J. Physiol. (1969), **202**, *pp.* 585–609
With 10 *text-figures*
Printed in Great Britain

RETICULO-RUMINAL MECHANORECEPTORS IN SHEEP

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(*Received* 4 *December* 1968)

SUMMARY

1. The nervous activity in single afferent gastric vagal units was recorded electrophysiologically from halothane-anaesthetized sheep with spontaneous reticulo-ruminal movements present.

2. Sixty-six afferent units innervating gastric mechanoreceptors were isolated from fifteen sheep. The receptors were located mainly in the medial walls of the reticulum and the cranial sac of the dorsal rumen, and also in the reticular groove, the reticulo-ruminal fold, the dorsal and ventral sacs of the rumen and the omasal canal.

3. The mean conduction velocity (C.V.) for twenty-seven units was $12{\cdot}4 \pm 1{\cdot}0$ m/sec (S.E.). For units with a pathway in the dorsal vagal trunk, the mean C.V. was $14{\cdot}5 \pm 1{\cdot}0$ m/sec (S.E.) and for units with a pathway in the ventral vagal trunk the mean C.V. was $6{\cdot}6 \pm 0{\cdot}5$ m/sec (S.E.).

4. From the receptors a slowly adapting response was elicited by tangential lengthening. These were tension receptors *in series* with contractile elements, as they were excited by increased tensions developed both passively by inflation of the viscus and actively by muscular contractions.

5. Receptors in the reticulum and the rumen appeared to be situated deep in the muscle layers, whereas those in the reticular groove structures seemed to be more superficial and gave the *in series* tension receptor response as well as a response to light pressure.

6. A resting discharge in tension receptor units was usually absent at low levels of distension but appeared and increased as the level of distension was raised. Intermittency and fluctuations in the resting discharge were related to intrinsic local movement involving the receptive fields. Increasing distension enhanced the intrinsic movements.

7. Even after the removal of the abomasum, reticular and ruminal (primary cycle) movements were evoked by distending the reticulum. It is possible that this manoeuvre enhanced intrinsic movements, which, in turn, caused an increased excitatory afferent input to the 'gastric centres' from *in series* reticular tension receptors.

8. The enhanced afferent discharge from reticular tension receptors elicited by an isometrically recorded reticular contraction reflexly inhibited the subsequent (primary cycle) contraction of the rumen.

9. Very few receptors were located in the caudal regions of the rumen whereas the cranial sac is richly supplied with tension receptors. The idea that the cranial sac may serve as the reflexogenic zone for secondary cycle movements of the rumen is discussed.

INTRODUCTION

Mechanical stimulation of the reticulo-ruminal mucosa reflexly affects gastric movement, salivary secretion, rumination and eructation (Wester, 1926; Weiss, 1953; Iggo, 1955; Titchen, 1958; Ash & Kay, 1959; Stevens & Sellers, 1959). Reticular distension, particularly, provides a potent afferent drive to the gastric centres and reflexly evokes reticulo-ruminal movements (Iggo, 1956; Titchen, 1958; Dussardier, 1960; Iggo & Leek, 1967*a*, *b*). The objects of the present experiments were to determine (*a*) the locations, (*b*) the types, (*c*) the afferent activities and (*d*) the physiological properties of mechanoreceptors in the reticulo-rumen of sheep. Using electrophysiological techniques similar to those described by Iggo (1954, 1956), the activity in single afferent gastric vagal units was recorded, as far as possible, when spontaneous gastric movements were present. This investigation is an extension of Iggo's earlier work and has been published briefly by Leek (1966, 1967*a*) and more fully by Leek (1967*b*).

METHODS

Experimental animals. Fifteen adult Scotch Blackface sheep were used. They were 8–24 months old, weighed 25–40 kg and were held indoors for at least a fortnight before use, during which time they received 200 g oats/day and hay *ad lib.*

Surgical procedures. Anaesthesia was induced with a 4% halothane B.P./oxygen mixture by a semi-closed method, employing a facemask. It was maintained, after endotracheal intubation, with a controlled mixture of halothane and oxygen administered by a circle-type closed-circuit method incorporating a Harvard 'variable phase large animal respirator' (Model 613). The level of anaesthesia was comparatively deep, so that swallowing and reflex limb movements did not interfere with the electrical recordings.

Both horns were sawn off. An intravenous cannula was inserted into the left lateral tarsal vein. A large rubber balloon was inserted into the reticulum through its ventral pole, by way of a median laparotomy. The sheep was then transferred to an experimental table and laid on its right side on an electric blanket, thermostatically controlled to maintain a rectal temperature of 38° C. Further surgery was delayed until reticulo-ruminal movements were recorded. If spontaneous movements were absent, it was usually possible to evoke them by distending the reticular balloon with 200–600 ml. air (Iggo & Leek, 1967*a*).

The left cervical vagus was exposed by incising the skin for 15 cm along the jugular groove and excising the left sternocephalic muscle. The edges of the skin wound were sutured to a horizontal ring of solder to form a pool for liquid paraffin B.P. A silver earth electrode was

embedded in the longus colli muscle. About 1·5 cm of vagus was freed from underlying connective tissue and a rigidly held black Perspex dissecting plate was placed beneath this region. A pair of Ag/AgCl stimulating electrodes was inserted beneath the nerve (peripheral to the recording site) for the purpose of measuring conduction velocity.

Later, during the course of the experiment, further surgery was required in order to manipulate the surfaces of the reticulum and the rumen for the location of receptors. A hand was inserted either through a dorsal sac rumenotomy wound or transthoracically. For the latter, ribs 7 to 9 and the left lung were removed. By incising the diaphragm the serosal surface of the left (lateral) wall of the reticulum could be observed directly or palpated and, by incising it, access to mucosal surface was gained. Removal of the left lung also facilitated, first, the recognition of gastric afferent discharges in fine strands as a result of largely abolishing afferent pulmonary discharges on the left side and, secondly, the application of stimulating electrodes to the dorsal and ventral thoracic vagal trunks.

In four sheep the abomasum was removed almost completely after ligating the fundus close to the omaso-abomasal opening and the duodenum about 5 cm distal to the pyloric sphincter.

Recording techniques. Fine strands were dissected from the left cervical vagus and placed across a pair of fine Ag/AgCl wire recording electrodes carried on a micromanipulator. The vagus and the fine strands were at all times immersed in a pool of liquid paraffin. The action potentials ('spikes') were amplified, displayed on a dual beam oscilloscope and recorded photographically on moving bromide paper.

Movements of the reticulum and rumen were recorded manometrically, using a strain-gauge manometer. Reticular contractions were recorded with either the isotonic or the isometric system described by Iggo & Leek (1967*b*) and were displayed on the oscilloscope simultaneously with those of the nervous discharge and also on heat-sensitive paper, using a Devices 8 channel pen-recorder. Inspiratory movements caused small pressure rises in the reticular balloon.

RESULTS

Sixty-six afferent units were isolated from fifteen sheep. From forty-one units the activity was recorded under conditions when spontaneous reticulo-ruminal movements were present. The sites of the receptors were located for thirteen of the forty-one units and the conduction velocities were measured for four of these units. The afferent activity in a further twenty-five units was examined in sheep with no spontaneous reticulo-ruminal movements, principally to determine the location of their receptors, the conduction velocity of the afferent fibres and, for eleven units, the thoracic vagal branch in which the fibres were to be found. Due to the inhibitory effect upon gastric movements caused by surgical procedures and the manipulating of wound edges and viscera (Iggo & Leek, 1967*a*), the manoeuvres necessary for locating receptors often resulted in the abolition of spontaneous movements.

