# THE MECHANISM OF REFLEX REGULATION OF ERUCTATION IN SHEEP

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# THE MECHANISM OF REFLEX REGULATION OF ERUCTATION IN SHEEP

by

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## ABSTRACT

Forestomach motility and its association with eructation was studied in sheep and some of the factors affecting the primary and secondary cycle contractions of the reticulo-rumen and eructation were investigated.

A new technique for recording the reticulo-ruminal movements from discrete locations was developed. This made it possible to assess the involvement of reticulo-ruminal musculature in the primary and secondary cycle contractions. It was found that the primary cycles started with a biphasic contraction of the reticulum and progressively involved the cranial, the middle and the caudal regions of the dorsal rumen, followed usually by a contraction of the ventral rumen. The secondary cycles usually started in the caudal wall of the caudo-ventral blind sac and progressively involved the caudal and then the cranial regions of the dorsal rumen, followed nearly always by a contraction of the ventral ruminal sac.

Eructation was principally associated with the secondary cycle contractions of the dorsal rumen and took place when the contraction had reached its peak. Eructation occurring during a primary cycle was rare. The frequency and the amplitudes of reticulo-ruminal contractions for the primary and secondary cycles and the frequency of eructation varied with the activity of the animal, i.e. resting, ruminating or eating. Eating exerted an over-all stimulatory effect on the motility of the reticulo-rumen and the frequency of eructation.

Gaseous distension always increased the frequency of secondary cycle contractions and eructation more than the primary cycle contractions of the reticulo-rumen which were not affected at moderate distension. The latter responded at higher degrees of free gas distension. The excitatory effects of anaesthetic bag distension in the dorsal rumen were more pronounced for the primary cycle contractions than the secondary cycle con-

:tractions of the forestomach. Extreme distension with free gas depressed the amplitudes of reticulo-ruminal contractions. The effect was more pronounced on the secondary cycle contractions of the rumen. Extreme distension with an anaesthetic bag was more inhibitory for the primary cycle contractions. Evacuation of ruminal gases depressed the cyclic activity of the forestomach. The over-all decrease was more apparent in the secondary cycle contractions than in the primary cycle contractions.

Addition of acid or alkali solutions into the rumen produced low or high pH of the rumen contents respectively. At these values of pH the primary cycle contractions of the reticulo-rumen were either depressed or completely abolished while secondary cycle contractions of the rumen accompanied by an eructation continued, though with reduced force and frequency.

It is concluded that the primary and secondary cycle contractions of the reticulo-rumen are under independent nervous control and that the eructation is regulated through its association with the presence of second-:ary cycle contractions of the rumen, whose frequency and amplitudes are determined by the degree and type of distension.

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# INTRODUCTION AND LITERATURE REVIEW

## Development of the ruminant stomach

The ruminant stomach consists of four compartments - rumen, reticulum, omasum and abomasum, the last named being equivalent to the true glandular stomach of other animals. The first three compartments are non-glandular and lined with stratified squamous epithelium (Sisson & Grossman, 1953). A brief anatomy of the internal structures of the rumen and reticulum has recently been described by Habel, (1965), and Sellers & Stevens, (1966) in different species of ruminants. All the four compartments develop from the gastric spindle by progressive specialization in which the important phenomena are the suppression of glandular epithelium and its replacement by stratified squamous epithelium (Lambert, 1948), with distinct motor activity of the gastric smooth muscle appearing after 70 days of foetal life (Duncan & Phillipson, 1951).

It has long been recognised that the forestomach of the new born ruminant is neither structurally nor functionally fully developed and shows marked changes with the growth and age of the animal. The investigations of McAnally & Phillipson, (1944), Wallace, (1948), Dziuk & Sellers, (1955a), Wardrop & Coombe, (1960), Flatt, Warner & Loosli, (1959), and Tamate, McGilliard, Jacobson & Getty, (1962), showed that the transformation of the digestive tract of the ruminant from an essentially non-ruminant state at birth to a ruminant state during development is markedly influenced by diet. This transformation is characterised by many changes in the basic anatomy and physiology of the young ruminant and the rumen and reticulum are the sites of most obvious changes. Their capacity increases rapidly and their walls develop the gross and histological characteristics of mature tissue. Closely associated with the structural

developments are changes in the pattern of forestomach motility, the establishment of an extensive microbial population and an increase in the metabolic activity of the mucosa. Walker & Walker, (1961), indicated that the rumen micro-organism population of three week old lambs, with differences in enzymic activity due to age and composition of diet, was capable of digesting as wide a variety of carbohydrates and proteins (the two principal constituents of food), as the adult ruminant. Flatt et al. (1959), demonstrated the occurrence of first regular eructation contract-:ions of the rumen in hay and grain-fed calves at the age of 18 to 21 days. It can be stated that with the change in the eating habits, the development of the reticulo-ruminal musculature and the growth of the microbial population in the rumen of the young ruminant, the first signs of eructation mechanism appear within three weeks of its post-natal life.

Gases in the rumen

As a result of microbial fermentation, vast quantities of gases are produced in the first two compartments of the ruminant stomach. The rates of gas production, as measured by both drawing off gas from rumen fistula and by the use of a face-mask and tracheal fistula (Colvin, Wheat, Rhode & Boda, 1957), have been reported to be about 30 l/hour from cattle on an alfalfa diet. Dougherty & Cook, (1962), using a face-mask and endotracheal catheter for collection of eructated gas estimated the rates to be about 42 l/hour in a resting cow in the standing position. Hungate, Fletcher, Dougherty, and Barrentine, (1955), have estimated that approximately 1.2 to 2 litres of gas are formed per minute in a 1000 lb. bovine animal. Principal gases produced in the forestomach are $CO_2$ and $CH_4$ but other gases such as $H_2$, $N_2$, $O_2$, $H_2S$ and CO are also present in small proportions. The mean percentage composition of each gas as determined by McArthur & Miltimore, (1961), using a gas-

solid chromatographic method, in close agreement with the earlier work (Cole, Mead, and Kleiber, 1942), is as follows:

| | |
|---|---|
| Carbon dioxide | 65% |
| Methane | 27% |
| Nitrogen | 7% |
| Oxygen | 0.6% |
| Hydrogen | 0.2% |
| Hydrogen sulphide | 0.01% |
| Carbon monoxide | 0.5% |

The $CO_2$ is produced by bacterial metabolism and by release from salivary bicarbonate. The relative importance of these two sources depends partly on the diet and partly on the pH of the rumen contents, because Cole, Huffman, Kleiber, Olson & Schalk, (1945), have pointed out that saliva which is secreted at pH 8 in equilibrium with 6% $CO_2$ will tend to absorb carbon dioxide when exposed to 70% $CO_2$ in the rumen until its pH is reduced below about 6.9. It has been shown by the same authors that $CH_4$, $H_2$ and $H_2S$ represent the end products of reductive bacterial metabolism and that $N_2$ and $O_2$ are either swallowed with food or diffuse into the rumen from the blood. The composition and the total amount of gases formed are not greatly affected by the kind of ration consumed but they vary greatly with the time elapsing after feeding (Cole, Mead & Kleiber, 1942). Kingwell, Oppermann, Nelson & Brown, (1959) confirm this observation by continuous collection of samples of rumen gases from cattle maintained on hay or concentrate rations. They found that the gas composition varied in a regular manner with the time after feeding. The ratio of $CO_2$ : $CH_4$ was narrowest after fasting (1:1). It became widest (3:1) within two hours after feeding, following which it narrowed until four hours after feeding when it again reached a

wide peak for the second time. Washburn & Brody (cited: Dukes, 1955), measuring percentage composition of rumen gases in dairy cows on alfalfa hay and grain ration, found approximately 66% $CO_2$ and 29% $CH_4$ three hours after feeding. $N_2$ and $O_2$ were found to be absent. After this, progressive decrease in the percentage amount of the $CO_2$ continued throughout the day, while the percentage proportion of $CH_4$ and $N_2$ con-:tinued to increase from about seven hours after feeding. At about the 16th hour after feeding, the percentage composition of $CO_2$ and $CH_4$ in the rumen gases was nearly equal (35%).

Elimination of rumen gases

The production of enormous quantities of gases (30 to 42 l/hour in cattle) in the rumen necessitates the animal of having some means of expelling or eliminating them, without which a serious condition called 'bloat' would develop. Dougherty, (1961) suggested that physiologically this was brought about by the following processes:-

(i) Eructation
(ii) By absorption from the ruminal wall and subsequent elimination with the expired air
(iii) Passage of some quantities to the lower alimentary tract.

The major part of the ruminal gases is eliminated by eructation - a complex reflex phenomenon involving synchronised movements of the forestomach, the cardiac orifice and the oesophagus (Weiss, 1953) including the coordinated opening and closing of prediaphragmatic and pharyngoesophageal sphincters (Dougherty, 1961). Most investigators have associated eructation with active reticulo-ruminal motility (Wester, 1926; Quin, Van der Wath & Myburgh, 1938; Cole et al. 1942; Weiss, 1953; Dougherty & Meredith, 1955; Reid & Cornwall, 1959; Stevens & Sellers, 1959, and Reid & Titchen, 1965). The pioneer work of Schalk &

Amadon, (1928) on cattle, established the occurrence of reticulo-ruminal movements in two cycles called primary and secondary. Since then they have been variously named as 'mixing' and 'belching' cycles (Reid & Cornwall, 1959), 'A' and 'B' sequences (Reid, 1963); 'backward-moving' and 'forward-moving' waves of contraction (Weiss, 1953; Reid & Titchen, 1965). To avoid confusion the original classification adopted by Schalk & Amadon, (1928) will be used.

Techniques of studying forestomach motility

A variety of methods has been used by different workers to establish the pattern of reticulo-ruminal motility. The most commonly used methods are:-

(i) Visual inspection

Visual inspection of the stomach after laparotomy in lightly anaesthetized or fully conscious animals has been practiced by Mangold & Klein, (1927). Visual inspection of the interior of the forestomach by a torch light and manual exploration through a rumen fistula has been used by Wester, (1926), Schalk & Amadon, (1928), Williams, (1955) and Ash & Kay, (1959). These methods could be profitably utilized for making general observations of the contractile events taking place in the stomach but suffer from the disadvantage of not providing a permanent record.

(ii) Palpation and auscultation

Palpation and auscultation of the rumen in the sub-lumbar triangle has been practiced by Williams, (1955). By placing the palm of the hand on this area the dorsal ruminal sac can be felt moving upwards during a contraction to meet the hand from which it is separated by skin, muscles and peritoneum. During relaxation receding of the organ is noticeable. Characteristic sounds due to the movements of the ingesta within the rumen

during a contraction can be heard by auscultation of the sub-lumbar triangle. Sounds of the ingesta due to a reticular contraction can best be heard on the ventral aspect of the seventh rib on the left side at its costo-chondral junction in cattle and sheep.

Mere application of an inflated balloon $3\frac{1}{2}$ inches in diameter to shaved areas of the sub-lumbar triangle for obtaining a permanent record of the ruminal movements in the intact cow was used by Alexander & Moodie, (1960).

These methods have their limitations particularly in relation to the study of events taking place in the ventral ruminal sac and the problem of transmitted pressures due to the movements of the skin render these methods inadequate for wider application.

(iii) Fluoroscopy

Cinefluorography or X-ray techniques have had only limited applica-:tion. They have successfully been employed in small ruminants - sheep, goats and calves, by Czepa & Stigler, (1926), Magee, (1932), Phillipson, (1939), Dougherty & Meredith, (1955), and Benzie & Phillipson, (1957). The methods suffer from poor contrast available in relatively large animals, the difficulty in the interpretation of results from an organ partly concealed by others (omasum) and their unsuitability for prolonged observation.

(iv) Partial exteriorization

Partial exteriorization of the wall of an organ to be studied has been advocated by Titchen, (1958b), Reid & Titchen, (1959) and Reid (1963) for observing the sequence of events taking place in the forestomach. To obtain graphic records of their observations, they tied the herniated parts to threads passed over a system of jockey pulleys. This system

like the others, also has the disadvantage of recording the passive move-:ments of the exteriorized part of the stomach due to contractions in another part, besided interference due to change in the position of the animal.

(v) Pressure recording through a fistula

Two types of fistulae - open and closed, have been used for observing the reticulo-ruminal activity in different ruminants. The term 'open fistula' is applied to a relatively large fistula that can be closed by a pressure or another type of plug, which can be removed at will for ready intra-ruminal examination and the introduction of different types of sensing devices to be placed at desired locations for obtaining a permanent record on the kymographic or other recording equipment. Operative techniques have been described by Phillipson & Innes, (1939) and Dougherty, (1955). Closed fistulae are more adaptable to sheep and other small ruminants though they have been successfully used in cattle. They are used when it is not necessary to enter the cavities of the reticulo-rumen for manual exploration. Metallic, ebonite, plastic, rubber and polythene cylindrical tubes have been employed by different investigators for closing the fistulae and at the same time leaving a possibility for physiological investigations without disturbing the interior of the forestomach. The commonest method of obtaining graphical records through these fistulae has been the introduction of slightly inflated toy balloons, (Schalk & Amadon, 1928), open-ended fluid-filled narrow-bore tubes (Dziuk & Sellers, 1955b) or other sensing devices. Electro-mechanical transducers were used by Reid & Cornwall, (1959) and pressure - sensitive transducers and induction coils attached to different structures within the cavity of reticulo-rumen for studying the sequence of muscular movements occurring during various digestive cycles were used by Lucas & Dougherty, (1964). The obvious drawbacks with these

devices are their forming a cavity within a cavity; recording of events from a wider area in the lumen, and the problem of transmitted pressures from one compartment to the other, and the undesirable use of clips on the muscular structures. Nevertheless, they provide a fair approximation of the events taking place inside the reticulo-rumen and have been most widely used by various investigators at different times for obtaining permanent records.

Reticulo-ruminal movements.

The reticulo-ruminal movements are closely associated with each other in a rhythmic way. Each primary cycle is initiated by a sharp biphasic contraction of the reticulum and reoccurs approximately every 60 seconds. Wester, (1926), Schalk & Amadon, (1928) and Dziuk & McCauley, (1965) produced evidence that reticulum in cattle showed two separate contractions with a definite pause between them, while Czepa & Stigler, (1926) and Magee, (1932), in sheep, found no relaxation between the two, the second contraction being superimposed upon the first. Phillipson, (1939) and Dziuk & McCauley, (1965) supported the latter authors but indicated that slight relaxation often occurred between the two phases of a reticular contraction. The amplitudes of the reticular contractions usually vary between 15 to 20 mm Hg. During rumination an extra-reticular contraction preceding the usual biphasic one has been reported by Schalk & Amadon, (1928), Phillipson, (1939), Balch, Kelly & Heim, (1951), Salmin, (1960) and many others, the functional importance of which is attributed to the process of regurgitation. Recently Seren, Molinari & Brambilla, (1965) have suggested that this reticular contraction due to its appearance and function does not belong to the typical biphasic reticular contraction and therefore, to the classic motor cycle of the stomach; instead it belongs to the rumination cycle and should be

considered a pre-contraction of the reticulum.

Just before the second reticular contraction reaches its peak the dorsal ruminal sac begins to contract at the cranial pillar accompanied simultaneously by the longitudinal pillars, dorsal coronary pillars and the intervening ruminal wall. This occupies 5 to 7 seconds in the cranial sac region with an amplitude of 10 to 20 mm Hg, and lasts 8 to 10 seconds in the caudo-dorsal blind sac with amplitudes of 6 to 12 mm Hg. Higher amplitudes of up to 20 mm Hg (Reid & Cornwall, 1959) and longer durations of about 15 seconds (McAnally & Phillipson, 1944) in the caudo-dorsal blind sac have been reported. During or after the dorsal ruminal sac has finished its relaxation, the ventral coronary pillar, the caudal pillar and the ventral ruminal sac contract with an amplitude of 10 to 20 mm Hg and lasting 10 to 15 seconds to mark the end of the primary cycle (Dziuk & Sellers, 1955b; Reid & Cornwall, 1959; the last named investigators indicated that during the ventral sac contraction the cranial pillar formed a low ridge between the cranial sac and the ventral sac and remained in that position till the following cycle).

Quite often in addition to the primary cycles, the dorsal rumen shows a contraction of the second type in which according to Weiss, (1953) the first noticeable change is an increase in pressure in the caudo-dorsal blind sac. Reid & Cornwall, (1959) suggested that this increase in pressure was associated with a powerful contraction of the dorsal coronary pillars and almost simultaneous contraction of the cranial pillar, dorsal sac and the caudo-ventral blind sac of the rumen. This is followed by a contraction of the ventral sac identical to the primary cycle contraction of the organ. Schalk & Amadon, (1928) were of the view that the secondary cycle contraction of the dorsal rumen was identical to the primary cycle. This view is still held by Ohga, Ota & Nakazato, (1965). Wester, (1926)

and Weiss, (1953) suggested that the secondary cycle contractions of the dorsal rumen originated in the caudo-dorsal blind sac but Reid, (1960) and Titchen & Reid, (1965) showed that the secondary cycle contractions originated in the caudo-ventral blind sac and then involved the more caudal regions before the more cranial regions of the dorsal rumen. Dziuk & Sellers, (1955b) and Dziuk & McCauley (1965) using open ended water-filled catheters for motility recording through strain-gauge pressure transducers reported that the ventral wall of the cranial sac did not contract in the secondary cycle.

The behaviour of the ventral ruminal sac has been reported to be variable in the primary and secondary cycle activity of the reticulo-rumen. Dziuk & Sellers, (1955b) indicated that the ventral sac contract-:ion did not occur with every primary cycle contraction of the dorsal rumen and Phillipson & Reid, (1960) reported four major patterns of reticulo-ruminal contractions for primary and secondary cycles in cattle. These were (1) a dorsal ruminal sac contraction which always started during the second phase of a reticular contraction unaccompanied by further pressure increments in the rumen; (2) a dorsal sac contraction followed by a con-:traction of the ventral rumen; (3) a dorsal sac contraction, then a second dorsal sac contraction followed by a contraction of the ventral ruminal sac; (4) as for No. 3 except that the first dorsal sac contraction was followed by a contraction of the ventral rumen. These measurements were made during resting, ruminating and eating states in cattle.

