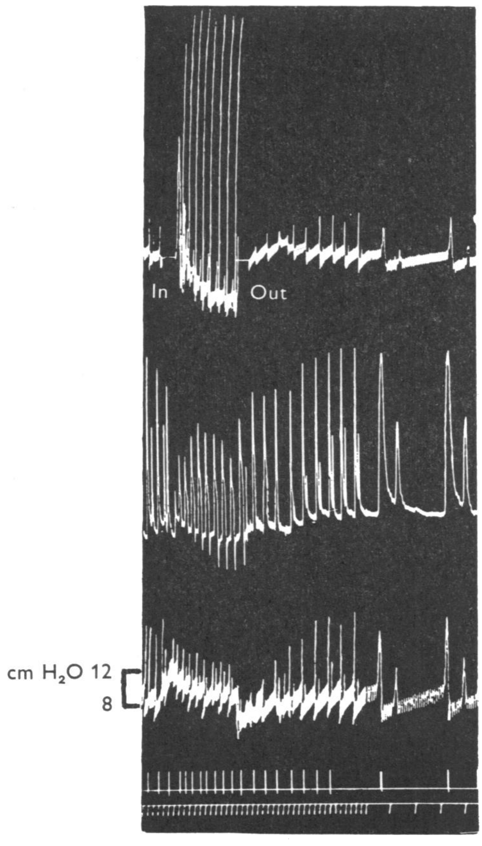

Fig. 8. Decerebrate sheep 13·5 kg. Records as in Fig. 1. Effect of distension of reticulum on movements of mid-dorsal sac of rumen. Gas (CH_4 : CO_2, 40:60) insufflated into rumen at 150 ml./min throughout, Interruption of reticulum trace at in indicates increase from 5 to 250 ml. of volume of water in reticulum balloon; interruption at out indicates return of volume in reticulum balloon to 5 ml. The fast section of the trace is included to show that (i) at the lesser degrees of distension of the balloon in the reticulum, the reticulum record reflected passively rumen contractions, and (ii) the diphasic character of the forward-moving rumen contractions. Time: 30 sec.

become diphasic 300 sec after the stimulus of reticulum distension had been withdrawn.

In the most extreme form of this inhibition there was a complete absence of forward-moving waves of rumen contraction. If eructation occurred it was only when the intrarumen gas pressure approached 20 cm H_2O. At such high intrarumen gas pressures there was a profound fall in blood pressure and generalized convulsive movements of the preparations. On the introduction of a tube into the oesophagus considerable resistance to its passage was encountered in the lowest thoracic regions. Dissection (both *pre* and *post mortem*) revealed that the reticulum balloon, although grossly distended, did not impinge on the cardia. Under these circumstances the administration of D-tubocurarine (0·1–0·2 mg/kg) led to a rapid and progressive deflation of the rumen.

Changes in conditions in the abomasum were examined. Attempts were made to study the effects of changes of the abomasal contents and of abomasal distension on the responses described. Repeatable responses to insufflation of gas into the rumen were not obtained in those preparations in which the abomasum was cannulated and isolated by ligatures tied at the omaso-abomasal and pyloric junctions. Thus no evidence was obtained of the effect of changes in the pH of abomasal contents on forward-moving waves of rumen contraction. Attempts to examine the effects of distension of the abomasum without its isolation gave equivocal results. In some experiments there was an increase in the frequency of eructation and of forward-moving rumen contractions. These changes were simultaneous with an increase in intrarumen gas pressure which appeared to be due to increased intra-abdominal pressure consequent on distension of the abomasum. Accompanying this increased frequency of eructation and forward-moving waves of rumen contraction, there was a reduction in the force of reticulum contractions. Attempts to define the effects of abomasal distension as mediated or not by afferent nerve fibres from the abomasum failed. In all experiments in which denervation of the abomasum or section of the splanchnic nerves was attempted, the dissection and manipulation involved appeared to inhibit completely the responses of the rumen to its distension as no contractions were obtained.

Transection of the spinal cord in its upper thoracic regions frequently led to the first appearance of rumen and reticulum contractions in preparations in which these had not been present previously, despite the application of a variety of appropriate stimuli. Transection of the spinal cord did not facilitate experimental analysis since the life of preparations in which it had been undertaken rarely exceeded 30 min. After this time circulatory collapse occurred associated with a gross pulmonary vascular congestion.

DISCUSSION

The experiments described above indicate that gaseous distension of the rumen serves as a potent reflex stimulus to forward-moving waves of rumen contraction. The efferent limb of the reflex arc appears to consist of cholinergic fibres in the vagus nerve, since the contractions are abolished by the administration of atropine, and by cutting the vagus nerves. These conclusions are supported by the observations that similar contractions of the dorsal sac of the rumen could be produced by stimulation in an efferent sense of the vagus nerve at low frequencies and that such responses were also abolished by atropine. The afferent limb of the reflex arc appears to consist of afferent fibres also contained in the vagus nerves. Thus it proved possible to evoke forward-moving contractions of the rumen by stimulation in an afferent sense of one vagus nerve cut in the neck provided that the other vagus nerve remained intact. Since the responses could be obtained in decerebrate preparations in which the spinal cord had been cut it is concluded that these responses of the rumen are medullary reflexes dependent on the integrity of both afferent and efferent fibres in the vagus nerves.