The location of receptors

The locations of the forestomach mechanoreceptors responsible for the discharge in thirty-eight single afferent units were determined by manual exploration of the mucosal surface of the reticulo-rumen. Access to the

interior of the reticulo-rumen was gained through fistulae made either in the dorsal ruminal sac, using a sublumbar approach, or in the reticulum, using a transthoracic approach. It was usually necessary to remove some of the rumen contents and to deflate partially or completely the reticular balloon, if present. The mucosal surface of the forestomach was stimulated mechanically by gentle stroking with a glass rod, by pinching, by pressing

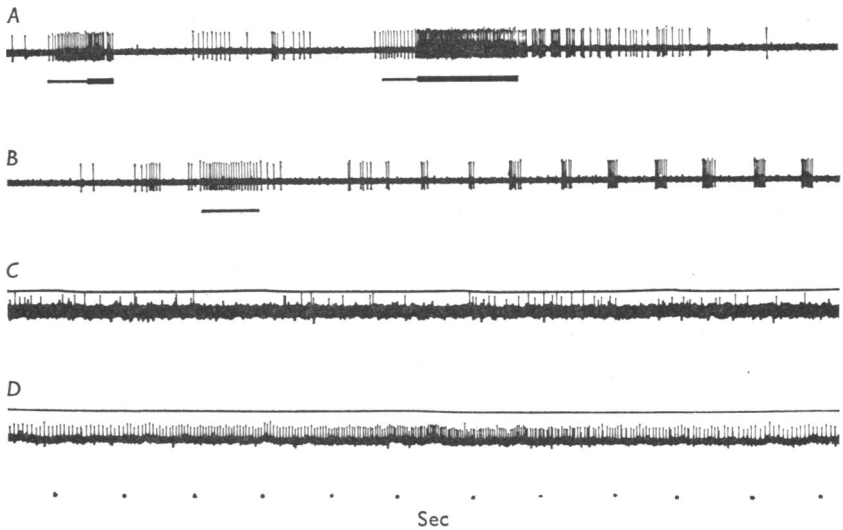

Fig. 1. The effect upon the afferent discharge, recorded from gastric units innervating 'in series' tension receptors in the reticulum, of manipulating the receptive field *per manus*.

A and *B* were recorded from the same unit. The receptors were stimulated by splaying open two fingers applied to the reticular wall containing the receptive field, thereby lengthening the reticular wall. The period of stimulation is indicated by the bars beneath the tracings; the narrow part representing a period of slight splay and the thick part representing a wide splay. Between the two periods of stimulation in *A*, a burst of spikes appeared spontaneously and was associated with a local contraction of the reticular wall, which was discernible as a 'ripple' beneath the finger tips. After the stimulation in *B*, spontaneous bursts of activity were present.

C and *D* were recorded from the same unit under conditions when cyclical reticulo-ruminal movements were present and the reticular balloon contained the same volume of air and was at the same pressure. Between *C* and *D*, the balloon was temporarily deflated and the reticulum manipulated, to locate the receptive field innervated by this afferent unit. Although recording conditions were returned to their former state before *D*, the 'resting discharge' was much greater than in *C*.

with one finger, by pulling on strips of mucosa and by stretching the wall by opening two fingers applied to adjacent areas of the wall. In this way the location of mechanoreceptor sites and their distribution were found (Table 1 and Fig. 2), and the afferent discharges elicited by manipulation are illustrated in Fig. 1*A*, *B*).

The majority of receptors (fifteen units) were found in the walls of the reticulum, predominantly in the medial wall adjacent to the lips of the reticular groove. Few receptor sites were found in the caudal wall and even fewer in the cranial wall. No receptors were located to the lateral (left) wall of the reticulum in these experiments. In only one of the forty-one units was it possible to elicit an afferent discharge when the mucosa was gently stroked. The receptive field of this unit was located in the cranial

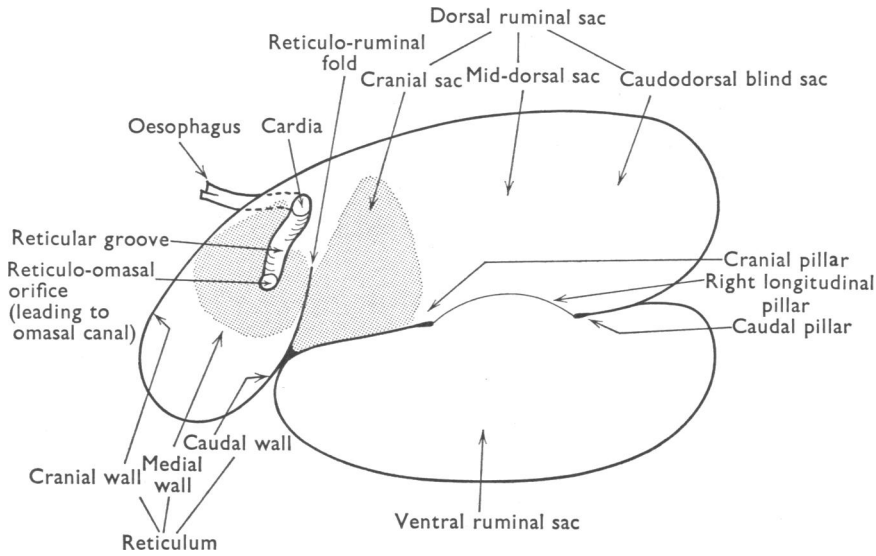

Fig. 2. A sagittal section through the reticulo-rumen of a sheep (diagrammatic) to show the region where mechanoreceptors were located (see text and Table 1 for details). The greatest densities of these receptors were found in the medial wall of the reticulum and of the cranial sac (shown as stippled areas).

TABLE 1. The locations of receptors innervated by thirty-eight gastric afferent vagal units and the conduction velocities (c.v.) of twenty-seven of these units. These locations are shown in Fig. 2

Site	No. of units	c.v. (m/sec)	Mean c.v. (m/sec)
Reticulum — cranial wall	2		
Reticulum — medial wall	8	15	11
Reticulum — caudal wall	5		
		6, 8	
		5, 7, 8, 10, 11	
		14, 21, 24	
Cardia	1	19	19
Omasal canal	1	*7*	7
Reticular groove	4	*5,* 15	10
Reticulo-ruminal fold	4	12, 16	14
Cranial ruminal sac	9	9, 10, 11, 11, 13, 16, 10	11
Caudodorsal blind sac (dorsal wall)	1	15	15
Mid-dorsal ruminal sac (medial wall)	1	16	16
Right longitudinal pillar	1	23	23
Ventral ruminal sac (cranial surface)	1	11	11
	Total = 38	Over-all mean = 12·4	

wall of the reticulum: stretching the wall also caused a short burst of afferent impulses but a sustained discharge could not be produced. In the remaining fourteen reticular units there was no response to pinching or gentle pressing. Harder pressing, pulling on the mucosa or stretching (in the manner described above) caused a sustained discharge. The frequency of the discharge increased as the stretch increased. It was established that the receptive field for one of the units was in the cranial wall of the reticulum, which had been exposed by the transthoracic approach. While the afferent discharge in this unit was being recorded, the receptive area was compressed between the finger (on the mucosal surface) and the thumb (on the peritoneal surface). No discharge was evoked by even moderate transmural compression, although a discharge was readily elicited by slight tangential stretch of the same region. Similarly, with 600–100 ml. air in the reticular balloon, it was not possible to evoke afferent discharges (in any of the several units tested) by exploring the peritoneal surface of the reticulum manually and pressing on the outer side of the receptor area.

Six units had receptive fields in or near the reticular groove. One of these was situated very close to the cardiac sphincter, another in the floor of the omasal canal, about 1 cm distal to the reticulo-omasal orifice, and two others in the floor of the reticular groove. All of these units gave a high-frequency sustained discharge when the site was pressed upon with a finger. The remaining two units had receptive fields located in the cranial and caudal lips of the reticular groove respectively. An afferent discharge appeared in these two units when the lips were stretched, and more particularly when they were pressed and pinched. By their response to pressing and pinching, the receptors around the reticular groove clearly differed from those in the reticulum.