Marked variations in the rate of primary and secondary cycles, in the amplitudes of contractions and in the ratio between primary and secondary cycles have largely been correlated with the state of digestion in the rumen and whether the animal is resting, ruminating or eating. An increased frequency of primary and secondary cycles of the reticulo-

rumen and eructation has been reported during rumination and feeding in different species of ruminants (Phillipson, 1939; Reid, 1963; Dziuk, Fashingbauer & Idstrom, 1963; Dziuk, 1965; and Dziuk & McCauley, 1965). Balch, (1952) and Dziuk & McCauley, (1965) showed that the rates of cyclic activity of the forestomach and eructation were less when the animals were recumbent than when they were standing. The usual ratio between primary and secondary cycles has been reported to be 2 : 1 or 3 : 1 during resting. It may change to 1 : 1 during feeding.

Rumen motility and eructation

Most investigators (Wester, 1926; Weiss, 1953; Dougherty & Meredith, 1955; Stevens & Sellers, 1959; and Reid & Titchen, 1965) have shown that eructation is usually associated with the secondary cycle contractions of the dorsal rumen, although its occasional occurrence with primary cycle contractions has also been recorded. Wester, (1926) was apparently the first to suggest that during the secondary cycle con-:traction of the dorsal rumen the gas was brought forward and downward to the cardia which in collaboration with the oesophagus eliminated the gases by a complex eructation reflex. This was later confirmed by Weiss, (1953) and Reid & Cornwall, (1959) who found that the eructation took place at the peak of a secondary cycle contraction of the dorsal rumen and was followed by a sharp drop in intraruminal pressure. The latter investigators and Stevens & Sellers, (1960) and Dziuk & McCauley, (1965) indicated that eructation was aided by a general rise in intra-abdominal pressure presumably due to a contraction of the abdominal wall. Weiss, (1953) showed that in sheep eructation was exclusively associated with the secondary cycles but Stevens & Sellers, (1959) found that about two thirds of the eructations occurred during the secondary cycles and one third during the primary cycles in cattle.

Although reticulo-ruminal motility may be a normal part of the eructation reflex there is evidence (Dougherty & Meredith, 1955) that eructation can occur during ruminal stasis under experimental conditions, but at much reduced rates as indicated by McCauley & Dziuk, (1965).

Other mechanical events associated with eructation

Other mechanical events involved in the eructation reflex will be briefly described as inferred from the investigations of Dougherty & Meredith, (1955), Dougherty & Habel, (1955), Dougherty, Habel & Bond, (1958) and Dougherty, (1961).

Two contractions of the reticulum clear that organ of much of its ingesta and the contraction of the rumino-reticular fold and the cranial pillar in sheep hold the ingesta away from the cardia and prevent the immediate return of ingesta into the relaxed reticulum. These events permit gas to come forward to the region of the cardia due to a secondary cycle contraction of the rumen so that it is in a position to be eructated. As the gas approaches the cardia, the latter relaxes along with the pre-diaphragmatic sphincter of the oesophagus, permitting the gas to enter into the oesophagus which is distended throughout its length. When the gas has entered the oesophagus, the cardia and the diaphragmatic sphincters are constricted and relaxation of the pharyngoesophageal sphincter takes place followed by an extremely rapid oesophageal con-:traction (160 cm/sec recorded by Hill, cited by Dougherty, Mullenax & Allison, 1966). Dougherty, Hill, Campeti, McClure & Habel, (1962) found that during the active phase of eructation the nasopharyngeal orifice was closed by elevation of the soft palate, thus preventing the gas from entering into the nasal cavity but enabling it to pass into the ventral part of the pharynx and oral cavity. They also indicated that the epiglottis did not move and the glottis remained open during the expulsive

phase of the eructation. In another publication Dougherty, Stewart, Nold, Lindahl, Mullenax and Leek, (1962) demonstrated that the eructated gases passed into the trachea at approximately the same pressures as in the oesophagus and then penetrated into the lungs where they were absorbed. Due to absorption of the gases, increased arterial $CO_2$ values were recorded during an eructation. They indicated that this increase in the arterial $CO_2$ content was not due to the reflex activation of the arterio-:venous shunts but due to direct passage of $CO_2$ into the pulmonary arterial circulation during eructation. Methane was found to be not excreted through the lungs. Insufflation with $CO_2$ at high intraruminal pressures (about 40 mm Hg) and with CO and $H_2S$ gave immediate clinical responses in sheep with patent trachea. They stated that a physiologically significant amount of various gases when placed into the rumen, was eructated and absorbed into the blood through the pulmonary route.

Innervation of the ruminant stomach and the nervous control of reticulo-ruminal movements

A detailed account of the innervation of ruminant stomach and the central control of the reticulo-ruminal movements is not required here but it seems essential to indicate that the ruminant stomach is dependent upon intact vagi for its varied reflex functions. This has been shown by Wester, (1926); Duncan, (1953); Weiss, (1953); Habel, (1956); Iggo, (1951, 1956); Stevens & Sellers, (1959) and Leek, (1963). It is also known, (Iggo, 1956; Habel, 1956) that both efferent and afferent nerve fibres to and from the stomach are contained in the vagi. The sympathetic nerve supply of the stomach comes from the splanchic nerves which are much less important in the maintenance of gastric motility (Duncan, 1953). However, when excited they cause inhibition of the reticulo-ruminal movements (Titchen, 1953; Comline & Titchen, 1961).

Marschall, (cited by Habel, 1956) found that stimulation of the peripheral end of the cut right cervical vagus resulted in a rapid, strong, total contraction of the reticulum, followed by a strong contraction of the dorsal ruminal sac, followed by a forceful contraction of the ventral rumen in stunned sheep whose viscera were exposed in a saline bath. Bilateral stimulation of the peripheral ends of the cut cervical vagi caused stronger contractions of all compartments. Duncan, (1953) in conscious sheep and Iggo, (1956) using decerebrate sheep, besides many others, showed that blocking or sectioning of the cervical vagi resulted in complete loss of rhythmic activity of the stomach. Unilateral or partial bilateral block of the cervical vagi reduced the amplitude and frequency of the gastric movements. Duncan, (1953) stated that unilateral cervical vagotomy in conscious sheep slightly disturbed the appetite and rumination for a few days, followed by an apparently complete compensation for the loss of half of the vagal fibres. It is also known that the dorsal vagal trunk plays a greater role in the innervation of the rumen than does the ventral vagal trunk. Thus Weiss, (1953) found that section of the dorsal abdominal vagal trunk markedly reduced the force and frequency of primary and secondary cycle contractions of the rumen and eructation for the first twenty days, after which progressive recovery took place. Section of the ventral vagal trunk has given variable results. Duncan, (1953) observed reticulo-ruminal motility was depressed only for one or two days while Weiss, (1953) found that the force of both primary and secondary cycle ruminal contractions was doubled and remained so for eight days after section of the ventral vagal trunk. From that time onwards progressive reduction in the force and frequency of primary cycle contractions took place without affecting the secondary cycle contractions and eructation. Conversely, electrical stimulation of the dorsal vagal trunk through surgically implanted electrodes cranial to the cardia, increased the force

and frequency of reticulo-ruminal contractions for primary and secondary cycles and the frequency of eructation, while stimulation of ventral vagal trunk, though increasing the frequency of reticulo-ruminal contractions, did not increase the frequency of eructation in cattle (Stevens & Sellers, 1959).

Electrical stimulation of the vagi in an afferent sense has also been found to alter the force and frequency of reticulo-ruminal movements. Thus, Iggo, (1951; 1956) using decerebrate sheep, demonstrated that in those preparations which did not show spontaneous gastric activity, movements were elicited by brief electrical stimulation (20 to 100 c/s for 5 to 20 sec) of the central cut end of the cervical, thoracic or abdominal branches of the vagi. Reid & Titchen, (1965) using similar preparations showed that secondary cycle contractions of the rumen could be evoked by electrical stimulation of the central end of a cut cervical vagus. This was brought about by establishing a background of excitability by gaseous distension of the rumen causing afferent nerve stimulation. Between 2 to 10 contractions followed stimulation of the cut central end of one cervical vagus. Such stimulation was ineffective when intraruminal gas pressure was less than 2 cm $H_2O$, or the other cervical vagus had also been cut or atropine at 0.1 to 0.2 mg/kg body weight had been administered. They also indicated that secondary cycle contractions of the rumen could be elicited by stimulation of the peripheral end of a cut cervical vagus at lower frequencies (6/sec) as compared to primary cycle contractions (20/sec or above).

Clark, (1953) using decerebrate sheep suggested that the reticulo-ruminal centre was located in a sub-cortical area anterior to the hypophysis cerebri and not in the medulla oblongata. This was contrary to an earlier postulation, by Iggo, (1951) that a 'reticulo-ruminal motor

centre' existed in the brain stem caudal to an intercollicular plane in decerebrate sheep. Bell & Lawn, (1955) by systematic exploration of the medulla oblongata produced evidence that electrical stimulation of the lateral reticular formation in a zone extending 6 mm rostral and 2 mm caudal to the obex evoked reticulo-ruminal contractions. These responses were consistent and reproducible even after transection of the rhombencephalon at pontine level and the spinal cord at the first cervical vertebra. The reactive loci were mainly in the dorsal part of the lateral reticular formation. Andersson, Kitchell & Persson, (1959) elicited reticulo-ruminal contractions by electrical stimulation of an area 2 mm rostral and 1 mm caudal to the obex in the medulla oblongata of conscious goats. The reticulo-ruminal movements were more pronounced if the site of stimulation was located near the mid line close to the raphe.

Iggo, (1951) suggested that the 'reticulo-ruminal motor centre' received vagal afferent impulses which could influence its activity and trigger the reticulo-ruminal contractions. Different forms of sensory stimuli (tactile, stretch, distension or chemical) from within the forestomach or other parts of the stomach (e.g. Phillipson, 1939; Weiss, 1953; Iggo, 1956; Stevens & Sellers, 1959; Iggo & Leek, 1966) have been known to influence the amplitudes, form and frequency of reticulo-ruminal contractions.

As yet very little is known about the central control of eructation reflex and no experimental proof has been presented of the existence of an eructation centre. The facts that the glottis remains open during the expulsive phase of eructation (Dougherty et al. 1962 b), the stimulation of an eructation inhibitory reflex due to the presence of ingesta, foam or other non-volatile material around the cardia (Dougherty et al. 1958) and the stimulation of eructation reflex by gaseous distension of the reticulo-

rumen and not by the irritation of walls by scabrous material (Weiss, 1953) are indications of the presence of an eructation centre in the brain stem.

Factors affecting the reticulo-ruminal motility and eructation

There is strong evidence (Comline & Titchen, 1957; Ash & Kay, 1959; Stevens & Sellers, 1959; and Titchen & Reid, 1965) that reticulo-ruminal motility, eructation and salivary secretion are governed in part by reflexes originating in the forestomach. Natural stimuli responsible for these reflex functions are provided by the feed taken and the end pro-:ducts of microbial digestion in the reticulo-rumen. Stimuli arising from other parts of the stomach as well as from the lower digestive tract reflexly influence the efficiency of these phenomena (Phillipson, 1939; Weiss, 1953; and Titchen, 1958 a). Broadly speaking these stimuli can be classified as tactile, pressure or tension, stretch and chemical.

An increase in the intraruminal pressure or tension on the fore-stomach wall and tactile stimulation of the mucosa, (especially of the cardiac area, rumino-reticulo fold, cranial pillar, ventral wall of the reticulum and reticular groove) increases the rates of reticulo-ruminal movements, eructation and salivation (Weiss, 1953; Comline & Kay, 1955; Titchen, 1958 a; Stevens & Sellers, 1959 and Salmin, 1960). Iggo, (1956) and Titchen, (1958 a) using decerebrate sheep showed that stretching the reticulum and rumen with air-or fluid-filled balloons resulted in a series of contractions of the organs which increased in force and frequency if the volume of air or fluid in the balloon was increased. When the balloon was returned to its original volume, the contractions disappeared or were reduced in frequency. This observation has been confirmed by Leek. (1966) who recorded reticular contractions in anaesthetized sheep and also indicated that insufflation of the reticular balloon beyond 1 l. reflexly caused a reduction both in the amplitude and

the rate of contractions of the organ.

The presence of receptors in the rumen sensitive to gas distension was suggested by Weiss, (1953) who thought that the greater sensitivity of the caudo-dorsal blind sac relative to the cranial sac, was responsible for the increased rate of secondary cycles and eructation when intra-ruminal pressure was raised by insufflation. Doughterty et al. (1958) surgically removed most of the rumen in decerebrate sheep and then clamped off and insufflated the remaining pocket of reticulum, cardia and cranial sac and found that eructation continued as before; this suggests that an important number of receptors are also located in these areas and are stimulated by pressure or distension. The presence of an eructation inhibition reflex was also demonstrated by the same investigators by sub-mersion of the cardia with ingesta or fluid. This reflex disappeared after the topical application of a local anaesthetic (Butacaine sulphate) to the area around the cardia. These results were later confirmed by Stevens & Sellers, (1959), who also showed that the application of a local anaesthetic (Butacaine sulphate 5 to 10% solution) to the dorsal ruminal walls including the cardia inhibited eructation and reduced the rate and amplitude of dorsal ruminal sac contractions. Anaesthesia of the caudo-dorsal blind sac alone had no apparent effect.

The reaction of the rumen contents is maintained within the pH range of approximately 5.5 to 7.3 (Kay & Hobson, 1963). This is partly due to the buffering action of the continuous inflow of alkaline saliva and partly due to the absorption of volatile fatty acids through the ruminal wall. Any change from the normal pH range has been reported to inhibit the reticulo-ruminal motility. Clark & Lombard, (1951) found that administration of alkali through a rumen fistula or by intravenous in-:jection in sheep caused ruminal paralysis. Weiss, (1953) gave graded doses of sodium carbonate through a rumen fistula in sheep and demonstrated

that the primary cycle contractions of the reticulo-rumen were reduced in both force and frequency; the secondary cycle contractions continued to occur. Ash, (1959) did not find any effect on reticular movements by the addition of alkaline buffer solutions (0.1 M sodium phosphate pH 7.9 to 8.1 and 0.1 M glycine - NaOH - NaCl pH 9.2 to 10.1) and 0.5 M $Na_2CO_3$ solution pH 9.0. In only one experiment did he find that the forestomach motility was inhibited for a short period after 30 minutes from the addition of 0.5 M $Na_2CO_3$ solution.

Clark & Lombard, (1951) stated that administration of 100 ml. of N. HCl into the rumen or 150 ml. of 1% solution of lactic or acetic acid intravenously did not elicit any change in reticulo-ruminal motility. Ash, (1956) on the other hand, found that (0.1 to 0.2 M) buffer solutions of acetate, propionate and butyrate in the pH range 3.6 to 4.0 completely abolished reticulo-ruminal contractions for 30 to 90 minutes within 3 minutes of the addition of acid solutions into the rumen. The same investigator (1959) demonstrated that acidification of the forestomach walls with acetic, propionic or butyric acid vapours inhibited the move-:ments when the intraruminal pH was 4.5 to 5.0 or less. Buffered solution of lactate (pH 3.6 to 4.0) phosphate and citric acid (pH 3.8 to 4.0) and glycine and HCl (pH 3.0) did not cause inhibition.

Inhibition of reticulo-ruminal movements during alkalosis was thought to be of central origin by Clark & Lombard, (1951) but Phillipson, (1955) suggested that the inhibition might be due to stimulation of sensory nerve endings in the rumen epithelium. This suggestion was later supported by Ash, (1959) who stated that the effects obtained with acid or alkali solutions were not a surface pH effect but were related to the rapid penetration of the free fatty acid solutions through the stomach epithelium and the stimulation of sensory nerve endings in the walls of rumen and

reticulum.

Despite the work of Schalk & Amadon, (1928), Weiss, (1953), Ash, (1959) and Reid, (1960) and many others, there was much uncertainty about the site of origin of the secondary cycle contractions of the rumen and of the influence of various regulating factors on the primary and secondary cycles of the reticulo-rumen. Since secondary cycles and eructation have been closely correlated, it was decided to make a detailed study of secondary cycle contractions of the rumen and the effect of some of the factors influencing them in the hope that this would throw some light on the regulation of the cyclic activity and also on eructation.

# METHODS

## 1. Experimental animals

Twenty-two Scottish Blackface, 2 Crossbreds and 1 Cheviot sheep all over 1 year old and weighing 27 to 49 kg were used.

Ten sheep were surgically prepared by chronic fistulation for fixation of rumen cannulae and 15 were used for the insertion of micro-:cannulae in the reticulo-ruminal wall.

### Management routine

(a) Pre-operative: The sheep were kept at pasture until 2 to 6 weeks before they were required and then transferred to an indoor pen in batches of up to 6. Hay and water were provided ad lib. This ration was supple-:mented with bran and crushed oats if and when required.

(b) Post-operative: After the operation the cannulated sheep, as well as those with microcannulae, were preferably housed in a separate pen and were given the same ration. They received 0.5 M units penicillin and 0.5 g. dihydrostreptomycin (brand 'Strypen' - M & B) injected intra-:muscularly for 4 to 5 days so as to avoid any infection. The cannulated sheep could live healthily for many months, unless some experiments involving the removal of ruminal contents were performed on them. Two cannulated sheep lived for more than a year.

The sheep with microcannulae were kept for 7 to 10 days after which they were killed because of the formation of fibrous tissue around the im-:planted microcannulae as a result of which the recorded pressure changes became less and ultimately disappeared. The positions of the micro-:cannulae were subsequently located by post-mortem examination.

## 2. Materials

### Rumen cannulae

The rumen cannulae of type shown in Fig. 1 varying from 2.5 cm 1.D; 3.0 cm O.D; to 3.7 cm 1.D; 4.4 cm O.D. were used throughout. This type was developed by Mr. B.F. Leek of the Department of Veterinary Physiology, Royal (Dick) School of Veterinary Studies, Edinburgh for chronic use in sheep. The cannulae were made from polythene tubing of diameters mentioned above. The preparation of this cannula for insertion into the rumen has recently been described by Howard (1966).