The differences in the form of rumen contractions obtained with stimulation of the vagus nerves in an efferent sense at low or higher frequencies may suggest that separate layers of the rumen muscle are differentially activated according to the frequency of vagus nerve stimulation. This must remain speculative in the absence of supporting evidence. There is no evidence that the different frequencies of stimulation adopted in these experiments bear any relation to what happens in conscious animals. It might have been expected that some such indication would have been provided in the experiments in conscious sheep in which Dussardier (1960) used diaphragmatic muscle action potentials as an index of efferent vagus nerve discharges after regeneration had occurred in vagus-phrenic nerve anastomoses. However, the appropriate nerve fibres may not have been involved in the anastomoses in Dussardier's experiments. This problem might be resolved by a direct examination of the activity in efferent vagus nerve fibres during rumen contractions with the use of electrophysiological techniques.

The observations on inhibition are of less value in these experiments than in previous ones in which more experimental analysis of the afferent pathways involved was possible (Titchen, 1958*b*, 1960). The marked reduction in inhibitory effects which resulted on cutting the spinal cord could be attributed not only to interruption of spinal afferent pathways but also to a loss of an inhibitory sympathetic discharge. Duncan (1953) observed no difference in the activity of the reticulum and rumen after chronic section of the splanchnic nerves. If there were a tonic inhibitory effect it might have been expected to be manifest as an increase in motility. However, at least in the case of the reticulum, section of the splanchnic nerves would not result in a sympathetic denervation: Comline & Titchen (1951*b*) found that sympathetic motor effects could be obtained with stimulation of the right thoracic sympathetic nerve trunk but not necessarily with stimulation of the right splanchnic nerve.

Dougherty, Habel & Bond (1958) did not appear to meet the same difficulty with inhibition encountered in the present experiments. In the decerebrate preparations employed in the present experiments the brain stem was transected at an intercollicular level and all of the nervous system anterior to transection removed, as previously described by Comline & Titchen (1951*a*) and Titchen (1958*b*, 1960). Dougherty *et al.* (1958) were largely concerned with the oesophageal responses to gaseous distension of the rumen. There is no evidence offered by them of having observed or recorded movements of the stomach or of having undertaken any of the discrete interferences such as distension of the reticulum or changes in the abomasum comparable to those employed in the present experiments.

In some decerebrate preparations contractions of the posterior ventral blind sac of the rumen were clearly seen to precede the forward-moving waves of contraction of its dorsal sac which were in turn followed by contractions of the main ventral rumen sac. This sequence of contraction is similar to one observed repeatedly in conscious animals (Reid, 1962) in which partial exteriorizations (Reid, 1960) permitted direct identification of the direction of rumen contractions. Weiss (1953) had contended that those contractions of the rumen associated with eructation moved anteriorly over the rumen from its more caudal parts. Benzie & Phillipson (1957) found that during 'extra' contractions of the rumen (Phillipson, 1939) there might be a translocation forwards of gas from more posterior regions towards the anterior regions of the rumen and the reticulum. This may provide an indication of the direction of contraction of the rumen. In experiments in decerebrate preparation described in this paper, the recording system adopted permitted a differentiation of the two forms of movements of the rumen.

It has proved possible in the experiments described to stimulate in decerebrate preparations two types of rumen movements which exhibit the same relation to reticulum contractions as do rumen contractions observed in conscious sheep and also to provide some evidence as to the stimuli which may produce such movements. These experiments taken together with those reported previously (Titchen, 1958*b*, 1960) indicate the reflex nature of contractions of the reticulum and rumen in intact conscious sheep. They strengthen the contention (Comline & Titchen, 1961) that these movements are influenced by conditions within the stomach itself.

SUMMARY

1. Two distinct types of rumen contractions have been obtained as reflex responses in decerebrate preparations of sheep.

2. One of these spreads over the dorsal sac of the rumen as a backward-moving contraction.

3. The other type of rumen contraction spreads over the dorsal sac of the rumen as a forward-moving contraction.

4. Eructation is most commonly associated with the forward-moving contractions in decerebrate sheep.

5. The stimulus used to elicit and maintain a series of forward-moving contractions was gaseous distension of the dorsal sac of the rumen.

6. The threshold stimulus for the initiation of forward-moving rumen contractions varied. It was not less than 4 cm H_2O intrarumen gas pressure.

7. Forward-moving contractions were obtained by electrical stimulation in an afferent sense of one vagus nerve cut in the neck, provided that the other vagus nerve remained intact.

8. Both types of rumen contraction were annulled by atropine and ceased after both vagus nerves had been cut.

9. Both forward-moving and backward-moving rumen contractions were produced by electrical stimulation of efferent fibres in the vagus nerves. The form of the rumen contraction obtained with stimulation of the vagus nerves varied according to the frequency of stimulation.

10. Inhibition of forward-moving rumen contractions by reticulum distension was demonstrated.

11. Experimental interferences with the abomasum inhibited both forward and backward-moving rumen contractions. The effect was more pronounced on the forward-moving contractions of the rumen than on backward-moving contractions.

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