Four units with receptors situated in the reticulo-ruminal fold were isolated. A high-frequency (up to 100 spikes/sec), sustained, regular afferent discharge was produced by stretching the fold, the frequency being directly related to the degree of stretch. The discharge in these units was not evoked by lightly pressing or stroking the fold, nor by compressing the fold between the finger and thumb. When a forceful stretch was maintained for several seconds, it often caused a local contraction of the fold, which could readily be felt beneath the fingers and which gave rise to a short burst of afferent activity with an even higher discharge frequency than that which could be evoked by stretch alone.

Thirteen units had receptors in the rumen and nine of these were in the cranial sac (dorsal rumen). Seven of the nine cranial sac units had receptors located in the medial wall, one in the ventral wall and one in the dorsal wall. Stretching, but not pinching or stroking, stimulated the receptors and caused a sustained discharge in the afferent unit. Usually the discharge

was not regular, however, because the stretch stimulus induced local contractions of the muscle in the area being stretched. As in the case of the reticulo-ruminal fold described above, these contractions were easily detected by the fingers and caused an extra burst of afferent impulses. After a series of these local contractions ('ripples') the afferent discharge sometimes diminished or ceased even though the stretch was maintained. During the preliminary exploration of the mucosal surface and before the actual receptive field was located and stretched, the resting discharge often increased in frequency. Moreover, after a series of applied 'stretches' the resting discharge often took the form of frequent bursts of activity, each of which was associated with a local contraction of that region. Once this pattern of resting discharge became established, it usually lasted for at least 5–10 min (Fig. 1).

Only four single units were isolated from other parts of the rumen (Table 1). In two experiments a deliberate attempt was made to isolate only ruminal afferent units and, during the process, afferent activity in multiunit strands was frequently detected when stretch was applied to the reticulum, reticular groove and cranial sac regions, whereas afferent activity arising from receptors in other parts of the rumen was observed very infrequently. Stretch was the effective stimulus for the four units which were eventually isolated. As for the cranial sac and the reticulo-ruminal fold, stretch evoked local contractions, which could be felt, and which enhanced the afferent discharge. In the case of the unit with receptors in the cranial wall of the ventral sac, the discharge during stretch was not sustained but fluctuated in time with these local contractions.

The paths and conduction velocities of gastric afferent fibres

For twenty-seven of the thirty-four units whose receptor sites were located, the conduction velocities were measured by the techniques of Paintal (1953, 1963) and Iggo (1958). Stimulating electrodes were placed either on the left cervical vagus (peripheral to the recording electrodes), on the left thoracic dorsal vagal branch or on the ventral thoracic vagal trunk. By stimulating the last two nerves, it was possible to decide whether a particular unit had its pathway in the dorsal or ventral vagal trunk. Excision of the left lung, besides largely abolishing respiratory afferent activity in the left vagus, facilitated access to the thoracic vagal branches, which were kept moist under a pool of warm liquid paraffin. If the nerve strand on the recording electrodes contained more than one live fibre, electrical stimulation evoked a compound action potential. The recognition of the contribution to the compound action potential by the gastric unit whose conduction velocity was being determined was based on the demonstration of a refractory period in the gastric unit. With the stimulating

electrodes close to the recording electrodes on the cervical vagus, the 'natural' spike was made to trigger the stimulator after an appropriate delay. When the delay was less than the refractory period, the evoked compound action potential was devoid of the spike component attributable to the gastric unit. Alternatively, the nerve could be stimulated repetitively and on occasions the gastric unit component would be absent from the evoked compound action potential, because, on these occasions, electrical stimulation would have occurred during the refractory period resulting from the natural spike. The latter method alone was used to identify gastric units when thoracic vagal branches were stimulated.

The path taken by eight of the afferent fibres was determined during the course of those conduction velocity measurements which involved stimulation of thoracic branches of the left vagus. The path of one other unit was determined by blocking nervous conduction, in turn, in the left dorsal and in the left ventral thoracic branches, by cooling with a thermode. This last unit had a receptive field on the medial wall of the reticulum about 2 cm caudal to and level with the reticulo-omasal orifice and the afferent discharge was abolished by cooling the left dorsal thoracic vagal branch. By the method of electrical stimulation, the dorsal vagal trunk was found to provide a path for afferent fibres with receptors in the medial wall of the reticulum (one unit) the caudal (right) lip of the reticular groove (one unit), the lateral region of the reticulo-ruminal fold (one unit), the floor of the omasal canal (one unit) and the medial wall of the cranial sac of the dorsal rumen (two units). The ventral vagal trunk contained afferent fibres innervating the medial wall of the reticulum (one unit) and the medial aspect of the reticulo-ruminal fold (one unit).

The mean value for conduction velocity in gastric vagal afferent fibres is $12{\cdot}4 \pm 1{\cdot}0$ m/sec (S.E. of mean) and the distribution of the conduction velocities is shown in Fig. 3. The individual values for conduction velocity are given in relation to the receptor sites in Table 1. These values have been arbitrarily divided into two groups according to whether the unit is known or is likely to have a pathway either in the dorsal or in the ventral vagal trunk, on the basis of the nerve distribution given by Habel (1956). In the case of units in which the path was not determined experimentally, it was presumed that units had a pathway either (*a*) in the *ventral* vagal trunk, if the receptors were located in the cranial and cranio-medial wall of the reticulum, the cranial lip and floor of the reticular groove and the floor of the omasum, or (*b*) in the *dorsal* vagal trunk, if the receptors were located in the cardia, caudal lip of the groove, caudal and caudo-medial wall of the reticulum, the reticulo-ruminal fold, cranial sac and other parts of the rumen (Fig. 3). On this basis, the mean conduction velocity for gastric afferent fibres with pathways in the ventral vagal trunk is $6{\cdot}6 \pm 0{\cdot}5$ m/sec

(S.E. of mean) and in the dorsal vagal trunk is $14{\cdot}5 \pm 1{\cdot}0$ m/sec. These values are statistically significant at the 0·1 % level ($P = < 0{\cdot}001$).

The nervous discharge in single gastric afferent units

The nervous discharge will be described as it occurs, first, during the quiescent part of the 'primary cycle' and, secondly, during the contractile or active phase of the cycle, recorded under isometric conditions.

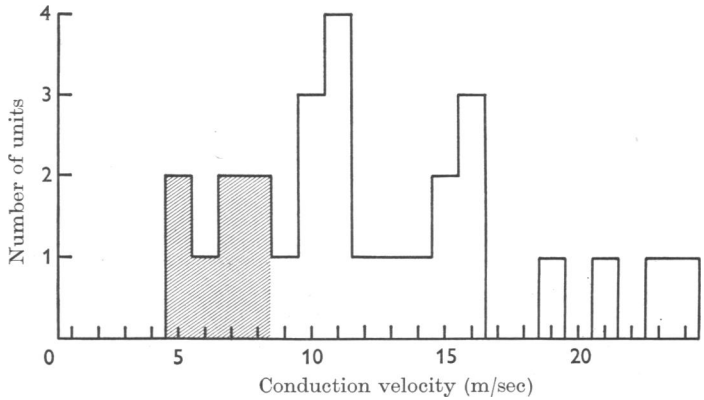

Fig. 3. The conduction velocities of twenty-seven gastric afferent units.

The over-all mean is $12{\cdot}4 \pm 1{\cdot}0$ m/sec (S.E. of mean). The mean for units either known or presumed to have pathways in the ventral thoracic vagal trunk (hatched area on histogram) is $6{\cdot}6 \pm 0{\cdot}5$ m/sec, and in the dorsal vagal trunk (clear area on histogram) is $14{\cdot}5 \pm 1{\cdot}0$ m/sec (see text for details).

The locations of the receptors innervated by these units are given in Table 1.

The values in the hatched part of the histogram comprise those in italics in Table 1.

Forty-one units were examined with reticulo-ruminal movements present and only four of these had no discharge during the quiescent phase of the cycle. The remaining thirty-seven units had one of the following 'resting' discharge patterns when first observed:

(*a*) An occasional spike (seven units).