### The microcannulae

The microcannulae (Fig. 2) were prepared from polythene tubing with varying internal diameter (1-2.5 mm) and external diameter (2.5-3.5 mm). Best results were obtained with a narrow-bore polythene tubing having 2.0 mm 1.D and 3.0 mm O.D. (brand Sterivac cannula, Allen & Hanburys Ltd., London, E.2.).

### Preparation of the sensitive portion of the microcannula

Depending upon the site into which the microcannula was to go in the reticulo-ruminal musculature, lengths varying between 10-25 cm of the narrow-bore polythene tubing were taken. One end of each tube was warmed on a low bunsen flame and clamped with artery forceps so as to form a broad 'head-end' of the tube with a fine hole in the centre made with a red-hot needle for subsequent use. Approximately $\frac{1}{2}$ to 1 cm from the head end, the tube was carefully warmed on the low bunsen flame to the extent that it did not melt or burn, after which gently stretching and blowing through the open end of the tube resulted in a small, sensitive, thin-walled 'bubble-like' portion on cooling. By careful warming the open end was drawn into a thread-like structure 2-3 cm long and then closed. This was called the 'tail-end'.

Fig. 1. The cannula assembly used for chronic insertion into the mid-dorsal sac of the rumen.

A = the cannula with its lugs which were tied together by a thread before insertion into the rumen.

B = rubber washer passed over the barrel of the cannula to keep it in position.

C = rubber bung used to close the open end of the cannula.

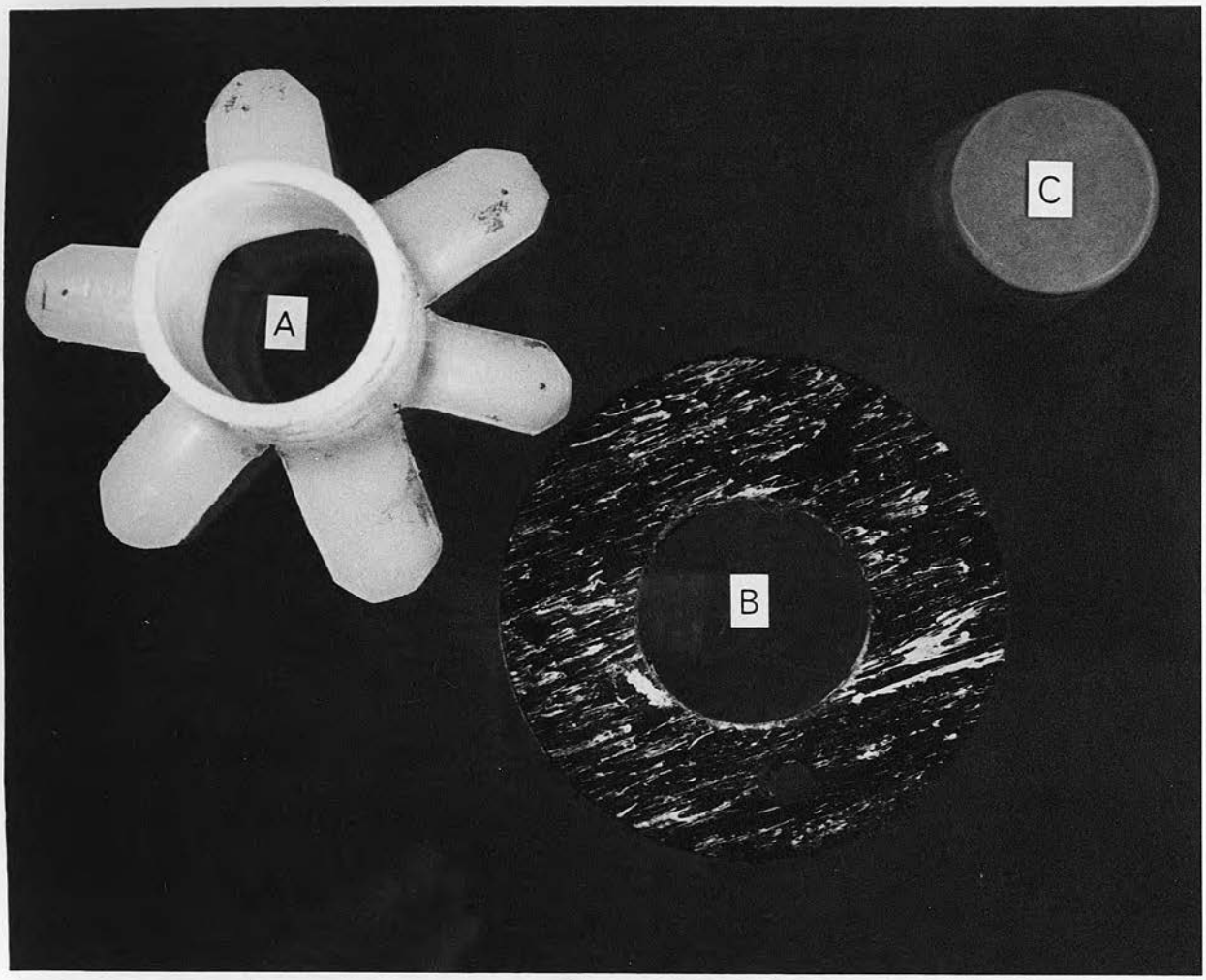

A
B
C

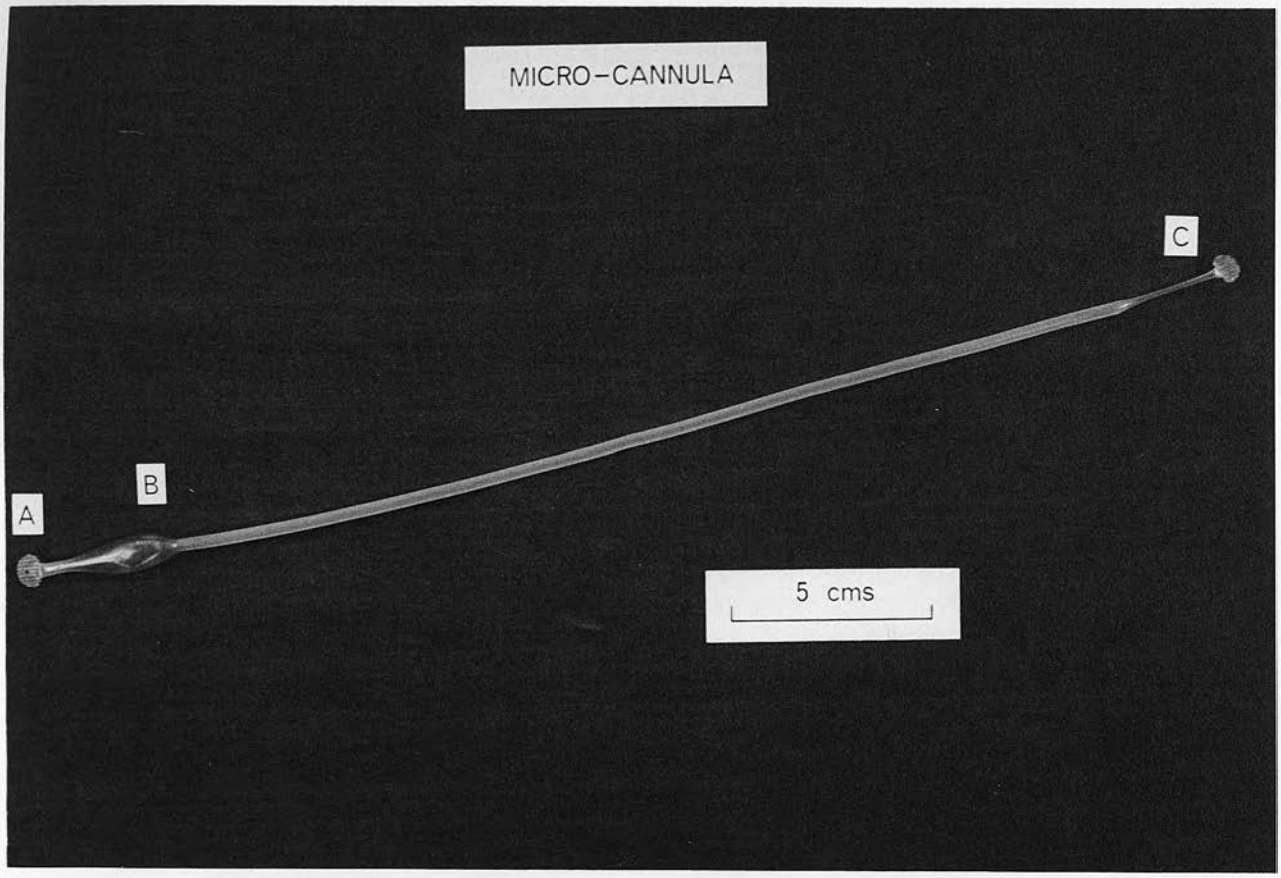
Fig. 2. A narrow-bore polythene microcannula used for insertion into the reticulo-ruminal wall at discrete locations.

A = head-end of the microcannula.

B = sensitive, bubble-like portion of the microcannula.

C = tail-end of the microcannula.

The bubble-like portion was inserted into the muscular layers of the reticulo-rumen.


MICRO-CANNULA
A
B
C
5 cms

Stiff polythene pressure lines, small balloons (3 cm diameter), 1 l. and 4 l. anaesthetic bags were used for recording the pressure events from different compartments of the forestomach.

Gas mixture for insufflation

The gas mixture used for insufflation in these experiments throughout was 95% oxygen and 5% carbon dioxide.

Solutions:

(i) o.9% (w/v) normal saline
(ii) 0.18 N- $Na_2CO_3$ pH 10.1
(iii) 0.18 N- KOH pH 12.4
(iv) 0.205 N HCl pH 0.74
(v) 0.205 N- acetic acid pH 2.7

These solutions were prepared and kept at 39°C in a warm water-bath.

Apparatus:

(i) Kymographic recording drum with paper and Marey Tambours.
(ii) Devices 8-channel hot-wire pen-recorder with heat sensitive paper.
(iii) Strain gauge pressure transducers.
(iv) Gas meter
(v) Vibret Laboratory pH Meter model 46A having 0-2.8 and 0-14 pH scales, with dual pH glass reference electrode system type SHDN 33/C and pH temperature compensator type T46A over the range 0-100°C (E.I.L. Surrey) The glass electrodes were calibrated at the working temperature of the solutions.
(vi) Dual phase respiration pump (Model 607 D. Harvard Apparatus Co., Dover, Mass. U.S.A.)
(viii) Vacuum pump (Type RBF 3. Vacuum pump and Compressor, Edwards High Vacuum Ltd. Crawley).

## 3. Surgical procedures

### (a) Rumen cannulation

Two sheep were each provided with two cannulae of the rumen, one at the level of the 12th rib and the other in the sub-lumbar triangle 13-14 cm apart. The other 8 sheep had each one mid-dorsal rumen sac cannula.

The operation was carried out under general anaesthesia using either pentobarbitone sodium 6.5% w/v solution (brand Sagatal - M & B) administered intravenously (0.5 ml/kg body weight) or fluothane (brand Halothane I.C.I.) administered from a shaped face-mask. Halothane was also used for maintenance anaesthesia and administered through an endotracheal tube by a circle type closed circuit method incorporating a respiration pump. An endotracheal tube was always passed into the trachea in order to combat respiratory failure or inhalation of regurgitated reticulo-ruminal contents. The left sub-lumbar triangle and requisite area around it was clipped, thoroughly scrubbed with soap solution and sterilized with absolute alcohol. The rumen was exposed by a vertical laparotomy incision of requisite length 4-5 cm caudal to the last rib and 3-4 cm below the transverse processes of the lumbar vertebrae under strict aseptic conditions. The wall of the rumen, after being withdrawn through the skin incision was held by a pair of peritoneal forceps. Using No. 1 catgut in a curved suturing needle, a purse-string pattern was sutured through the muscular layer of the small selected portion of the ruminal wall. Interrupted mattress sutures were then applied involving the rumen muscle, peritoneum, abdominal muscles and the skin on either side of the vertical skin incision. A slit was made in the centre of the purse-string sutured area of the ruminal wall for the insertion of the polythene cannula prepared and sterilized in the manner described by Howard (1966). This

was followed by invagination of the lips and tightening of the purse-string sutures, and slipping of the rubber washer over the barrel of the cannula to lie against the skin. The washer was secured in position by wrapping zinc oxide adhesive tape around the barrel. A rubber bung was used to close the opening of the cannula.

In the case of double cannulation, the cranial cannula was inserted at the level of the 12th rib. The skin was incised, rib exposed, periosteum separated, and requisite length of the rib excised 2-3 cm from its costo-vertebral junction to reach the cranial dorsal rumen. The rest of the procedure was similar to that described above.

In one sheep a 'split cannula' was inserted in the mid-dorsal ruminal sac using the same surgical procedure. A split cannula could be easily taken out of the rumen fistula after the surgical wound had healed.

The whole operation took half to one hour after which the animal was allowed to recover. Recovery was fast on halothane anaesthesia and the sheep were found eating hay within an hour after the operation. After pentobarbitone sodium, recovery was delayed for 1 to 2 hours or more.

(b) Implantation of microcannulae

The sites of insertion of sensitive parts of the microcannulae in the reticulo-ruminal musculature of different sheep are shown in Table 1, (opposite page 39)

(i) The rumen. The operations were carried out under general anaesthesia using the drugs already mentioned. The left sub-lumbar triangle and an area 8-10 cm cranial and ventral from it was clipped, thoroughly scrubbed with soap solution and sterilized with absolute alcohol. Laparotomy was performed by a vertical incision 6-7 cm long,

4-5 cm behind the last rib in the sub-lumbar triangle and the rumen exposed under strict aseptic conditions. Desired areas of the rumen musculature were manually explored, brought to the surface one by one and held in peritoneal forceps. A straight needle with the tail-end of the polythene tubing passed through its hole was gently pulled through the muscle layers so as to make the sensitive portion of the tube lie at its intended place of insertion. Comparatively less resistance to the passage of tube was encountered if it was passed across the direction of the muscle layers. To check the movements of the sensitive portion of the polythene tubing or its being pulled out by other external means (sheep in the pen or movements of the animal during recording) it was ligatured to the ruminal wall by a nylon thread through the fine hole in the head-end and close to the sensitive portion of the tube on the other side. After having inserted the sensitive portion in a discrete location of the rumen musculature, the organ was gently pushed back to its position in the abdominal cavity.

In a few cases approach to the cranial ruminal sac was made through the same site and using the same procedure as for reticulum described below.

(ii) The reticulum. In eight out of these fifteen sheep sensitive portions of the narrow-bore polythene tubing were also inserted into the layers of reticular musculature. Access to the reticulum was obtained through a separate skin incision at the lower level of the 10th rib. The rib was exposed, periosteum separated and approximately 5 cm of the rib excised 3-4 cm from its costo-chondral junction. The diaphragm was incised for 2-3 cm to reach the abdominal cavity. The reticulum was located manually, brought to the body surface and held in peritoneal forceps. The rest of the procedure for inserting the sensitive portion of

the narrow-bore polythene tubing into the reticular wall was similar to that of the rumen. The usual site of insertion was the cranial wall of the reticulum near its ventral pole. The organ was gently pushed back into the abdominal cavity after the insertion.

During the insertion of the sensitive portion of the polythene tube in the reticular wall, positive pressure respiration was applied with a dual phase respiration pump (stroke volume 300 to 350 ml, rate 24/min) through the endotracheal tube.

The abdominal wound in the sub-lumbar triangle was closed by two layers of continuous gut sutures followed by interrupted horizontal mattress sutures to close the skin wound using No. 2 B.P.C. nylon thread. Similarly the thoracic wound was closed using two layers of continuous sutures and one row of interrupted mattress sutures for the skin. During the final closure of the thoracic wound the lungs were fully distended by blowing down the endotracheal tube so as to remove the air from the thoracic cavity.

The tail-ends of all the microcannulae were kept outside the body surface and labelled with a tape for future recognition.

4. Recording of jaw, oesophageal and reticulo-ruminal activity

The sheep were trained to stand in a metabolism cage for recording the reticulo-ruminal activity. The techniques used were:

(a) In cannulated sheep

(i) Direct visual observation and manual exploration of the internal surfaces of the reticulo-rumen in sheep with large rumen fistulae.

(ii) Classical manometric recording of the contractions of different compartments of the forestomach using air-filled pressure lines consisting

of stiff polythene tubing, ending in small balloons (3 cm diameter) intro-:duced through ruminal cannulae. The stiff polythene tubes bearing the balloons were passed through holes made in a rubber bung which fitted in the opening of the cannula. The pressure events associated with the con-:tractions were recorded either on smoked kymographic paper using Marey tambours or on heat sensitive paper using a Devices 8-channel hot-wire pen-recorder and strain-gauge pressure transducers.

(b) In sheep with implanted microcannulae

The pressure events associated with contractions of the reticulo-ruminal musculature were recorded on heat sensitive paper using a Devices 8-channel hot-wire pen recorder and strain-gauge transducers. In those cases in which a microcannula was not implanted in the reticular wall, intraluminal contractions were recorded from a finger-cot balloon tied to one end of an alkathene tube passed intranasally. The usual com-:bination of these microcannulae in a chronic preparation recording was as shown in Table 1 (opposite page 39)

The jaw movements were recorded from a slightly inflated balloon tied at one end of a stiff polythene pressure line and placed underneath the jaw. The oesophageal activity was recorded either by a slightly inflated balloon tied to the neck so as to lie in the jugular furrow where the oesophagus was superficial or by a finger-cot balloon tied to one end of an alkathene tube passed intranasally to lie in the lower third of the cervical oesophagus, through a pressure transducer.

Any variation from the above mentioned recording techniques will be dealt with in the section concerned.

## RESULTS

The nomenclature of the structures referred to in the text is that used by Habel (1965) and adopted by International Committee on Veterinary Anatomical Nomenclature. An attempt has been made to follow it as far as possible except for 'rumino-reticulum' which has been mentioned as reticulo-rumen.

### Visual observation and manual exploration of the internal surfaces of the reticulo-rumen

Visual observation of the internal surfaces of the reticulo-rumen through a large rumen fistula was limited to the dorsal ruminal sac in two sheep with full rumen after morning feeding. The top layer of the ingesta consisted of freshly ingested moist hay fibres of different dimensions floating on the rest of ingesta in the cavity of the dorsal rumen. With each primary cycle contraction of the dorsal ruminal sac, the coarse hay fibres were seen to be pushed backward from the cranial region and forward from the caudal region towards the central opening, between the dorsal and ventral ruminal sacs and then pressed into the latter. Four to seven seconds later the ingesta started moving upwards in the directions of cranial and caudal regions of the dorsal ruminal sac. This was not a constant observation and was thought to be due to a contraction of the ventral ruminal sac. During the primary cycle contraction the walls of the dorsal ruminal sac tend to converge towards the centre of the organ. The intervals between successive primary cycles, were recorded by a stop-watch and varied between 57 to 86 sec for a period consisting of 60 contractions. In between these primary cycles, movements of the ingesta due to secondary cycle contractions of the dorsal rumen at variable intervals (13 to 39 sec) also occurred after every 2 to 3 primary cycles. In this case the ingesta were noticed to be pushed forward and downward

into the ventral sac, followed by an upward and forward push similar to primary cycles due to a contraction of the latter organ. During the period of observation gases continuously escaped from the dorsal rumen and when a primary or a secondary cycle contraction took place, gas escaped more rapidly.

When the semi-solid fibrous shelf of rumen ingesta was removed and the forestomach explored manually, the reticulum and the ventral sac were found to contain semi-liquid contents having a gruel-like consistency. For observing the movements of the reticulo-rumen and their contents, the semi-liquid ingesta were either left as such or completely removed, the organs washed and then filled with warm water slightly above the level of the cranial pillar. The right hand was inserted through the fistula in such a way that the first finger rested in the middle of the reticular cavity, the thumb on the ventral wall of the cranial dorsal sac, the second finger touched the medial wall of the cranial sac and the third and small finger over the cranial pillar and into the ventral ruminal sac. The fore-arm could sense the contraction of the wall of the dorsal ruminal sac. During the first reticular contraction the reticular contents made a swirling move-:ment within the organ and partly overflowed into the cranial dorsal sac. Immediately following this the reticulum underwent a second but powerful contraction together with the rumino-reticular fold and bringing its ventral pole towards the rumino-reticular opening poured its contents into the cranial sac which being in a state of relaxation was ready to receive this addition. Before the second reticular contraction had reached its peak, the cranial pillar and the cranial ruminal sac started contracting. In order to observe the activity in the caudal regions of the rumen, the right hand was taken out and the left hand inserted so that the thumb rested in the caudo-dorsal blind sac, the palm touched the caudal pillar and the

rest of the fingers lay in the ventral ruminal sac. The movements of the dorsal wall could be simultaneously observed by the arm. The activity of the caudal pillar, the dorsal coronary pillar and the caudo-dorsal blind sac closely coincided with the activity observed in the cranial region. The activity of the ventral ruminal sac presented a varied observation and has been quantitated by balloon recording method (Table 2). However, frequently the ventral ruminal sac showed a con-:traction 7 to 10 sec after the dorsal rumen had finished its relaxation. The contraction began at the ventral coronary pillars accompanied by the caudal pillar and the musculature of the ventral sac. The movements of the liquid ingesta or warm water, if the digesta had been removed, observed visually or detected by hand showed the directions mentioned previously.

In the case of secondary cycle contraction of the dorsal rumen, the activity was first noticeable in the dorsal coronary pillars and the caudo-dorsal blind sac accompanied by a contraction of the cranial and caudal pillars. No activity could be observed by hand in the ventral wall of the cranial sac for the secondary cycles. The ventral ruminal sac contraction resembled the one for primary cycle. The movements of the ingesta were found to be downward and forward during the dorsal ruminal sac contract-:ion and upward and forward during the ventral sac contraction.

When the fistula was completely closed by the arm or by wrapping paper towels around the arm and keeping the semi-liquid ingesta inside the forestomach, it was possible to observe an eructation taking place at the peak of the secondary cycle contraction of the dorsal rumen.

The sequence of movements of ingesta as observed visually and by manual exploration is represented diagramatically in Fig. 3.

Fig. 3. Schematic representation of the sequence of movements of ingesta during the primary and secondary cycle contractions of the reticulo-rumen as observed visually and by manual exploration.

I. Movements of ingesta due to primary cycle contraction of the reticulum and dorsal ruminal sac.

II. Movements of ingesta due to secondary cycle contraction of the dorsal ruminal sac.

III. Movements of ingesta due to contraction of the ventral ruminal sac in both primary and secondary cycles.

Primary cycle

Secondary cycle

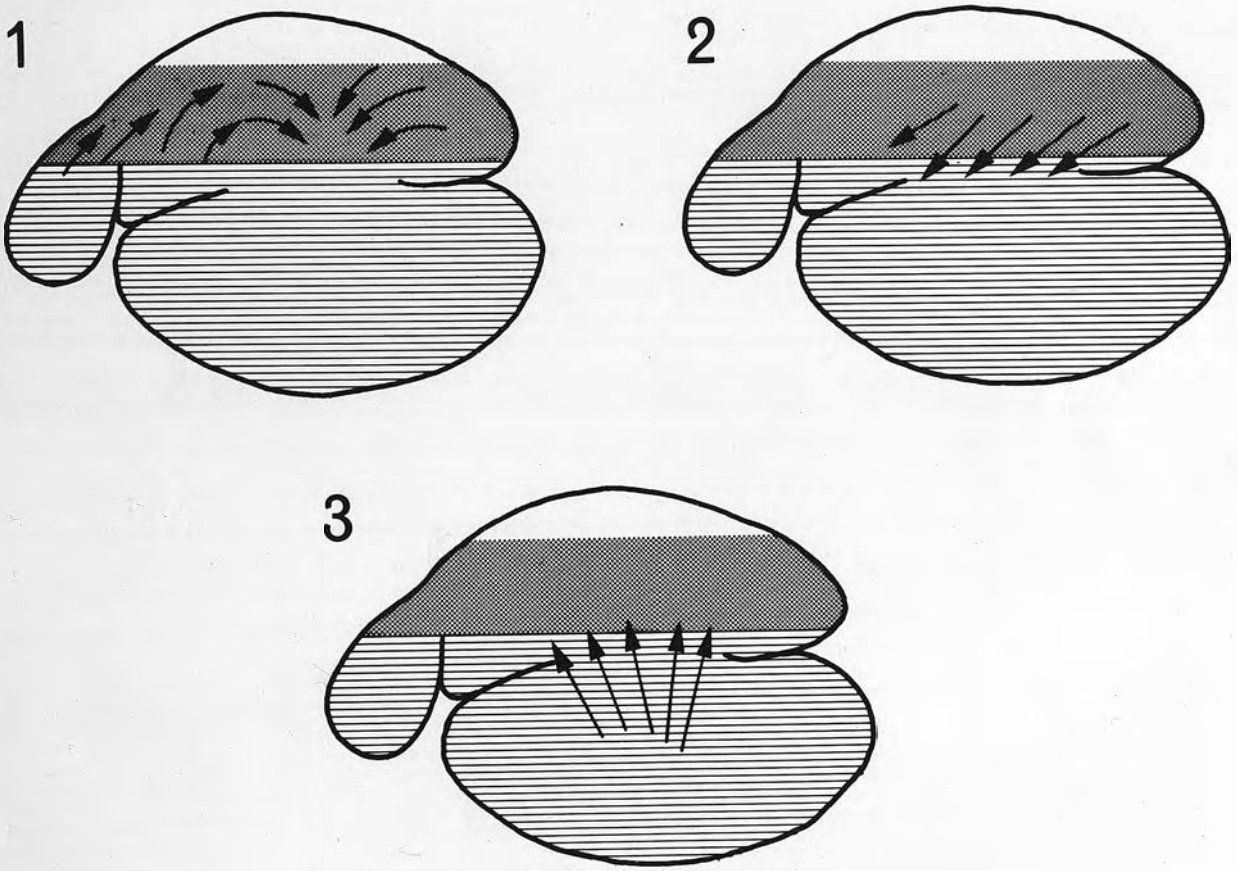


Table 2. Incidence of contractions (mean %) in the rumen in respect of primary and secondary cycles in sheep.

| Sequence of Contractions | $D_1$ | $D_1$ $V_1$ | $D_1$ $V_1$ $D_2$ $V_2$ | $D_1$ $V_1$ $D_2$ | $D_1$ $D_2$ $V_2$ | No. of Contractions for each group |
|---|---|---|---|---|---|---|
| Resting | 11.6 | 34.7 | 27.2 | 3.5 | 23.0 | 1785 |
| Ruminating | 24.2 | 32.2 | 8.0 | 1.7 | 33.9 | 337 |
| Eating | 0 | 35.3 | 60.7 | 0 | 4.0 | 219 |

$D_1$ = Dorsal Rumen contraction for primary cycle.

$D_2$ = Dorsal Rumen contraction for secondary cycle.

$V_1$ = Ventral Rumen contraction for primary cycle.

$V_2$ = Ventral Rumen contraction for secondary cycle.

The respective compartments of the rumen contracted in the order indicated in the top column.

These values have been obtained from a total of 2341 contractions from 5 sheep.

During 'ruminating' 24.2% of dorsal ruminal sac ($D_1$) contractions include 43 contractions from 1 sheep in which the ventral sac did not contract for primary cycles. This was unusual.

The reticulo-ruminal movements and eructation in sheep recorded by toy balloons

The normal movements for both primary and secondary cycles from different compartments of the reticulo-rumen in cannulated sheep were recorded for varying periods between 10.00 a.m. and 5.00 p.m. on many occasions. The form, frequency and force of these movements and their relationship to eructation was studied according to the state of the animal, i.e. (a) resting, (b) ruminating and (c) eating. Figures 4, 5 and 6 respectively show the activity of the reticulo-rumen during different states of the animal. The movements during the resting state of the animal were considered as control and then compared with those during ruminating or eating.

The form of the forestomach movements

Each primary cycle was initiated by a biphasic contraction of the reticulum. The first reticular contraction was always small, followed immediately with or without relaxation in between by a more powerful and sharp contraction. The relaxation between the two contractions was rarely complete and varied from day to day and sheep to sheep. The peaks of the two reticular contractions were separated from each other by a mean interval of 2.6 sec ($\pm$ S.D. 0.4 sec). Within a second of the beginning of the second reticular contraction and before it had reached its peak, the balloons placed near the ventral surface and in the upper regions of the cranial sac, the mid-dorsal and caudo-dorsal blind sac started recording a contraction of the primary cycle; if this was not followed by a secondary cycle, the ventral ruminal sac started contracting 6.8 sec (S.D. $\pm$ 1.6 sec) after the dorsal rumen had finished its contraction. The usual order of contraction in the rumen during primary cycles was

cranial sac, mid-dorsal sac, caudo-dorsal blind sac and ventral ruminal sac. Quite often if a secondary cycle closely followed a primary cycle, the ventral ruminal sac was found to miss its primary cycle contraction and contracted only after the secondary cycle contraction of the dorsal rumen (Fig. 7 and 8). The ventral ruminal sac presented a varied activity for both primary and secondary cycles. Table 2 shows the percentage incidence of ruminal contractions in respect of both primary and secondary cycles during the three recording states. Quite often the balloons placed in the mid-dorsal and caudo-dorsal blind sacs recorded a secondary cycle contraction, without the reticulum, while that placed near the ventral surface of the cranial sac did not register any increment in the base-line pressure. Immediately following the dorsal sac contraction, the ventral ruminal sac balloon started recording a contraction to mark the end of the secondary cycle (Fig. 7 and 8). The usual order of start of a contraction during a secondary cycle was caudo-dorsal blind sac, mid-dorsal sac and a slight rise in the base-line pressure in the cranial sac region, followed by a ventral ruminal sac contraction. It was rare to find the ventral rumen missing a contraction for the secondary cycle.

The primary and secondary cycle contractions of the caudo-dorsal blind sac were separated from each other by a mean interval of 15.98 sec during resting, 18.23 sec during ruminating and 19.27 sec during eating (Table 3). These differences between the intervals of primary and secondary cycles in the three states were found to be not statistically significant ($P > 0.05$) even in individual experiments. The mean durations of both primary and secondary cycle contractions of different compartments of the reticulo-rumen during resting, ruminating and eating states of sheep are shown in Fig. 4, 5, 6 and Table 4. The reticular contractions during rumination were found to be of longer duration (8.7 sec)

Table 3. Interval in seconds between primary and secondary cycle contractions of the caudo-dorsal blind sac. The measurements have been made from the peak of primary cycle contraction to the peak of secondary cycle contrac-:tion from 3 sets of 10 successive contractions in each experiment on different days. Three sheep were used.

| | | Resting | | | Ruminating | | | Eating | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Range | Mean | S.D. | Range | Mean | S.D. | Range | Mean | S.D. |
| Sheep I | (1) | 10-30 | 15.89 | 5.819 | 13-47 | 25.40 | 13.050 | 13-40 | 20.50 | 7.810 |
| | (2) | 10-27 | 16.69 | 5.570 | 13-30 | 21.43 | 5.798 | 10-30 | 21.34 | 6.572 |
| Mean | | | 16.29 | | | 23.41 | | | 20.92 | |
| Sheep III | (1) | 10-40 | 15.78 | 9.589 | 13-27 | 16.14 | 5.146 | 10-30 | 19.06 | 5.434 |
| | (2) | 7-30 | 13.07 | 9.211 | 6-19 | 15.78 | 2.809 | 7-27 | 16.61 | 6.321 |
| Mean | | | 14.42 | | | 15.96 | | | 17.83 | |
| Sheep V | (1) | 10-47 | 10.00 | 9.781 | 7-30 | 14.44 | 8.354 | 13-30 | 20.50 | 3.486 |
| | (2) | 13-53 | 24.50 | 13.308 | 13-30 | 16.21 | 4.441 | 10-43 | 17.62 | 9.557 |
| Mean | | | 17.25 | | | 15.32 | | | 19.06 | |
| Over-all mean from 3 sheep | | | 15.98 secs | | | 18.23 secs | | | 19.27 secs | |

The intervals between primary and secondary cycle contractions of the caudo-dorsal blind sac were not significantly different from each other during the three recording states.

Table 4. Mean duration in seconds ± S.D. of primary and secondary cycle contractions of different compartments of reticulo-rumen during resting, ruminating and eating. The measurements have been made from the onset of a contraction to the end of its relaxation in each compartment from 12 successive contractions in three sheep on different days. Recordings were made with intraluminal balloons.

| | Reticulum | | Dorsal Rumen | Caudo-dorsal blind sac | | | Ventral sac | |
|---|---|---|---|---|---|---|---|---|
| | Primary cycle | P | Primary cycle | Primary cycle | Secondary cycle | P | Primary cycle | Secondary cycle |
| Resting | 5.9 ± 0.7 | <0.05 | 7.8 ± 0.7 | 7.8 ± 0.7 | 6.2 ± 1.1 | 0.05 | 7.8 ± 1.0 | 7.9 ± 1.7 |
| Ruminating | 8.7 ± 0.9 | 0.01 | 8.0 ± 0.8 | 8.0 ± 0.8 | 6.1 ± 0.9 | <0.05 | 9.2 ± 1.2 | 7.4 ± 0.4 |
| Eating | 5.7 ± 0.9 | | 9.0 ± 1.0 | 9.0 ± 0.9 | 7.8 ± 0.8 | >0.05 | 8.1 ± 1.0 | 8.3 ± 1.0 |

The value of P in the reticular column was obtained by comparing the duration of reticular contractions during 'resting and ruminating' and during 'eating and ruminating'.

The value of P in the caudo-dorsal blind sac column was obtained by comparing the duration of primary and secondary cycle contractions of the compartment during the three recording states.

The secondary cycle contractions of the caudo-dorsal blind sac have significantly less duration than the primary cycle contractions of that compartment during resting and ruminating.

than those during resting or eating (5.9 and 5.7 sec respectively). This was due to an extra reticular contraction, at the peak of which regurgita-:tion took place, preceding the usual biphasic contraction during resting or eating. Additionally the first reticular pressure change following regurgitation was either of a very low amplitude or absent. The mean durations of the ruminal contractions for primary cycles were not signifi-:cantly different ($P > 0.1$-$0.05$) during all the three states. The secondary cycle contractions of the caudo-dorsal blind sac were found to be of shorter duration and had finer peaks as compared to the primary cycle contractions from the same region during resting, ruminating and eating.

The secondary cycle contractions of the dorsal rumen on reaching their peaks were usually accompanied by an eructation. The respiratory movements were checked in their expiratory phase and an eructation took place during a comparatively low intra-oesophageal pressure. The oesophageal balloon recorded 1 to 4 quick contractions during the process of eructation. The sheep when standing calm and undisturbed were also found to raise their head slightly when an eructation took place. On some days during an experiment extending over a period of 2 to 3 hours, 1 to 3 secondary cycle contractions of the dorsal rumen were found to be not accompanied by an eructation. An eructation rarely accompanied a primary cycle contraction of the dorsal rumen.

The frequency and the amplitudes of the reticulo-ruminal movements

Figures 9, 10 and 11 show the mean frequencies of both the cycles, and eructation, the ratio between primary and secondary cycles and the amplitudes of contractions of different compartments of reticulo-rumen. These parameters were found to vary with the activity of the animal and from day to day in the same animal. Fig. 9 displays the mean frequencies

of primary and secondary cycles and eructation in the same sheep over a five day period. During standing and resting, the means ranged from 7-10/10 minutes for primary cycles and 4-6/10 minutes for secondary cycles and eructation. These values increased during rumination to 11-14/10 minutes for primary cycles and 6-8/10 minutes for secondary cycles and eructation. During eating the values ranged 11-13/10 minutes and 7-9/10 minutes respectively on different days. The mean intervals between successive primary cycles varied from 58.5 to 69.5 sec, 49.5 to 53.2 sec and 47.8 to 54.3 sec during resting, ruminating, and eating while for secondary cycles and eructation they ranged between 102.5 to 135.5 sec, 48.4 to 108.0 sec and 45.7 to 104.3 sec respectively. This increase in the frequencies or decrease in the mean intervals between successive primary cycles during rumination or eating was found significant ($P \leq 0.01$) while in the case of secondary cycles and eructation the increase was significant at values of P varying between 0.05 to 0.01.