(*b*) Rhythmic bursts of spikes lasting 1–2 sec, recurring every 4 sec and related to inspiration (positive pressure ventilation). When the left lung was removed, as was the case in most experiments, the intrareticular pressure was scarcely affected by respiratory excursions and this type of resting afferent discharge was not seen. When both lungs were present, the resting discharge frequently had a respiratory rhythm superimposed on it (three units).

(*c*) Intermittent bursts of spikes with a non-respiratory rhythm. The bursts lasted 2–5 sec and recurred every 4–10 sec (Fig. 4*B*, *C*) (nineteen units).

(*d*) A sustained discharge with frequencies ranging from 1/sec to 28/sec (Fig. 4*D*, *E*) (eight units).

A particular afferent unit often possessed either one or more of the types of resting discharge outlined above, depending principally on the recording conditions. In general there was a gradation from either no discharge or an occasional spike to an intermittent discharge and then to a sustained, regular discharge as the reticular balloon was progressively distended

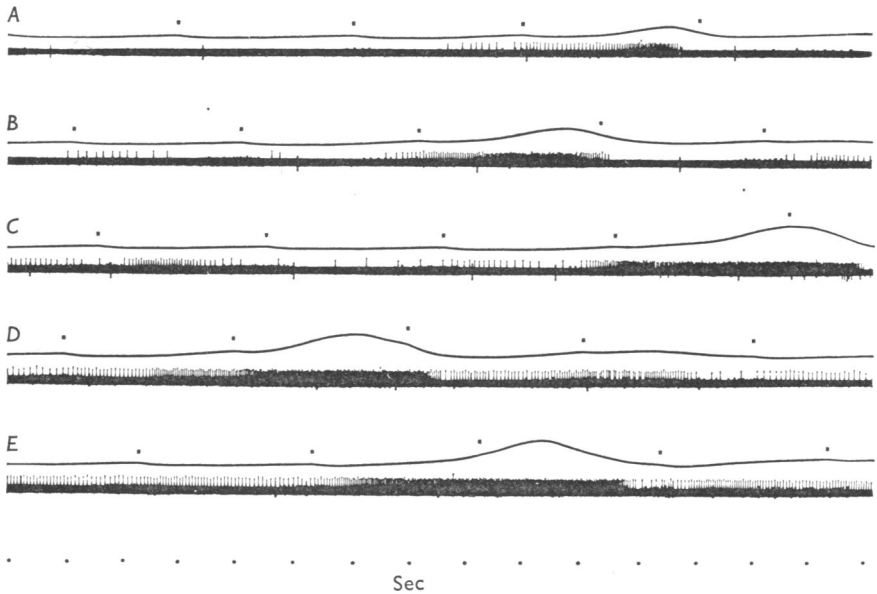

Fig. 4. The delayed effects upon the afferent discharges, recorded from a unit innervating reticular tension receptors, of increasing the volume of air in the reticular balloon.

In *A*, *B*, *C*, *D* and *E*, the reticular balloon contains 100, 200, 300, 400 and 600 ml. air respectively. All the records were obtained from the same unit. Each record was obtained not less than 5 min after adding more air.

In *A* there is negligible 'resting discharge': a doublet of spikes (not shown) occur approximately every 7 sec. The reticular contraction has a small amplitude and the afferent discharge is correspondingly of relatively low frequency. As the level of distension is increased the 'resting discharge' is also increased. At first, intermittent bursts of spikes appear which are unrelated to respiratory movements (*B*) and, upon further inflation, the interval between bursts is reduced and the peak discharge frequency reached during each burst is increased (*C*). Finally, the 'resting discharge' becomes continuous, although it fluctuates at a rhythm related to respiration (*D* and *E*).

At the higher levels of distension the durations and amplitudes of the reticular contractions are greater and, associated with these, the afferent discharges are enhanced. In *E*, the peak frequency is greater than 100 spikes/sec.

A small non-gastric 'contaminant' spike, which extends below the base line, is also present but should be disregarded.

The end of inspiration is marked with a dot.

(Fig. 4). In some units it was possible to relate the intermittent bursts which had a non-respiratory rhythm to local contractions, which were felt as 'ripples' during manual exploration. When the reticular balloon was suddenly emptied, the resting discharge was usually abolished for 1–10 min and thereafter reappeared but at a much lower frequency.

TABLE 2. The afferent discharge in twenty-eight 'reticular' units. The spike frequency represents the number of spikes occurring in 1 sec. Several values for the interval between the bursts of activity of the 'resting discharge' have been given to illustrate their variability. The right-hand column shows the interval between the main peak of the discharge and the reticular contraction (i.e. that of its second peak)

	Resting discharge			Contraction discharge				
	Spike frequencies (sec^{-1})		Interval between bursts	Spike frequencies (sec^{-1})				
Unit and site	Min	Max	(sec)	1st phase	2nd phase	3rd phase	Duration (sec)	Peak to peak
1 ret-cd	5	5	reg	17	45	28	12	−0·2
2	2	2	reg	11	11	7	9	1·0
3 ret-cd/md	0	5	1, 3	12	19	5	12	−0·2
4	9	10	reg.	24	36	0	5	0
5	6	11	4, 6	17	60	0	6	0·5
6	0	0	—	47	40	0	—	2·5
7 (100 ml.)	0	2	4, 6	2	42	—	3	0·5
8 (300 ml.)	16	28	3, 6	51	> 100	38	14	−0·2
9	0	8	13	8	18	0	4	0·5
10	0	21	3	54	> 70	0	7	0·3
11	0	20	5, 7	26	44	20	10	0·3
12 ret-cd	0	1	reg	18	12	0	5	3·0
13 groove-cr	11	35	4, 6	35	50	28	10	0·5
14 groove-cd	1	7	2, 4	14	27	0	4	0·1
15	0	8	5	10	11	0	4	0·4
16 ret-cr/md	0	10	2, 4	17	28	16	9	0·4
17	3	6	3 (resp)	12	22	22	11	−0·2
18	0	1	10	0	16	8	6	0·8
19 ret-cr/md	1	2	reg	6	8	4	9	0·7
20	0	6	4, 6	36	45	12	10	−0·3
21	0	3	3	0	8	0	4	0·2
22	0	4	4 (resp)	9	16	6	10	0·7
23	0	7	6, 8	0	11	8	13	0·4
24	0	4	6	4	11	4	12	−0·3
25 ret-cd/md	0	20	3, 8	33	53	0	9	0·0
26	0	9	3, 6	7	19	0	7	0·0
27 ret-cr/md	0	37	10, 20	0	58	0	8	−0·7
28 groove floor	0	10	3, 6	25	40	0	6	−0·2
Mean ± S.E.	1·9 ± 0·8	10·4 ± 1·9	5·7 ± 0·6	17·7 ± 3·0	33·2 ± 4·1	7·4 ± 2·0	8·1 ± 0·6	0·4 ± 0·1

ret = reticulum, cr = cranial, cd = caudal, md = medial, resp = respiratory rhythm, reg = regular.

A resting discharge was still present in many of the units examined either when there were no reticulo-ruminal movements or after the contents of the reticulum had been more or less removed. This discharge took the form of a low frequency, steady discharge or infrequent bursts of activity, the latter being particularly common in units innervating the cranial sac of the dorsal rumen.