The mean amplitudes (measured as a pressure increment) ranged between 9 to 13.0 mm Hg for reticular, 8 to 12 mm Hg for caudo-dorsal ruminal blind sac and 2.5 to 5.0 mm Hg for ventral ruminal sac con-:tractions for primary cycles during resting over a five day period. For secondary cycle contractions the ruminal compartments registered pressures in the same range as for primary contractions but it was unusual to find them having the same values for individual contractions during an experiment, particularly in the dorsal rumen. In some experiments the secondary cycle contractions of the dorsal rumen showed comparitively low pressures throughout while in others the opposite was true even if the contractions were recorded from the same region.

Figure 11 shows the mean frequencies of primary and secondary cycles and eructation and the mean amplitudes of different reticulo-

ruminal compartments and oesophagus during resting, ruminating and eat-:ing, measured on half an hour basis from three sheep. Besides the usual increase in the frequency of cyclic activity and eructation during rumina-:tion and eating, the magnitude of pressure changes in different compart-:ments of reticulo-rumen was also affected. The increased frequency during rumination and eating was highly significant ($P = 0.001$) for primary cycles and significant ($P = 0.01$) between resting and ruminating and highly significant ($P < 0.01$) between resting and eating for secondary cycles and eructation. The values for secondary cycles and eructation between rumination and eating were also found to be increased significantly ($P \leq 0.01$). The mean reticular pressures during rumination decreased from resting values of 13 mm to nearly 7 mm Hg while during eating they increased to 16.0 mm Hg. The differences in reticular amplitudes between resting and ruminating or ruminating and eating were highly significant ($P \leq 0.001$) while between resting and eating they were significant at values of P varying between 0.01 to 0.002. The mean amplitudes of primary cycle caudo-dorsal blind sac contractions were found to increase from the resting values of 10 mm Hg to 12.5 mm Hg during rumination and 16.5 mm Hg during eating while for secondary cycle contractions, the values increased from 8.5 to 11 mm Hg during rumination and 16.5 mm Hg during eating. Resting and ruminating amplitude differences of the caudo-dorsal blind sac contractions were significant ($P \geq 0.01$) while for resting and eating or ruminating and eating they were highly significant ($P < 0.001$) for both primary and secondary cycles. The mean amplitudes of the ventral ruminal sac contractions ranged between 3 to 4 mm Hg and were found to be not significantly different during resting, ruminating or eating. The mean oesophageal contraction amplitudes, measured only for eructation, from the lower third of the cervical oesophagus by a balloon passed intra-nasally, were 15 mm Hg during resting and ruminating and 20.5 mm Hg

during eating. Whereas resting and ruminating oesophageal contraction amplitudes for eructation were not significantly different, resting and eating or ruminating and eating were highly significant (P = 0.001). Mean amplitudes of 7.6 mm Hg (± 1.86) from upper third of the cervical oesophagus and 28.72 mm Hg (± 6.65) from the thoracic region of the organ for eructation contractions were also recorded from different sheep. As mentioned previously (p. 34) the force of contactions of different compartments of the reticulo-rumen varies from day to day and animal to animal according to its activity. Except for reduced and steady reticular amplitudes during rumination, different compartments of the forestomach showed a varying range of amplitudes during resting and eating in different sheep on different days. Usually the reticular con-:tractions attained mean amplitudes of 7 to 13 mm Hg, dorsal rumen in its various compartments 8 to 12 mm Hg, while ventral rumen and caudo-ventral blind sac reached mean pressures of 2 to 6 mm Hg which showed little variations between themselves during resting.

The rhythm between primary and secondary cycles during resting was 2 : 1. During rumination it usually remained 2 : 1. The increase in the number of secondary cycles and eructation corresponded to that of the primary cycles and hence was rarely found to change the rhythm even if rumination continued as long as half an hour, but during eating with the increase in the frequency of secondary cycles and eructation the rhythm kept shifting between 2 : 1 and 1 : 1. A change from resting pattern to rumination or eating patterns always occurred more quickly than from ruminating to resting (the latter took 2 to 3 minutes). In one experiment two quiescent periods of 5 to 10 minutes were also recorded. A change from eating to resting patterns was not noticeable because during the last few minutes of eating the motility patterns closely resembled the resting ones.

Table 5. Comparison of intervals between primary cycles being followed by a secondary cycle (Group A) and primary cycles not followed by a secondary cycle (Group B) during resting.

| Sheep No. | | Group A Range (sec) | Group A Mean | Group A S.D. | Group B Range (sec) | Group B Mean | Group B S.D. | Significance of difference between (A&B) P | No. of cycles in each group |
|---|---|---|---|---|---|---|---|---|---|
| I | (1 | 53-80 | 69.13 | 8.493 | 50-83 | 65.95 | 8.764 | 0.05 | 45 |
| | (2 | 53-77 | 64.78 | 7.579 | 60-70 | 64.44 | 4.157 | >0.1 | 28 |
| | (3 | 50-73 | 59.94 | 6.412 | 47-73 | 53.71 | 6.031 | <0.05 | 54 |
| III | (1 | 67-97 | 73.70 | 8.845 | 60-67 | 63.86 | 3.185 | 0.01 | 40 |
| | (2 | 57-83 | 70.56 | 6.324 | 60-79 | 65.34 | 4.165 | <0.05 | 45 |
| V | (1 | 47-80 | 58.50 | 8.706 | 40-69 | 54.20 | 7.259 | <0.05 | 30 |
| | (2 | 50-90 | 61.18 | 10.285 | 47-77 | 61.00 | 9.659 | >0.1 | 35 |

The values have been obtained from 3 experiments in sheep I and two each from sheep nos. III and V on different days.

The measurements were made from the peak of one primary cycle contraction to the peak of the next primary cycle contraction of the caudo-dorsal blind sac.

The secondary cycles when present probably influence the frequency of the oncoming primary cycle.

Sheep starved for 16 to 24 hours showed slightly reduced frequencies of the cyclic activity and eructation and amplitudes of different compartments of the reticulo-rumen during resting but not during rumination. These values when compared with those of the same sheep recorded one day before were not significantly different ($P > 0.05$). If during an experiment the sheep were provided with food, there was an immediate increase in the frequency of cyclic activity and eructation and the force of reticulo-ruminal contractions. This increase in the frequency of reticulo-ruminal motility and eructation was highly significant ($P = 0.002$).

In order to ascertain whether the occurrence of a secondary cycle influenced the period between one primary cycle and the next primary cycle, the intervals between successive primary cycles from 7 experiments in 3 sheep were classified into groups A and B. Group A consisted of those primary cycles being followed by a secondary cycle, and Group B of those which were not followed by a secondary cycle, during resting. It was noticed that usually the interval between two successive primary cycles having a secondary cycle in between, was greater by 3 to 5 sec than those without a secondary cycle. These results when put to statistical analysis showed that in a majority of cases the value of P was 0.05 (Table 5). It is probable that the secondary cycles influence the occurrence of the following primary cycle.

Fig. 4. Hot-wire recorder tracing showing the pattern of reticulo-ruminal motility during primary and secondary cycles in the resting state. The balloons were placed (from above downward) under the jaw, and in the oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac. The oesophageal balloon was passed intra-:nasally to lie in the lower third of the cervical oesophagus. Note the occurrence of eructation (indicated by small dots under the oesophageal record) at the peak of each secondary cycle contraction of the caudo-dorsal blind sac. The secondary cycle contractions of the caudo-dorsal blind sac had finer peaks and were comparatively shorter than the primary cycles. Note also the frequency of primary and secondary cycles.

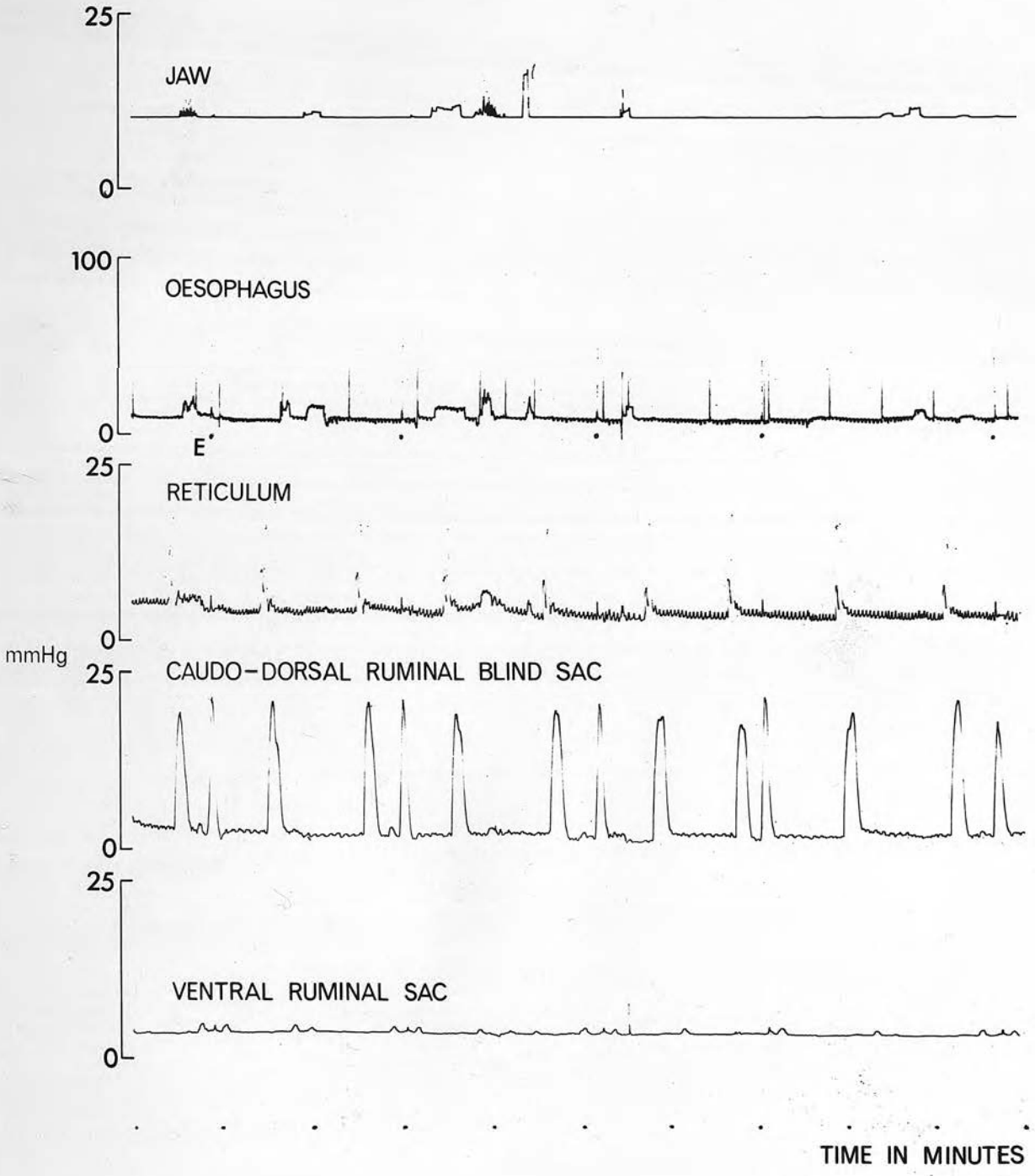

25
JAW
0
100
OESOPHAGUS
0
E
25
RETICULUM
0
mmHg
25
CAUDO-DORSAL RUMINAL BLIND SAC
0
25
VENTRAL RUMINAL SAC
0
TIME IN MINUTES

Fig. 5. Hot-wire recorder tracing showing the pattern of reticulo-ruminal motility in primary and secondary cycles during rumination. Balloons were placed (from above downward) under the jaw, and in the oesophagus, reticulum, caudo-dorsal blind sac and ventral rumen. The oesophageal balloon was passed intranasally to lie in the lower third of the cervical oesophagus.

Note the movements of the jaw during the remasticating phase of rumination, the frequency of primary and secondary cycles and eructation (indicated by small dots under the oesophageal record) and the form and amplitude of reticular contractions.

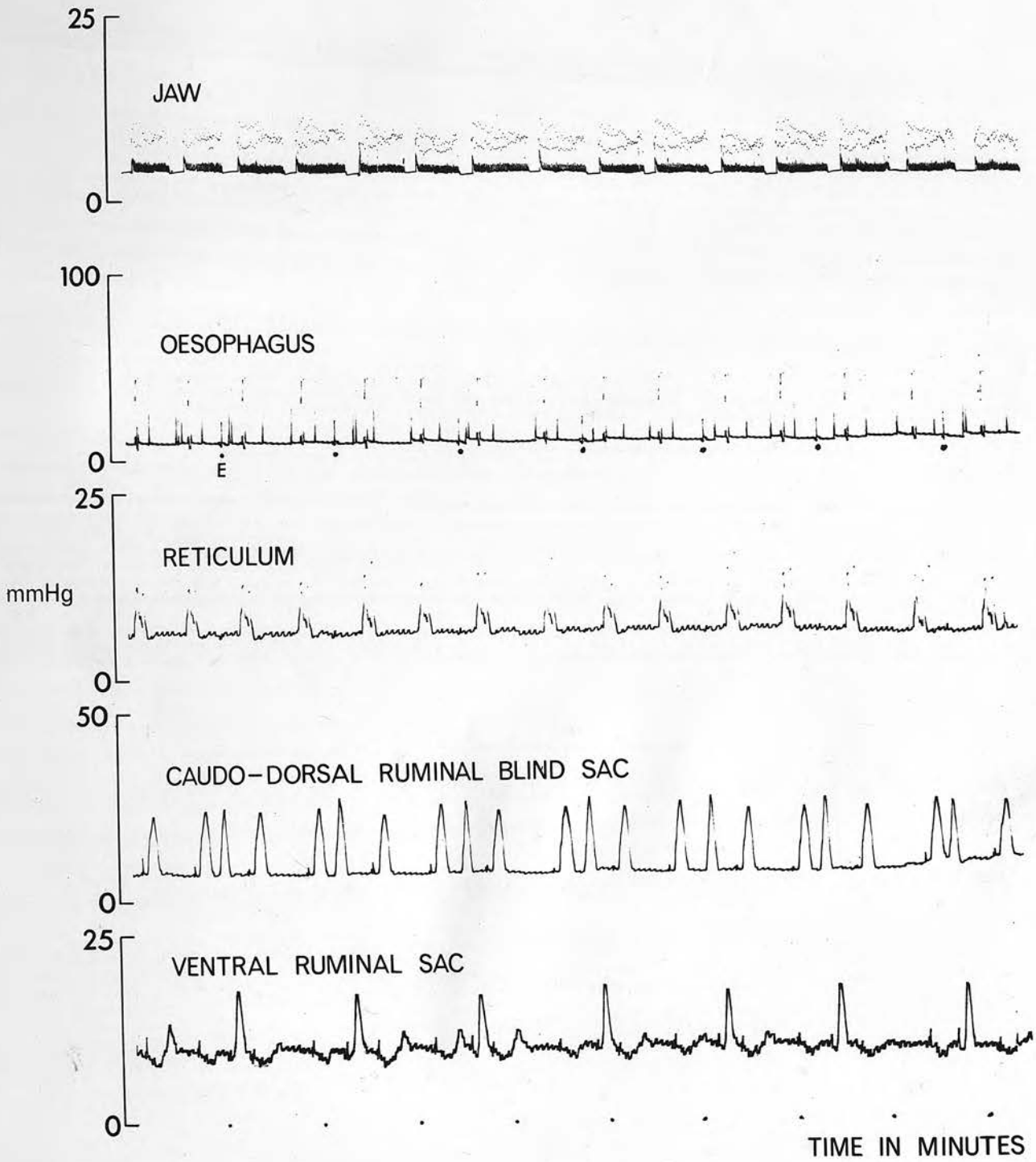

25
JAW
0
100
OESOPHAGUS
0
E
25
RETICULUM
mmHg
0
50
CAUDO-DORSAL RUMINAL BLIND SAC
0
25
VENTRAL RUMINAL SAC
0
TIME IN MINUTES

Fig. 6. Hot-wire recorder tracing showing the pattern of reticulo-ruminal motility in primary and secondary cycles during eating. Balloons were placed (from above downward) under the jaw, and in the oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac. The oesophageal balloon was passed intranasally to lie in the lower third of the cervical oesophagus. Note the move-:ments of the jaw, the frequency of primary and secondary cycles, eructation (indicated by small dots under the oesophageal record) and the amplitude of the reticulo-ruminal contractions.