The pattern of the afferent discharges associated with the active phase of the primary cycles may be divided into two groups. The first group (Table 2) contains twenty-eight units (henceforth termed 'reticular' units) whose discharge either started or increased above the resting level 3–5 sec before the second peak of the reticular contraction, reached its maximum discharge frequency at about the same time as this second peak and

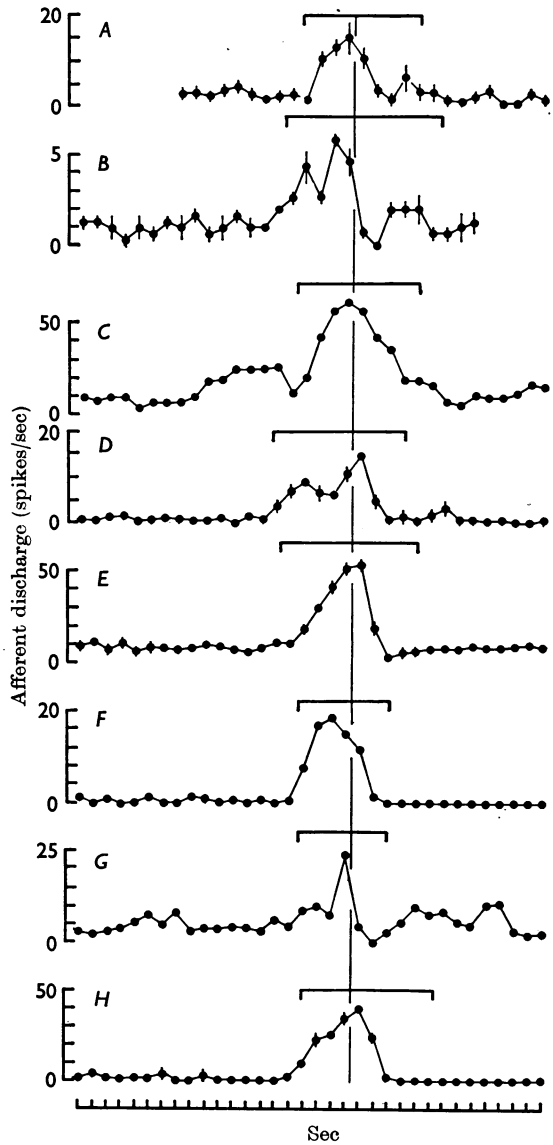

Fig. 5. For legend see opposite page.

decreased 1–2 sec afterwards. Between the start and the maximum of the discharge, there was often a raised level of activity corresponding to the first phase of the reticular contraction when this was clearly present (Fig. 9*B*). The receptive fields of eight 'reticular' units (Fig. 5) were localized to sites in or near the reticulum, namely, the medial wall of reticulum (three units), the caudal wall of reticulum (two units) and the reticular groove (three units: one in each lip and one in the floor).

The second group is comprised of eleven units (henceforth termed 'cranial sac' units), in which the afferent discharge consisted of a submaximal burst of spikes (occasionally absent) at the time of the second peak of the reticular contraction and a maximal burst 2–9 sec afterwards (Table 3). Two of these units were found to innervate receptors in the medial wall of the cranial sac, one of which was active 6–9 sec after the reticular contraction peak (Fig. 6*B*), whereas the other (from a different sheep) showed submaximal activity at the time of this peak and maximal activity 3 sec after it (Fig. 6*C*). A third unit was found to innervate receptors in the lateral part of the reticulo-ruminal fold and although slight activity occurred coincident with the peak of the reticular contraction, the greatest activity occurred 5–8 sec afterwards (Fig. 6*A*). The receptive fields of the other eight units were not located but the pattern of the afferent discharge in six of them (Table 3) resembled that in the unit with receptors located in the cranial sac (of the dorsal rumen) described above. The seventh unit had a steady discharge of 4 spikes/sec lasting from 1 sec before to 7 sec after the second peak of the reticular contraction.

The remaining four units had afferent discharge patterns which were substantially different from either of the previous groups. In two of these

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Legend to Figure 5

Fig. 5. The afferent discharges of eight 'reticular' units recorded during spontaneous reticular contractions. The locations of the receptors innervated by these units were subsequently established by manipulation.

The locations of the receptors in the reticulum were: *A*, *B* and *C*, cranio-medial wall, about 2 cm cranial to the reticulo-omasal orifice. *D* and *E*, medial wall, 1–2 cm caudal to reticulo-omasal orifice. *F*, caudal wall, about 1 cm ventral to the reticulo-ruminal fold. *G*, reticular groove, ventral end of caudal (right) lip. This unit responded to pinching > stretching. *H*, reticular groove, middle of floor. This unit responded to light pressure as well as during a contraction.

For each unit the graph of spike frequency shows mean values for a number of contractions. Where the S.E. of the mean exceeds the diameter of the points in *A*, *B*, *D*, *E* and *H*, they have been shown by a vertical bar. The graphs have been aligned so that the peaks of the contractions are coincident (shown by the vertical line). The horizontal bar above each graph represents the period from the start to the end of the pressure increment caused by an isometric contraction. Only *F* and *G* were recorded from the same sheep.

TABLE 3. The afferent discharge in eleven 'cranial sac' units. The spike frequency is the number of spikes occurring in 1sec. Several values for the interval between the peaks of bursts of activity in the 'resting discharge' have been given to illustrate their variability. The interval given in the right-hand column (Peak to peak) is measured from the peak of the afferent discharge to the second peak of the reticular contraction

	Resting discharge			Contraction discharge				
	Spike frequencies (sec^{-1})		Interval between bursts	Spike frequencies (sec^{-1})				
Unit and site	Min.	Max.	(sec)	1st phase	2nd phase	3rd phase	Duration (sec)	Peak to peak (sec)
29	0	2	4	0	8	28	7	−2·7
30	0	1	2, 6	0	14	13 and 16	14	−4·0 and −9·0
31	0	0	0	0	0	7	2	−6·0
32	0	5	4 (resp)	21	26	41	14	−7·0
33	0	6	4 (resp)	29	21	31 and 31	12	−4·7 and −6·5
34	0	1	3	6	0	32 and 50	12	−2·5 and 6·2
35 c.s.-md	0	3	3, 6	3	0	15	13	−8·0
36 (two units)	8	27	4 (resp)	61	65	82	8	−3·2
37 fold-lat	0	8	4 (resp)	21	19	54	15	−6·5
38	1	3	reg	10	0	11	11	−6·7
39 c.s.-md	0	8	4, 6	17	32	35	7	−2·5
					18	27 and 24	9	−2·2 and −4·7
Mean ± S.E.	0·8 ± 0·7	5·8 ± 2·3	4·3 ± 0·6	15·3 ± 5·5	16·9 ± 5·4	33·2 ± 6·2	10·3 ± 1·1	−5·2 ± 0·5

c.s. = cranial sac, fold = reticulo-ruminal fold, md = medial, lat = lateral, resp = respiratory rhythm, reg = regular.

units the discharge occurred during only the active phase of the cycle but had a variable time relationship to the reticular contraction. The discharge consisted of a burst of activity lasting 3–4 sec and started, for example, 11, 9, 6, 2 and −3 sec before the second peak of the reticular contraction. Another unit had no resting discharge but was active from 5 sec before to 3 sec after the peak of the reticular contraction and two maxima occurred, which were 3 sec before and 1–2 sec after this peak. The fourth unit was active from 1 sec before to 3 sec after the reticular peak.

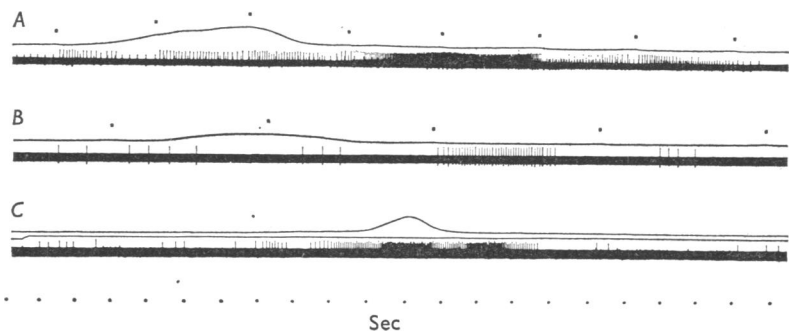

Fig. 6. The afferent discharge in three 'cranial sac' units recorded during spontaneous gastric contractions. The location of the receptors innervated by these units was subsequently established by manipulation.

The locations of the receptive fields were: *A*, reticulo-ruminal fold: (left) lateral border; *B*, rumen: cranial sac, medial wall; *C*, rumen: cranial sac, medial wall.

The reticular pressure is shown in the upper trace. The small spikes in *A* and the middle trace in *C* are incidental and should be disregarded. The end of inspiration is marked by a dot.

The afferent discharge recorded under isotonic conditions

The afferent discharges in seven units were examined under both the isometric and the isotonic recording conditions described by Iggo & Leek (1967*b*). The duration of the afferent discharge was the same in four units and shorter in three units, when recording under isotonic conditions. During the course of the isotonic reticular contraction, despite an increase in pressure of not more than 2 mm Hg, the spike frequency of the afferent discharge associated with the early or first phase of the reticular contraction was similar to that occurring under isometric recording conditions, but that related to the second phase of the reticular contraction was much lower in all the units. It was, however, always greater than the 'resting' discharge.

After switching from isometric to isotonic recording conditions in the reticulum, that part of the spike discharge which occurred 2–9 sec after the peak of the reticular contraction was altered; in 2 'reticular' units, the number of spikes and the peak frequency of this part of the discharge

(i.e. the third phase) were reduced, whereas in one 'cranial sac' unit the number of spikes and the peak frequency were increased (Fig. 7). The receptors for the two 'reticular' units were not localized. The 'cranial sac' unit had a receptive field in the medial wall of the cranial sac. The remaining four units, which did not have a third phase of activity, innervated receptors in the floor of the reticular groove (one unit), the caudo-medial wall of the reticulum (one unit) and unlocated regions presumably in the

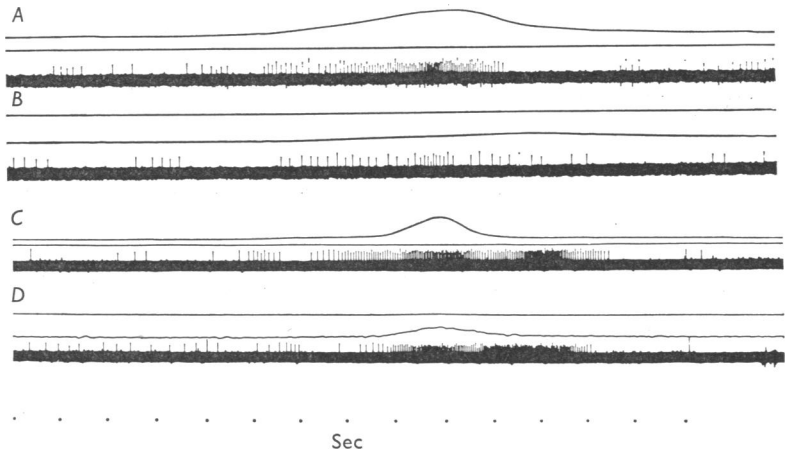

Fig. 7. The effects on the afferent discharges in a 'reticular' unit (records *A* and *B*) and in a 'cranial sac' unit (records *C* and *D*) of changing the recording conditions *in the reticulum* from isometric (*A* and *C*) to isotonic (*B* and *D*).

The 'reticular' unit innervated receptors in the reticulum and its discharge was less under the isotonic conditions (*B*), whereas the 'cranial sac' unit innervated receptors in the cranial sac of the rumen and its discharge (particularly that part occurring 2 sec after the peak of the reticular contraction) was enhanced under the isotonic conditions (*D*). The peak of the discharge in *D* was associated with the peak of the ruminal contraction (not shown).

In each record, the top trace shows the pressure change in the reticulum, the middle trace shows the volume change in the reticulum and the bottom trace shows the afferent discharge.

the reticulum (two units). In all the units, the 'resting discharge' was the same under both isometric and isotonic recording conditions, provided that the pressure head in the aspirator bottles had been adjusted so that it was equal to the existing intrareticular pressure before removing the clamp.

The effect on the afferent discharge of suddenly inflating or deflating the reticular balloon

The effects of progressively inflating and deflating the reticular balloon in steps of 200 ml. were examined in sixteen afferent units. Intrareticular

volumes of not more than 1200 ml. were used, because, at high levels of distension, the frequency of afferent impulses became too great to photograph except on fast film speeds, and because reticulo-ruminal movements were less readily maintained on subsequently deflating the reticular balloon. The effects of inflation will be described below. The effects of deflation were the converse of these and will not be described.

As detailed earlier, most units were inactive or had a low 'resting' discharge frequency when the reticular balloon was empty. When the balloon was inflated the 'resting' discharge frequency increased, resulting in a low-frequency, sustained and regular discharge or in intermittent bursts of activity unrelated to respiratory or cardiac movements. Further inflation caused an increase in the resting discharge and took one of several forms:

(*a*) low-frequency regular discharges increased in frequency,

(*b*) intermittent discharges became sustained discharges with intermittent fluctuations in frequency and the interval between these periods of enhanced activity was reduced, and

(*c*) intermittent discharges became sustained regular discharges. These changes are illustrated in Fig. 4.

If the left lung had not been removed, a rhythm due to respiratory movements was often superimposed on the above patterns of the resting discharge. When 200 ml. was suddenly added or removed from the reticular balloon during the course of $\frac{1}{4}$–$\frac{1}{2}$ sec, a change in the frequency of the afferent discharge was observed about 100 msec after the start of the inflation or deflation. After inflation a high discharge frequency was reached $\frac{1}{4}$–$\frac{1}{2}$ sec later and persisted for about 3 sec before falling to its new value during the course of a further 7 sec. This is illustrated in Fig. 8.

Inflating the reticular balloon caused the interval between primary cycle contractions to be reduced (i.e. the frequency of movements to be increased) and the amplitude and the duration of the reticular and the ruminal contractions to be increased. If ruminal contractions were absent at low levels of distension, inflation usually evoked them (Fig. 9). Associated with these changes in the form of the contractions were increases in all parameters of the afferent discharges related to the first and second phases of the reticular contraction and, in some 'reticular' and 'cranial sac' units, an enhancement or an appearance of a third phase of activity 2–9 sec after the second peak of the reticular contraction. In Fig. 9*C* and *D* is shown the discharge recorded from a 'cranial sac' unit at low and at moderate levels of reticular distension. In Fig. 9*C* a burst of activity occurs only in association with the second peak of the reticular contraction and there is no ruminal contraction, whereas in Fig. 9*D*, in addition to this activity, there is a pronounced burst of spikes occurring at the time of the

third phase of the reticular contraction shown on the record, which itself coincided with a prominent dorsal ruminal sac contraction (not shown). Despite the reticular contraction being much greater in *D* than in *C* (Fig. 9), the burst of activity associated with the second peak of the reticular contraction is only slightly enhanced. The 'cranial sac' unit innervated receptors in the cranial sac and, for the reasons discussed below, it was

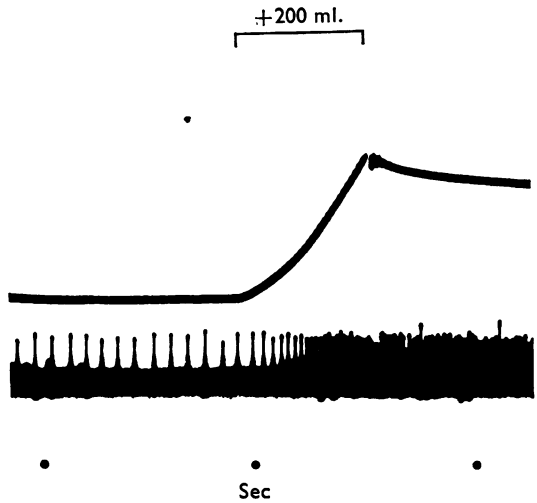

Fig. 8. The immediate effect upon the afferent discharge, recorded from a unit innervating reticular tension receptors, of suddenly injecting 200 ml. air into the reticular balloon.