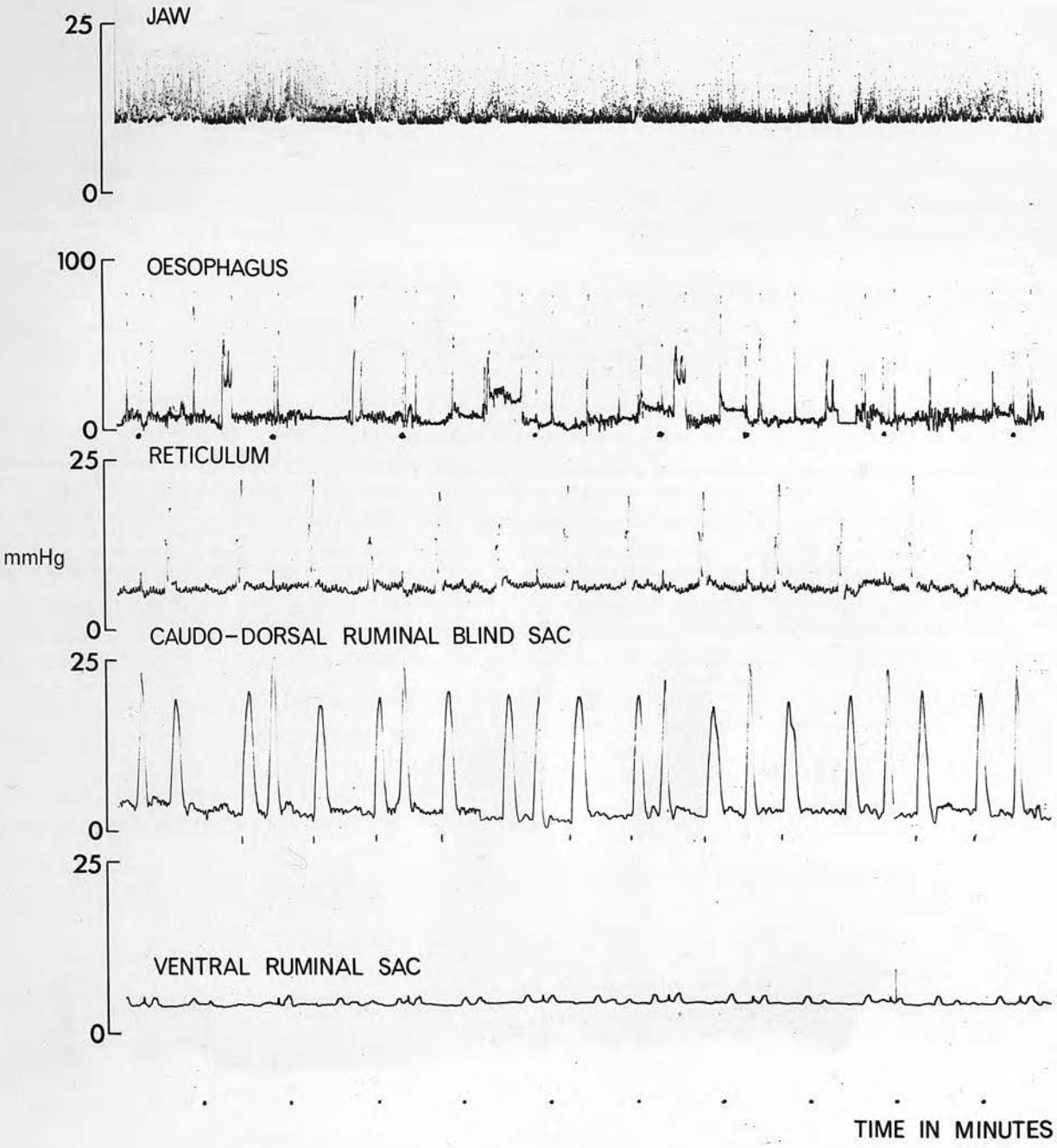

25
JAW
0
100
OESOPHAGUS
0
25
RETICULUM
mmHg
0
CAUDO-DORSAL RUMINAL BLIND SAC
25
0
25
VENTRAL RUMINAL SAC
0
TIME IN MINUTES

Fig. 7. Kymograph tracing showing the involvement of the reticulum, and different regions of the dorsal rumen in primary and secondary cycle contractions when the animal was resting in the standing position. Balloons were placed in (from above downward) the reticulum, near the ventral wall of the cranial sac, upper region of the cranial sac, mid-dorsal sac and caudo-dorsal blind sac.

Note the absence of any pressure increment in the cranial region of the dorsal rumen during the secondary cycles.

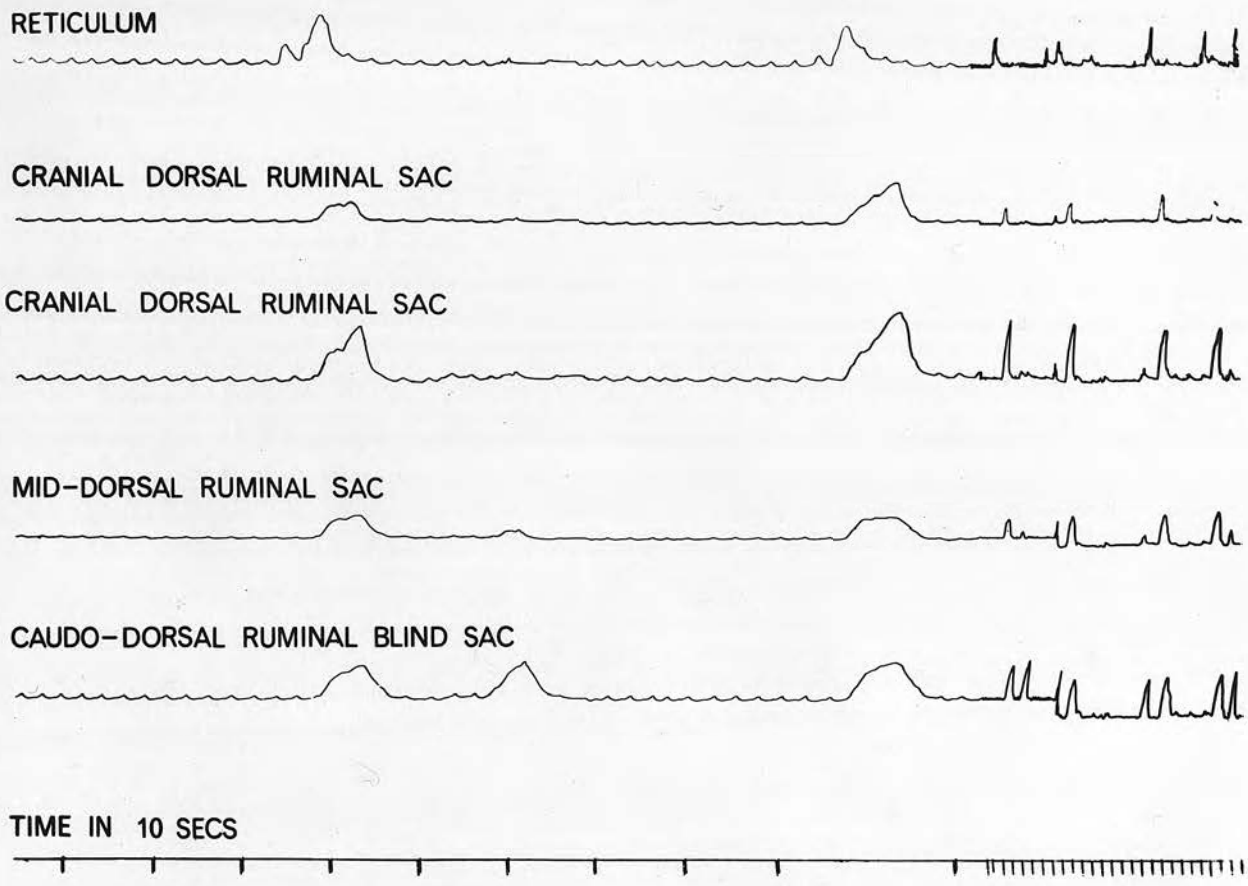

RETICULUM
CRANIAL DORSAL RUMINAL SAC
CRANIAL DORSAL RUMINAL SAC
MID-DORSAL RUMINAL SAC
CAUDO-DORSAL RUMINAL BLIND SAC
TIME IN 10 SECS

Fig. 8. Kymograph tracing showing the involvement of the reticulum and different regions of the rumen in primary and secondary cycle contractions when the animal was resting in the standing position. Balloons were placed in (from above downward) reticulum, cranial sac, mid-dorsal sac, caudo-dorsal blind sac and ventral rumen.

Note that the ventral rumen did not contract during the primary cycle but contracted at the end of the secondary cycle con-:traction of the dorsal rumen in the two instances.

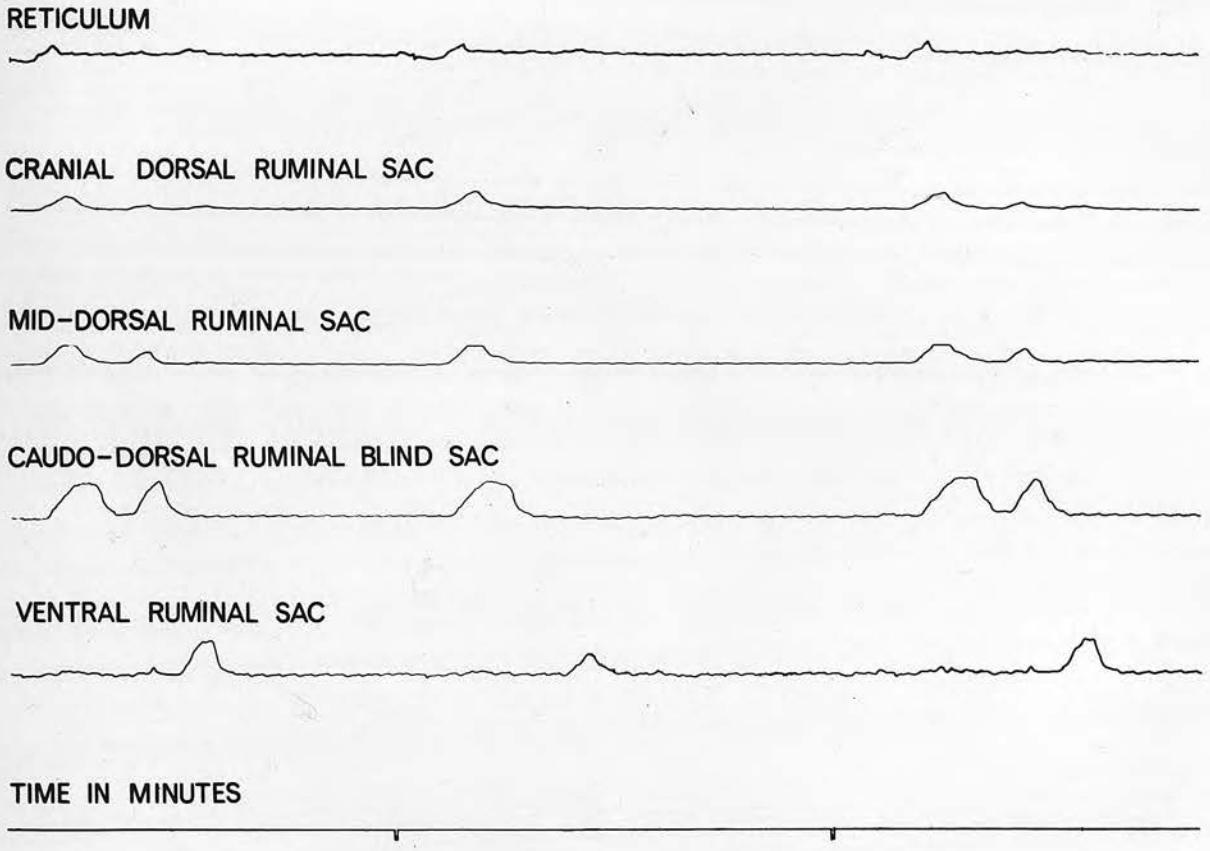

RETICULUM
CRANIAL DORSAL RUMINAL SAC
MID-DORSAL RUMINAL SAC
CAUDO-DORSAL RUMINAL BLIND SAC
VENTRAL RUMINAL SAC
TIME IN MINUTES

Fig. 9. The mean frequency of primary and secondary cycle con-:tractions and eructation during resting, ruminating and eating, in the same sheep on different days under routine feeding and mainten-:ance conditions. The measurements have been made from three 10-minute observations in each case between 11.00 a.m. and 5.00 p.m.

The standard deviation is indicated by vertical bars in each measurement and the horizontal dotted-lines represent the over-all mean of the values obtained over 5 days.

Eructation frequency during eating is not given because of the difficulty of distinguishing oesophageal movements due to eructa-:tion and those due to the swallowing of food for the five-day period.

Note that the primary and secondary cycle contractions and eructation increased significantly during rumination and eating.

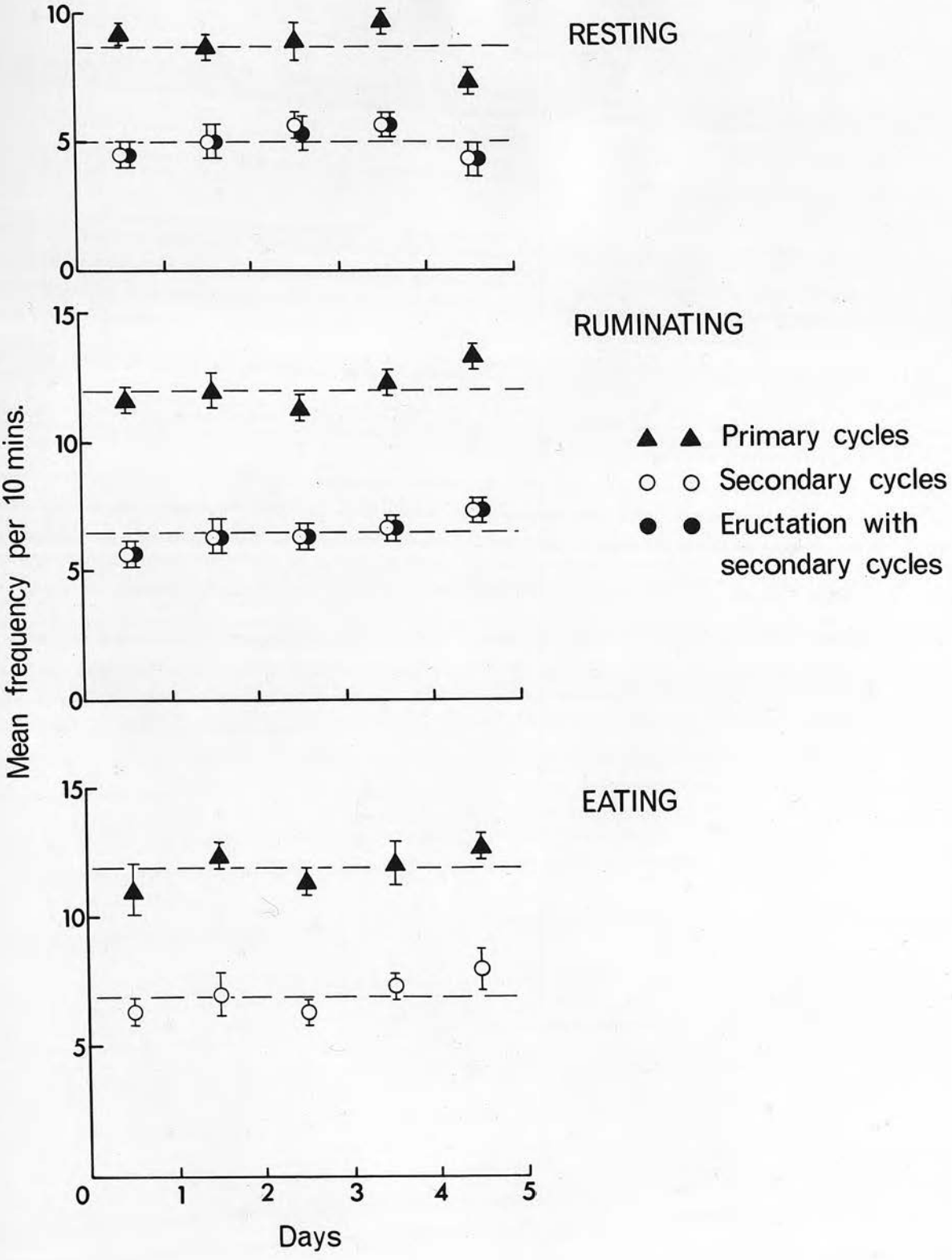

RESTING
RUMINATING
EATING
Mean frequency per 10 mins.
Days
Primary cycles
Secondary cycles
Eructation with secondary cycles
0
5
10
15
1
2
3
4

Fig. 10. Mean pressure increments in mm Hg recorded from the reticulum, caudo-dorsal blind sac and ventral ruminal sac for primary and secondary cycles during the resting state of the same sheep on different days under routine feeding and maintenance con-:tions. The measurements have been made from 10 successive con-:tractions of each compartment. The standard deviations are indicated by vertical bars for each measurement and the horizontal dotted-line represents the over-all mean of the values obtained over five days. In the case of primary cycles the top dotted line shows the over-all mean of reticular pressure, the middle dotted line re-:presents the caudo-dorsal blind sac pressure and the bottom dotted line shows the over-all mean of the ventral ruminal sac pressure increment.