The latency between the rise in pressure (upper trace) and the increase in afferent discharge (middle trace) is approximately 100 msec.

The high frequency discharge occurring at the end of inflation falls steadily over the course of the next 10 sec to a new rate, which is greater than that before inflation.

This unit is the same as that shown in Fig. 4. Tension receptors are excited not only during the active part of the primary cycle in the reticulum (Fig. 4), but also during passive distension of the reticulum. This behaviour characterizes the receptors as being 'in series' with the smooth muscle cells.

concluded that that part of its discharge which occurred at the time of the reticular contraction was due to a passive increase in ruminal tension resulting from the reticular contraction, whereas the rise in ruminal tension signalled 5 sec later in the discharge shown in Fig. 9*D* was actively developed by a ruminal contraction. Moderate but not low levels of reticular distension evoke ruminal contractions reflexly. The form of the ruminal contractions and their temporal relationships to the reticular contraction are shown in Fig. 10.

The effect of removing the abomasum

The abomasum was removed from four sheep during the present investigation and from a further ten halothane-anaesthetized sheep during a different investigation. Reticulo-ruminal movements were subsequently

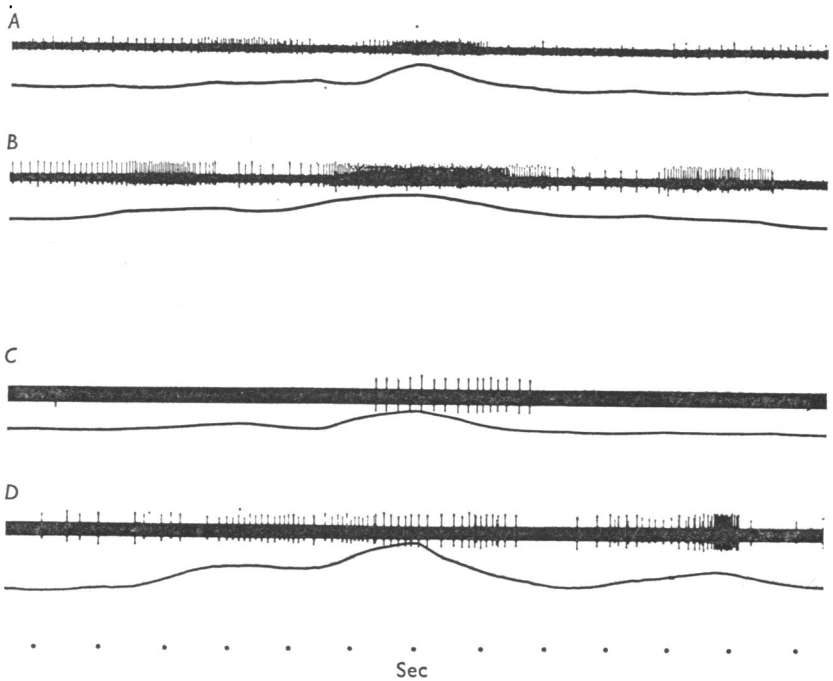

Fig. 9. The effect of distending the reticulum upon the afferent discharges in a 'reticular' unit (records *A* and *B*) and in a 'cranial sac' unit (records *C* and *D*). A 'reticular' unitary discharge (thin spikes) is also seen in *D*. This unit was inactive under the conditions of *C*.

Compared with that in *A* (at 400 ml.), the afferent discharge in *B* (at 800 ml.) shows an enhanced resting discharge, a greater discharge associated with the first phase of the reticular contraction, a more prolonged discharge but with a lower peak frequency associated with the more slowly developed, protracted second phase contraction and the presence of a burst of activity associated with the third phase of the reticular contraction which is absent from *A*. The spikes are taller in *B* because a slight movement of the fine strand lying on the electrodes in the interval between *A* and *B* improved recording conditions.

Compared with that in *C* (at 300 ml.), the afferent discharge (thick spikes) in *D* (at 900 ml.) shows the appearance of a resting discharge, a very slight increase associated with the second phase of the reticular contraction and the presence of a discharge which reaches a peak 5 sec after the peak of the ruminal contraction (not shown in this record). At the low level of reticular distension in *C*, no ruminal contractions were present.

The volumes given above refer to the amount of air in the reticular balloon. In each record, the lower trace registers the reticular pressure.

evoked in twelve of these fourteen sheep. The form of the contractions was unaltered but the frequency of primary cycle movements in six sheep was much faster (about 2/min) than was usual in sheep in which the abomasum was present (about 1/min).

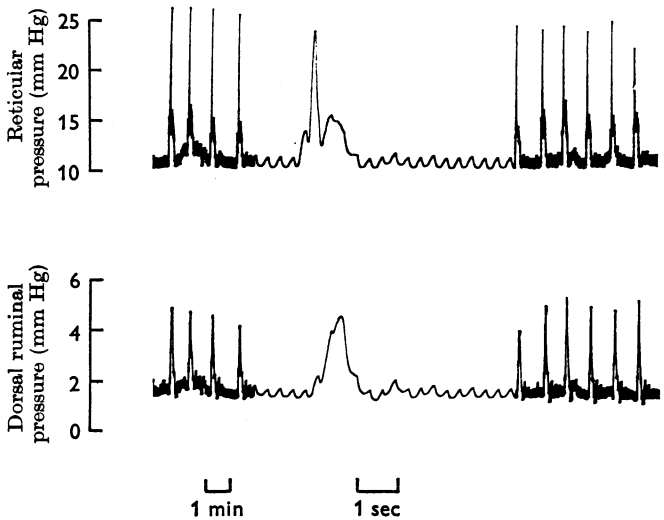

Fig. 10. The form and temporal relationship of reticular and dorsal ruminal sac contractions in a halothane-anaesthetized sheep.

In the middle part of the record, the paper speed was increased. On the dorsal rumen trace, the first and second notches correspond to the second and third peaks of the reticular contraction respectively. The peak of the dorsal ruminal sac contraction occurs about 5 sec and about 2 sec after the second and the third peaks of the reticular contraction respectively. The ventral sac contraction (not shown) reached a peak about 11 sec after the peak of the dorsal sac contraction and was responsible for the slight rise in dorsal sac pressure shown on the lower trace.

The base-line oscillations are due to respiratory movements.

DISCUSSION

In the present investigation, the reticulo-ruminal mechanoreceptors studied were located predominantly in the reticulum (especially in its medial wall), in the reticulo-ruminal fold, in the lips of the reticular groove and in the medial wall of the cranial sac of the rumen. This distribution accords with that found by Ash & Kay (1959), whose conclusions were based on observing the reflex effects of localized mechanical stimulation of the reticulo-rumen. The distribution is wider than that observed by Iggo (1955), who located five receptive fields near the reticular groove and possibly one other in the cranial wall of the reticulum.

The afferent discharges recorded from all the units except one were enhanced by increasing the tension in the wall of the appropriate viscus. Such units, therefore, innervated tension receptors, which appeared to be

excited by manoeuvres which caused tangential lengthening. Iggo (1955) gives the criteria by which visceral tension receptors may be typed as either 'in series' or 'in parallel' with the contractile elements of the viscus. These criteria are based on those given by Matthews (1933) for mechanoreceptors in skeletal muscle. In the present experiments, the tension receptors were of the 'in series' type and were slow-adapting, because they gave (*a*) an increased sustained discharge in response to passively distending the viscus and (*b*) an increased phasic discharge during an isometrically recorded contraction. The increased discharge in response to an isotonically recorded contraction was small, which argues against the possibilities of the receptors being of the 'in parallel' type or being 'tactile receptors' located in the superficial layers of the mucosa, where deformation of the tissues would probably be greater under isotonic recording conditions. In the reticulum and in the rumen, 'in series' tension receptors appeared to be situated deep in the muscle layers, whereas receptors located in reticular groove structures seemed to occupy a more superficial position, so that, in addition to giving the 'in series' type of response, they also responded to light pressure applied to the mucosal surface.