CDBS = caudo-dorsal blind sac

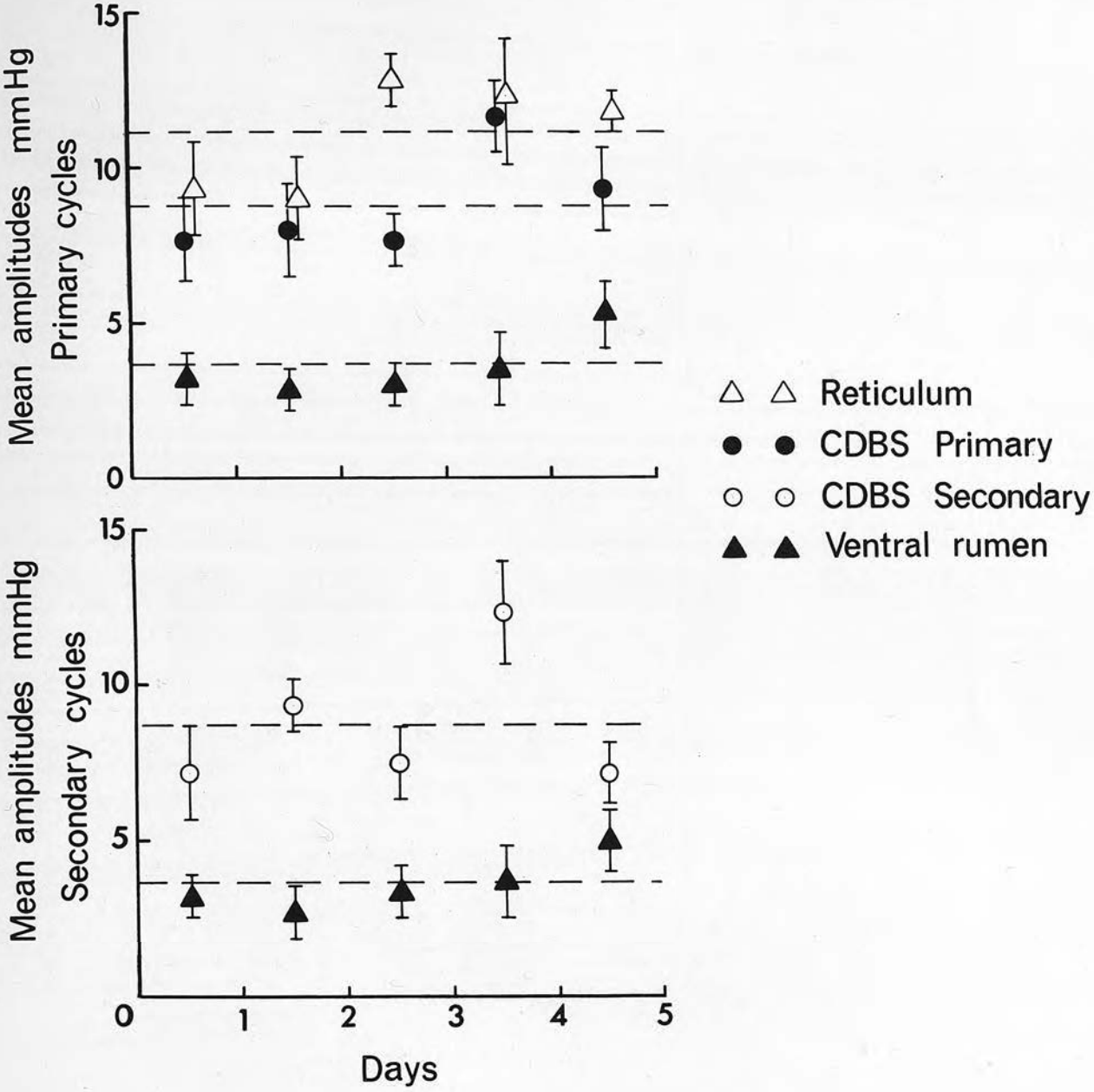

Mean amplitudes mm Hg
Primary cycles
15
10
5
0
Mean amplitudes mmHg
Secondary cycles
15
10
5
0
1
2
3
4
5
Days
Reticulum
CDBS Primary
CDBS Secondary
Ventral rumen

Fig. 11. The mean frequency of primary and secondary cycles and eructation and the amplitudes of oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac contractions during resting, ruminating and eating. The eructation contractions of the oesophagus were measured from the lower third of its cervical part by a balloon passed intranasally. The data presented are mean values obtained from three sheep on different days maintained under routine con-:tions. The standard deviations are indicated by vertical bars for each measurement lasting half an hour in each sheep.

CDBS = caudo-dorsal blind sac.

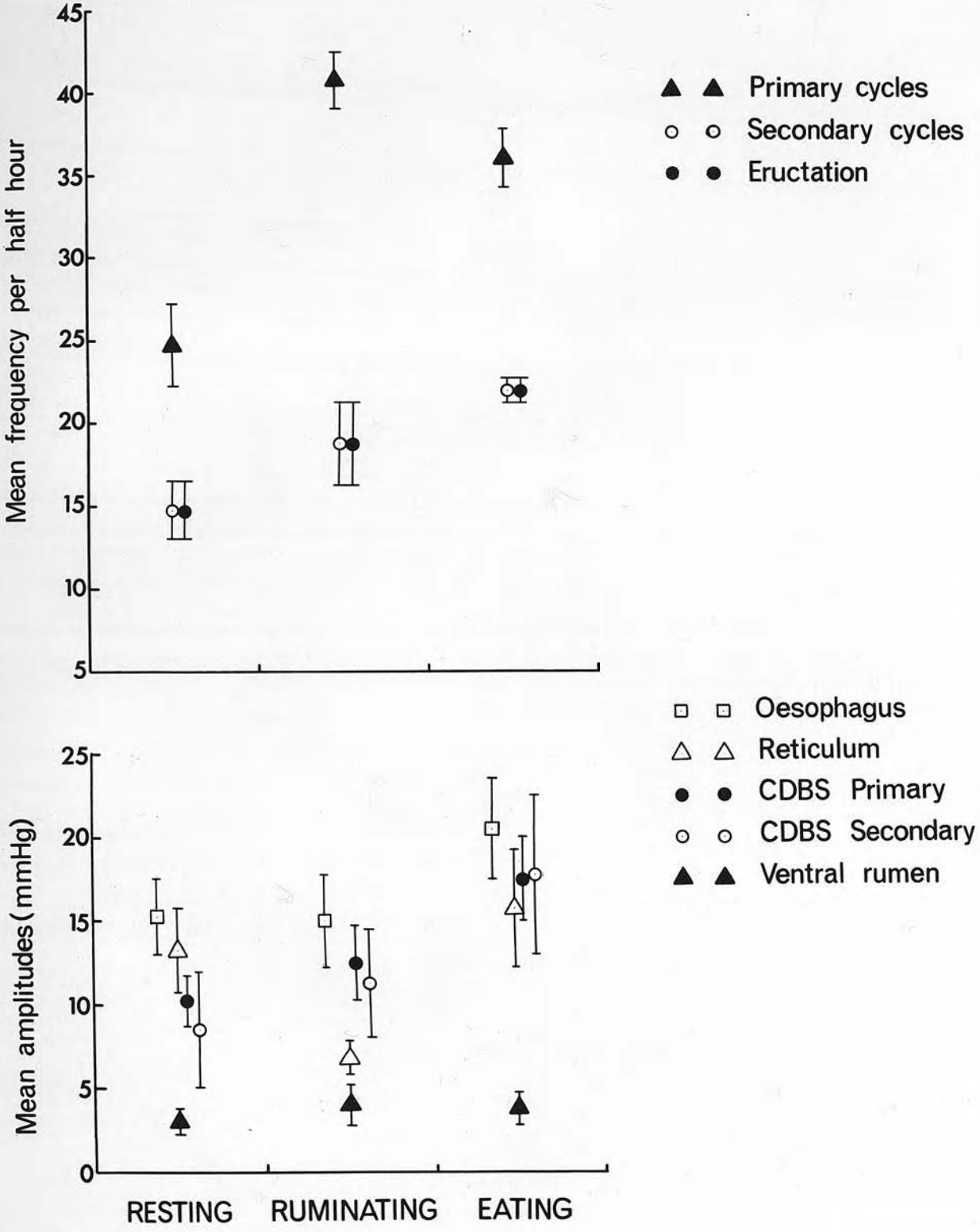

Mean frequency per half hour
45
40
35
30
25
20
15
10
5
Primary cycles
Secondary cycles
Eructation
Mean amplitudes (mmHg)
25
20
15
10
5
0
Oesophagus
Reticulum
CDBS Primary
CDBS Secondary
Ventral rumen
RESTING
RUMINATING
EATING

Table 1. Sites in the reticulo-ruminal wall where microcannulae were inserted in different sheep.

| Sheep | Reticulum | Cranial sac | Dorsal ruminal sac | Caudo-dorsal blind sac | Ventral ruminal sac | Caudo-ventral blind sac |
|---|---|---|---|---|---|---|
| 1 | - | - | Lateral wall | Lateral wall | - | Lateral wall |
| 2 | - | Lateral wall | - | Lateral wall | - | Lateral wall |
| 3 | - | Lateral wall | - | Lateral wall | - | Lateral wall |
| 4 | - | - | Lateral wall | Caudal wall | - | Caudal wall |
| 5 | Cranial wall | - | Dorsal wall | Lateral wall | Lateral wall | Ventral wall |
| 6 | Cranial wall | - | - | Lateral wall | Lateral wall | Dorsal wall |
| 7 | Ventral pole | Lateral wall | - | Lateral wall | Lateral wall | - |
| 8 | Cranial wall | Lateral wall | - | Lateral wall | Lateral wall | - |
| 9 | Cranial wall | - | Lateral wall | - | Lateral wall | Caudal wall |
| 10 | Ventral pole | - | - | Lateral wall | Lateral wall | Caudal wall |

The reticulo-ruminal movements of sheep recorded by implanted micro-:cannulae

These experiments were performed to ascertain the involvement of discrete regions of the reticulo-rumen in the mechanical activity of the forestomach particularly for the secondary cycle contractions of the rumen. Pressure events due to the contractions of the reticulo-ruminal musculature for primary and secondary cycles were recorded from locations shown in Table 1.

In five sheep no records were obtained for technical reasons i.e., the tube kinked or became displaced postoperatively. They have not been included in Table 1.

The relative intervals in seconds were measured from the peak of the second phase of a reticular contraction to the peak of contraction in different ruminal compartments for ascertaining the temporal involvement of the two sacs in a primary cycle. For establishing the origin of a secondary cycle contraction in the caudo-dorsal or caudo-ventral blind sac, the start of pressure increment in the caudo-dorsal blind sac was taken as zero.

Figures 12, 13, 14 and 15 represent the typical records obtained from discrete locations of the reticulo-rumen in different sheep (No. 6, 8 and 10, Table 1). Each primary cycle was initiated by a biphasic contraction of the reticulum. The second phase of the reticular contraction was accompanied by a contraction of the dorsal rumen which progressively involved the cranial, the mid-dorsal rumen and the caudo-dorsal blind sac. This was followed by a contraction of the ventral rumen and caudo-ventral blind sac in those primary cycles which were not followed by a secondary cycle. The mean intervals taken by different regions to reach the peak of their respective contraction relative to the peak of second reticular contraction has been

Table 6. Mean intervals in seconds ± S.D. between the second peak of reticular contraction and the peak of the contractions of various regions of the rumen during primary cycles. The measurements were obtained during 1 - 2 hours of uninterrupted activity in the resting state between 10 a.m. and 5 p.m., 1 - 3 days after the insertion of microcannulae in the reticulo-ruminal wall.

| Sheep | Cranial sac | Dorsal rum-inal sac | Caudo-dorsal blind sac | Ventral rumen | Caudo-ventral blind sac | No. of contrac-tions examined |
|---|---|---|---|---|---|---|
| 5 | - | 4.0 ± 0.7 | 5.0 ± 1.0 | 13.5 ± 2.0 | 15.0 ± 2.5 | 147 |
| 6 | - | - | 4.0 ± 0.5 | 7.2 ± 1.5 | 9.0 ± 0.7 | 133 |
| 7 | 2.5 ± 0.6 | - | 4.5 ± 0.5 | 10.0 ± 2.0 | - | 169 |
| 8 | 2.5 ± 0.7 | - | 4.5 ± 0.5 | 10.0 ± 1.0 | - | 105 |
| 9 | - | 3.7 ± 0.4 | - | 16.0 ± 1.5 | 17.0 ± 4.0 | 58 |
| 10 | - | - | 4.0 ± 0.5 | 16.5 ± 2.5 | 18.0 ± 3.5 | 156 |
| Over-all mean (secs) | 2.5 | 3.8 | 4.4 | 12.0 | 14.7 | |

shown in Table 6. In some preparations the caudal wall of the caudo-ventral blind sac was not found to register any increment in pressure for the primary cycle for varying intervals of up to 60 to 90 minutes during an experiment. It was usual to find that with the start of the first reticular contraction, the ventral ruminal sac recorded a fall in pressure and remained in that position till the second reticular contraction had reached its peak. This was also the case in some preparations having the sensitive part of a microcannula inserted in the lateral or ventral wall of the caudo-ventral blind sac (Fig. 12 and 14).

The mean amplitudes of reticulo-ruminal contractions for primary and secondary cycles ranged between the following values for reticulum 1.00 to 2.7 mm Hg; cranial sac 0.69 to 1.7 mm Hg; mid-dorsal ruminal sac 1.00 to 2.30 mm Hg; caudo-dorsal blind sac 0.53 to 2.57 mm Hg; ventral rumen 0.48 to 1.11 mm Hg; and caudo-ventral blind sac 0.8 to 1.43 mm Hg in different sheep on different days. These values were, besides the animal factors, very much dependent upon the efficacy of the insertion of the sensitive part of the microcannula and the day of recording the mechanical activity of the organs after the operation. A decrease in the amplitude of contractions of different regions was recorded with an increase in the number of days after the operation due to the formation of fibrous tissue around the site of insertion.

The reticular contraction amplitudes recorded by a finger-cot balloon passed intranasally ranged over 7 to 15 mm Hg in different sheep.

The mean frequency of the primary and secondary cycles was not consistently different from that recorded by the toy balloon method. Only in one preparation (sheep No. 9, Table 1) the frequency of both the primary and secondary cycles was significantly lower. A primary cycle contraction of the reticulo-rumen occurred every 2 to 3 minutes followed

Table 7. Relative incidence (%) for the start of the contraction in the caudo-ventral blind sac to the start of the contraction in the caudo-dorsal blind sac for secondary cycles. The start of a contraction in the caudo-ventral blind sac was either before (A), at the same time (B) or after (C) the start of contraction in the caudo-dorsal blind sac. The measurements have been obtained during 1 to 2 hours of uninterrupted activity under resting conditions between 10 a.m. to 5 p.m., 1 - 3 days after the insertion of the microcannulae in the reticulo-ruminal wall.

| Sheep No. | % Each | | | No. of contractions | Site in the caudo-ventral blind sac |
|---|---|---|---|---|---|
| | A | B | C | | |
| 1 | 19.7 | 42.0 | 38.3 | 138 | Lateral wall |
| 2 | 29.5 | 48.8 | 21.7 | 126 | Lateral wall |
| 3 | 15.9 | 57.6 | 26.5 | 167 | Lateral wall |
| 5 | 16.7 | 63.3 | 20.0 | 103 | Ventral wall |
| Over-all mean % | 20.4 | 52.9 | 26.7 | | |
| 4 | 46.7 | 37.0 | 16.3 | 154 | Caudal wall |
| 6 | 54.5 | 31.0 | 14.5 | 97 | Dorsal wall |
| 9 | 42.1 | 34.3 | 23.6 | 38 | Caudal wall |
| 10 | 78.0 | 15.0 | 7.0 | 128 | Caudal wall |
| Over-all mean % | 55.3 | 29.3 | 15.4 | | |

The secondary cycle contraction of the rumen usually started earlier in the caudo-ventral blind sac in those preparations having the micro-cannula inserted in the caudal or dorsal wall of that region of the rumen.

by a secondary cycle.

Eructation was associated with the secondary cycles and usually occurred as the contractions involved the caudal, the middle and cranial regions of the dorsal ruminal sac when they reached their peaks. Eructation taking place with a primary cycle in these preparations was rare.

The relative involvement of different regions of the ruminal sacs, particularly of the caudo-dorsal and caudo-ventral blind sacs, in the secondary cycles has been measured from the point of start of a con-:traction in the compartment involved. In two sheep (No. 7 and 8, Table 1) it was found that the successive involvement of the caudal and cranial regions of the dorsal rumen 16 -18 cm apart selected for recording, was separated by an interval of 1.2 to 2.4 sec (Fig. 15). The relative involvement of the caudo-ventral blind sac and caudo-dorsal blind sac was not consistent. The former either started contracting before, at the same time or after the signs of pressure increment were observed in the latter. The relative percentage incidence of each form in different sheep is shown in Table 7. It was found that the earlier start of the secondary cycle contraction in the caudo-ventral blind sac was dominant in those sheep (Nos. 4, 6, 9 and 10) in which the microcannula had been inserted in the dorsal or caudal wall of the caudo-ventral blind sac. Those prepara-:tions with the sensitive part of the microcannula inserted in the lateral or ventral wall of the caudo-ventral blind sac were predominantly found to record the start of a contraction at the same time as did the caudo-dorsal blind sac. In some experiments the ventral ruminal sac microcannula recorded a fall in pressure (Fig. 12) at the start of secondary cycle con-:tractions in the caudo-ventral blind sac.

Fig. 12. Hot-wire recorder tracing showing the movements of the reticulo-rumen recorded by implanted microcannulae in sheep No. 10. For locations of the microcannulae see Table 1. The oesophageal activity was recorded by a finger-cot balloon passed intranasally. The letter 'E' under the oesophageal record indicates eructation. From above downward; oesophagus, reticulum, caudo-dorsal blind sac, ventral ruminal sac and caudo-ventral blind sac.

Note the fall in pressure in the ventral ruminal sac tracing with the start of the first reticular contraction. The secondary cycle contraction in the caudal wall of the caudo-ventral blind sac started 2.4-6.0 sec before the caudo-dorsal blind sac (arrow).