By observing the motor effects of electrically stimulating the peripheral end of sectioned vagal trunks, Habel (1956) determined the differential distribution to various gastric regions of efferent nerve fibres in the ventral and in the dorsal vagal trunks. Where it was possible to determine the vagal pathways of afferent units in the present experiment, it was found that their differential distribution was consistent with that found by Habel (1956) for efferent fibres. By applying this differential distribution arbitrarily to those units whose conduction velocities were measured but whose vagal pathways were not determined experimentally, it was found (Fig. 3) that units known or presumed to have pathways in the dorsal vagal trunk had statistically significantly higher conduction velocities (14·5 m/sec) than those in the ventral vagal trunk (6·6 m/sec), the over-all mean being 12·4 m/sec. The values accord with those obtained by Iggo (1955) for four units innervating the reticular groove, i.e. 12, 6, 5 and 2 m/sec. It is possible that the observed conduction velocities are biased in favour of the larger diameter fibres, and are, therefore, high, owing to the greater difficulty of measuring conduction velocities in very small fibres. It is unlikely, however, that receptors innervated only by small fibres would have been overlooked in the present experiments, because studies of compound action potentials evoked by electrical stimulation in fine strands showed that C fibre activity was clearly recordable.

Most of the reticular tension receptor units had a resting discharge which was sustained at high levels of reticular distension, intermittent at lower levels and infrequent or absent at very low levels. The intermittent

discharges, when not due to diaphragmatic movements, appeared to be associated with localized contractions (i.e. intrinsic movements) of the wall in the receptor region and these could be felt as 'ripples' during manual exploration of the mucosal surfaces. They were particularly evident in the cranial sac. The frequency and amplitude of the 'ripples' and the extent of the corresponding afferent discharge were increased by manipulating the surfaces more forcibly. Likewise the number of spikes per discharge was increased and the interval between each discharge was reduced by distending the viscus or by administering drugs which cause contraction of smooth muscle (unpublished observations). It is possible that tension receptor activity may largely be determined by the extent of the intrinsic movements of the smooth muscle cells, with which they are 'in series'. The intrinsic movements increase as the degree of distension rises. When gastric movements are evoked at the beginning of an experiment by inflating the reticular balloon with 400–600 ml. air, the increased afferent (excitatory) input to the gastric centres may, therefore, be the indirect result of inflation enhancing intrinsic movements, which, in turn, elicit or increase the resting discharges in 'in series' tension receptors.

Ash & Kay (1959) described potent reflex effects by stroking the mucosa of the reticulum, etc. In the present experiments, light stroking did not directly elicit afferent discharges in gastric units. Several possibilities may account for this discrepancy: (*a*) if the fibres innervating the mucosa were very small, they may have been overlooked, although this seems unlikely; (*b*) the stroking used by Ash & Kay (1959) may have been sufficiently heavy to stimulate tension receptors directly; or (*c*) mucosal receptors may exist, which excite intrinsic movements through intramural nervous connexions with the smooth muscle layers, thereby eliciting tension receptor activity indirectly. The results illustrated in Fig. 1 are consistent with this last possibility.

In decerebrate preparations, it has been shown that primary cycle (reticulo-ruminal) movements are evoked or are enhanced by distension of the reticulum (Iggo, 1956; Iggo & Leek, 1967*a*, *b*; Titchen 1958), and by increased abomasal acidity (Titchen, 1958). Although, under most circumstances when gastric movements are present, an excitatory drive may be derived from both the reticulum and the abomasum, the drive provided by the latter is evidently not essential. Moreover, the increased frequency of reticulo-ruminal contractions observed in some sheep after removing the abomasum may be interpreted as being due to the abolition of an overall inhibitory drive arising from the abomasum. Titchen (1958) has shown that reticulo-ruminal contractions may be inhibited reflexly by distending the abomasum. Movements were still present in halothane-anaesthetized sheep after the removal of the abomasum and it was not

necessary to compensate for this loss by increasing the level of reticular distension; moderate distension of the reticulum was sufficient to evoke extrinsic movements reflexly. This manoeuvre appears to enhance intrinsic movements and to lead to an increased resting discharge from 'in series' tension receptors. Hitherto, the role of intrinsic movements in the reticulo-rumen has been regarded as insignificant, whereas it now seems that, although the movements *per se* are ineffective for moving the voluminous contents of the reticulo-rumen, they may be very effective indirectly: by exciting tension receptors, they may reflexly evoke the powerful contractions which constitute the primary cycle movements of the ruminant forestomach.

Examination of the discharges from receptors in the cranial sac have confirmed the conclusions of Leek (1966) and Iggo & Leek (1967*b*) that tensions in the reticulum reflexly affect the amplitude and duration of rumen contractions. Moderate tension in the reticulum during the quiescent period reflexly evokes rumen movements but high tensions developed in the reticulum during an isometrically recorded reticular contraction reflexly inhibit the ruminal contraction which occurs 2–9 sec later. The inhibition of the rumen contraction does not occur during an isotonically recorded reticular contraction, when there is little or no change both in reticular tension and in the afferent discharge from reticular tension receptors.

One mechanism postulated by Iggo & Leek (1967*b*) to account for the differing reflex response to moderate and to high levels of reticular tension is the existence of two sets of tension receptors: the one set having a low threshold of response to reticular tension and providing an excitatory input to the gastric centres, the other set having a high threshold of response to reticular tension and providing an inhibitory input to the gastric centres. The results of the present experiments accord with this postulation in so far as different units had different thresholds of response and some units (e.g. the 'reticular' unit in Fig. 9*D*) were active only at the higher levels of reticular tension.

Despite repeated attempts to locate mechanoreceptor sites in the caudal regions of the rumen, few sites were actually found there. It is difficult, therefore, to accept those hypotheses which postulate that reflexogenic zones situated in the caudo-dorsal regions of the rumen are responsible for the excitation of secondary cycle movements and eructation (Weiss, 1953; Stevens & Sellers, 1959). For several reasons, the effective receptor zone may be located more cranially than was supposed previously. Weiss (1953) himself observed that secondary cycles were enhanced by raising the sheep's hindquarters and conversely were reduced by raising the fore-quarters: an effect which I have confirmed recently (unpublished observations). Weiss (1953) concluded that the former manoeuvre would cause

distension (by rumen gas) of the caudo-dorsal region of the rumen, whereas it actually causes distension (by rumen contents) of the cranial regions. Eructation can also be evoked in decerebrate sheep by insufflating the rumen with gas even after most of the (caudo-)dorsal and ventral ruminal sacs have been ablated (Dougherty, Habel & Bond, 1958). The present experiments have demonstrated that the cranial sac of the rumen (particularly its medial wall) is richly supplied with tension receptors and it seems likely that this receptive area, rather than a more caudally situated one, may be responsible for those rumino-ruminal reflexes which elicit secondary cycle movements.

Most techniques used for recording reticulo-ruminal movements are capable of discerning only gross effects, whereas the discharge from 'in series' tension receptors indicates discrete movements in a localized part of the musculature. The afferent discharge elicited by a tension developed actively (i.e. by a contraction) is greater than one developed passively by the same overall tension, as Iggo (1955) also observed. On this basis it appears that, in halothane-anaesthetized sheep, the reticulum and the reticular groove undergo a contraction which is usually biphasic but occasionally monophasic, and sometimes triphasic, the third phase occurring at the time of the cranial sac contraction. The cranial sac of the rumen contracts monophasically, reaching a peak 2–9 sec after the peak of the reticular contraction and the reticulo-ruminal fold undergoes a triphasic contraction corresponding to the biphasic contraction of the reticulum and the monophasic contraction of the rumen.

I am indebted to the Agricultural Research Council for financing this investigation, to Professor A. Iggo for advice and to Miss Sheila Valentine and Mr Roger Taylor for prolonged and invaluable technical assistance.

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