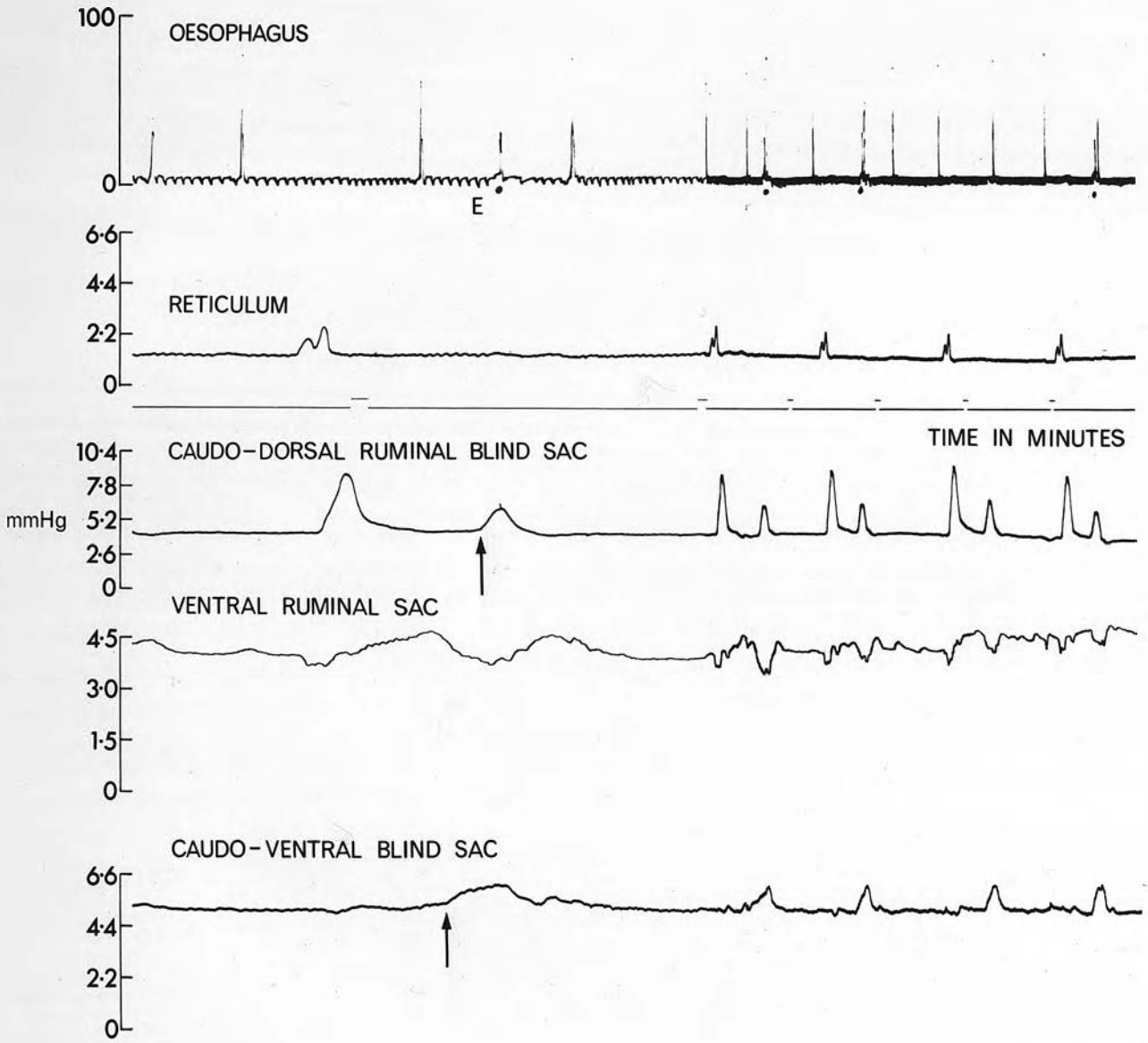

100
OESOPHAGUS
0
E
6·6
4·4
RETICULUM
2·2
0
TIME IN MINUTES
10·4
CAUDO-DORSAL RUMINAL BLIND SAC
7·8
mmHg
5·2
2·6
0
VENTRAL RUMINAL SAC
4·5
3·0
1·5
0
CAUDO-VENTRAL BLIND SAC
6·6
4·4
2·2
0

Fig. 13. Hot-wire recorder tracing showing the movements of the reticulo-rumen recorded by implanted microcannulae in sheep No. 10. For locations of the microcannulae see Table 1. Oesophageal activity was recorded by a finger-cot balloon passed intranasally. The letter 'E' under the oesophageal record indicates eructation.

Note that the caudo-ventral blind sac and the caudo-dorsal blind sac contracted at the same time during the secondary cycle (arrow 1). Eructation occurred with each secondary cycle. The caudo-ventral blind sac contracted after the ventral ruminal sac in the primary cycle (arrow 2).

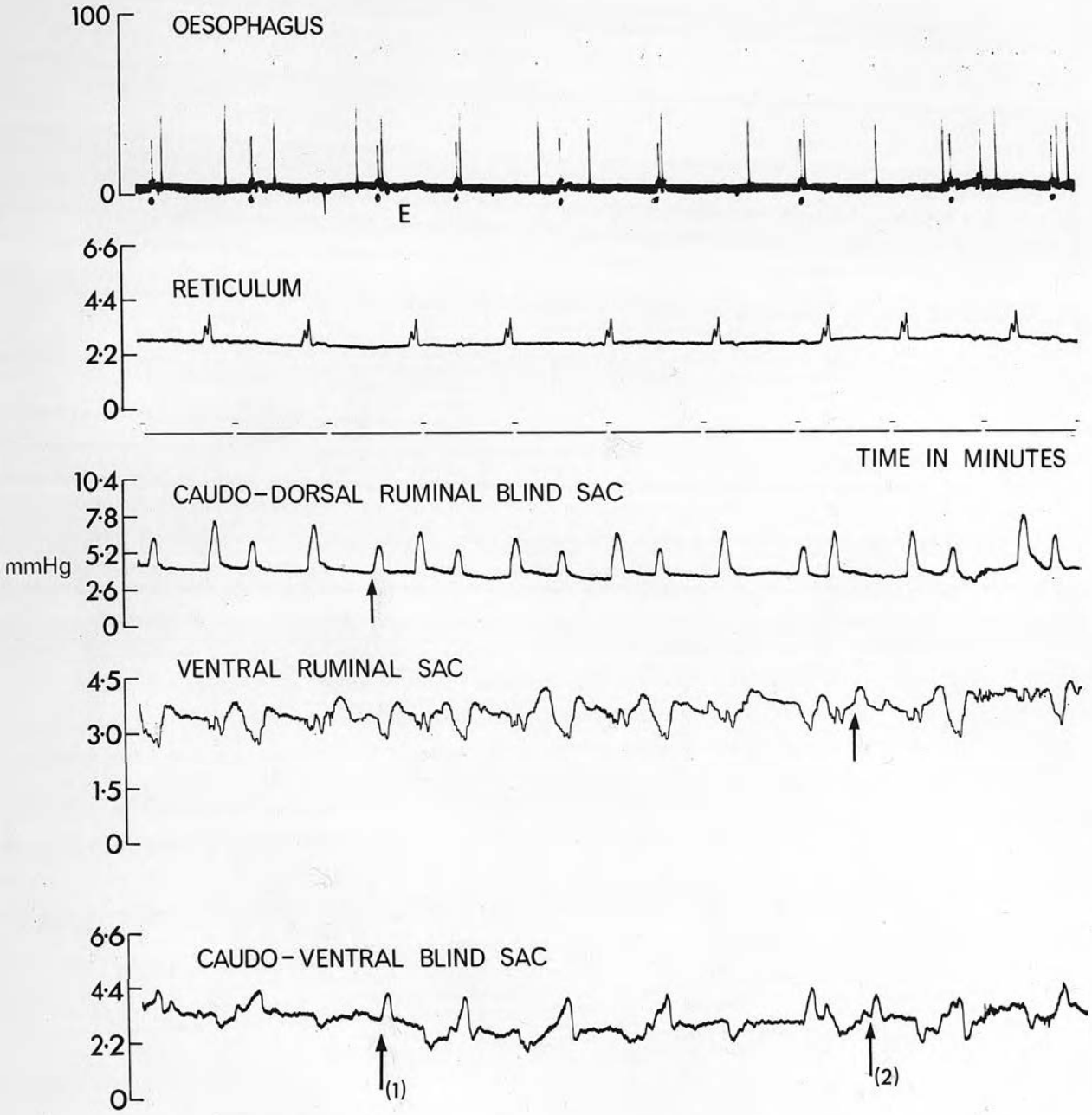

100
OESOPHAGUS
0
E
6·6
4·4
RETICULUM
2·2
0
TIME IN MINUTES
10·4
7·8
CAUDO-DORSAL RUMINAL BLIND SAC
mmHg
5·2
2·6
0
4·5
VENTRAL RUMINAL SAC
3·0
1·5
0
6·6
4·4
CAUDO-VENTRAL BLIND SAC
2·2
(1)
(2)
0

Fig. 14. Hot-wire recorder tracing showing the movements of the reticulo-rumen recorded by implanted microcannulae in sheep No. 5 (Table 1). Oesophageal activity was recorded by a finger-cot balloon passed intranasally. The letter 'E' under the oesophageal record indicates eructation.

Tracings represent (from above downward) pressures in the oesophagus, reticulum, caudo-dorsal blind sac, ventral ruminal sac and the caudo-ventral blind sac.

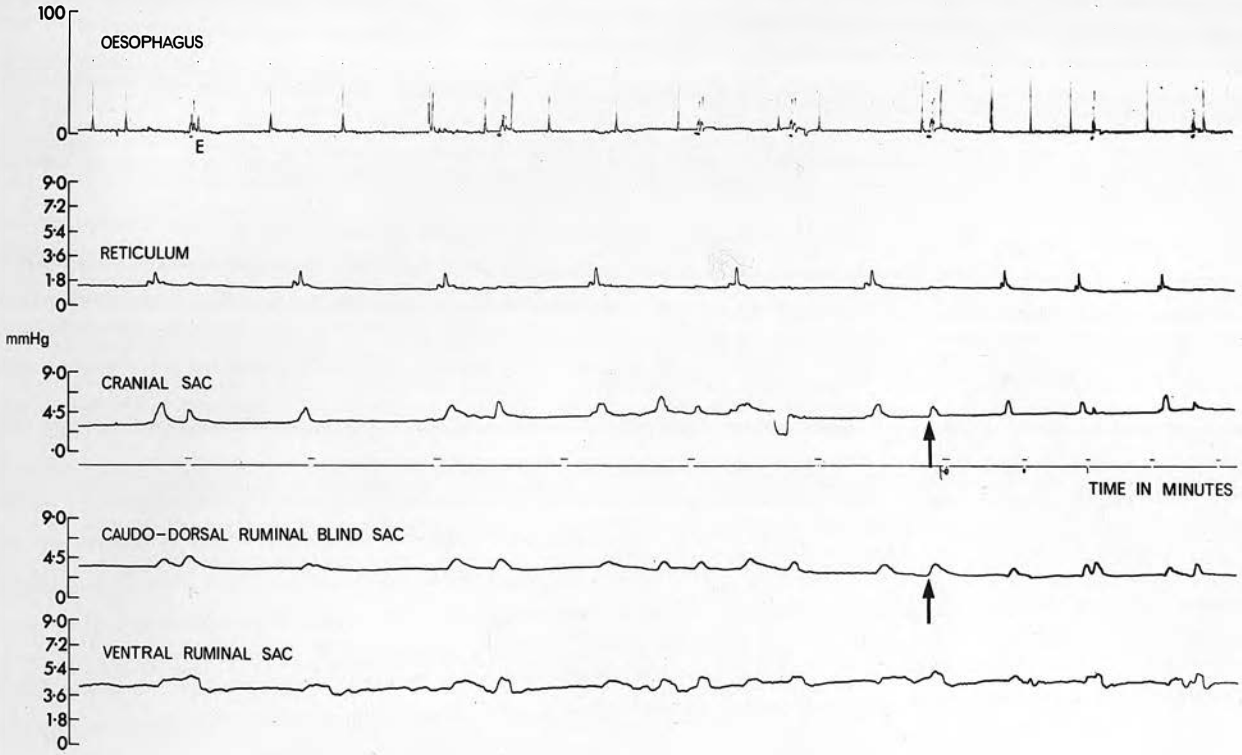
Note the caudo-ventral blind sac contracted after the caudo-dorsal blind sac during the secondary cycle contraction (arrow).

100
OESOPHAGUS
0
E
4·5
RETICULUM
2·25
0
7·5
TIME IN MINUTES
mmHg
6·0
4·5
CAUDO-DORSAL RUMINAL BLIND SAC
3·0
1·5
0
VENTRAL RUMINAL SAC
6·75
4·5
2·25
0
CAUDO-VENTRAL BLIND SAC
4·5
2·25
0

Fig. 15. Hot-wire recorder tracing showing movements of the reticulo-rumen recorded by implanted microcannulae in sheep No. 8 (Table 1). Oesophageal activity was recorded by a finger-cot balloon passed intranasally. The letter 'E' under the oesophageal record indicates eructation.

From above downward the tracings show pressures in the oesophagus, reticulum, cranial sac, caudo-dorsal blind sac and ventral ruminal sac.

Note that the caudo-dorsal blind sac contracted earlier than the cranial sac during the secondary cycle (arrow).


100
OESOPHAGUS
0
E
9·0
7·2
5·4
3·6
1·8
0
RETICULUM
mmHg
9·0
4·5
·0
CRANIAL SAC
TIME IN MINUTES
9·0
4·5
0
CAUDO-DORSAL RUMINAL BLIND SAC
9·0
7·2
5·4
3·6
1·8
0
VENTRAL RUMINAL SAC

The effect of insufflation on reticulo-ruminal motility and eructation

The effect of insufflating 95% $O_2$ + 5% $CO_2$ gas mixture on fore-stomach motility and eructation is shown in Fig. 16. The gases entered the dorsal rumen at the rate of 0.5 l./min, 1 l./min, and 1.5 l./min for 10 minutes each, except for 0.5 l./min which was continued for half an hour.

Insufflation at the rate of 0.5 l./min did not affect the frequency of primary cycles appreciably but the secondary cycles and eructation showed an increase which was not significant during the first 10 minutes. In the following two periods of 10 minutes each, the increase in the frequency of secondary cycles and eructation was significant ($P = 0.01$). During in-:sufflation at 1 l. or 1.5 l./min the increase in the number of secondary cycles and eructation was highly significant ($P = 0.002-0.001$). Eructation took place not only with every secondary cycle but also at the peak of 3 to 6 primary cycle contractions of the dorsal rumen. An extra secondary cycle accompanied by an eructation occurring between two successive primary cycles was not uncommon. The increase in the frequency of primary cycles was found significant ($P = 0.01$) only during insufflation at the rate of 1.5 l./min. This increase in the frequency of cyclic activity and eructation persisted so long as the insufflation was maintained and reverted to normal patterns within 5 to 6 minutes after it was stopped. In the case of sheep starved for 16 to 24 hours the effects of insufflation of 95% $O_2$ + 5% $CO_2$ gas mixture at 1 l./min were similar. There was an immediate change in the rhythm from 3 or 2:1 to 1:1 and the secondary cycles closely followed the primary ones but remained within the mean range of intervals (15 to 20 sec) between primary and secondary cycles. The frequency of eructation contractions of the oesophagus increased 3 to 4 minutes after the start of insufflation. With increasing

intraruminal gas volume, up to six quick oesophageal contractions per eructation were recorded. When the gas mixture was introduced at the rate of 1 l./min the resting base-line pressure registered an increase of 3 to 5 mm Hg at the end of 10 minutes of insufflation. The increase in the intrareticular resting pressure was negligible, if any.

The effect of insufflation at 0.5 l./min for $\frac{1}{2}$ hour on the amplitude of reticular and caudo-dorsal blind sac contractions is shown in Fig. 17. The mean values of reticular and caudo-dorsal blind sac contractions for primary cycles did not show significant differences from the resting mean values during the period of insufflation ($P \geqslant 0.05$). When the insufflation was stopped the reticular contraction amplitude showed an increase which was significant ($P = 0.01$) while that of the caudo-dorsal blind sac dropped to 6 mm Hg which was highly significant ($P < 0.001$). In the following 10 minutes both of these compartments tended to return to normal resting values. The secondary cycle contractions of the caudo-dorsal blind sac registered resting mean values of 7.5 mm Hg which dropped to 4 to 5 mm Hg during insufflation. This decrease in the amplitude of secondary cycle contractions of the caudo-dorsal blind sac was significant ($P < 0.01$). Insufflation at 1 l. and 1.5 l./min for 10 minutes were found to be excitatory for the first 2 to 3 contractions after which the amplitudes registered decreased values. In one experiment (Fig. 18) insufflation was carried out at 1 l./min, 1.5 l./min and 2 l./min each for 10 minutes, allowing the same period of rest between two successive periods of insufflation. Besides the usual increase in the frequencies of cyclic activity of the forestomach and eructation, the amplitudes of reticulum and caudo-dorsal blind sac showed reduced mean values as the volume of insufflation was increased. Except for insufflation at the rate of 1 l./min, the reduction in the mean amplitudes was highly significant ($P < 0.001$). The amplitudes remained depressed for 15 minutes after which the experiment

was discontinued.

In sheep with inserted microcannulae the rumen was insufflated at the rate of 1 l. /min for 10 minutes through an alkathene stomach tube passed intranasally. The frequency of both primary and secondary cycles and of eructation increased. There was an initial enhancement in the amplitudes of reticulo-ruminal contractions, followed in 3 to 4 minutes by a marked reduction below the pre-insufflation values. They gradually recovered in 5 to 10 minutes after the insufflation had been stopped. During insufflation it was not uncommon to find the caudal wall of the caudo-ventral blind sac showing two contractions for each primary and secondary cycle.

Effect of distension with an anaesthetic bag on reticulo-ruminal motility

The effects of rumen distension with 1 l. and 4 l. anaesthetic bags on reticulo-ruminal motility are shown in Figs 19 and 20 respectively. Part of the digesta was removed before introducing the anaesthetic bag through the rumen cannula. The bag was intended to lie in the caudo-dorsal blind sac but when fully distended it was found to occupy part of the dorsal rumen during an experiment. The air was introduced with a syringe at 200 ml each time, during an interval of 10 minutes, through a tap in the stiff polythene pressure line. The bag was deflated through the same tap when required.

A one litre anaesthetic bag was used for moderate distension (Fig. 19 and table); it contained 600 ml of air initially and 800 ml more was introduced within 3 minutes of the first 10 minute interval. The distension was maintained for 30 minutes after which the bag was deflated save its initial volume. At this level of distension the frequency of both the primary and secondary cycles was not significantly affected. The

pressure increment of the reticular contraction did not show any significant differences throughout the period of recording ($P > 0.05$). The primary cycle contraction of the caudo-dorsal blind sac registered a mean pressure increment of 9.14 mm Hg during (a), to 15.71 mm Hg during (c) which dropped to 14.17 mmHg during (d). The difference between the resting mean values and the subsequent increase on distension was highly significant ($P < 0.001$). The difference between the peak mean value of 15.71 mm Hg and the subsequent drop to 14.17 mm Hg was also found to be significant ($P = 0.01$). On removal of the introduced air from the bag, the mean pressure increment decreased to 10.8 mm Hg and then to 9.3 mm Hg in the following two intervals of 10 minutes each.

The secondary cycle amplitudes of the caudo-dorsal blind sac contraction increased from the resting mean values of 9.5 mm Hg during (a) to 13.0 mm Hg during (c) which dropped to 9.8 mm Hg during (d). This pressure increase of 3.5 mm Hg was highly significant ($P = 0.002$) while the subsequent decrease in the next 10 minutes of maintained dis-:tension was significant at values of $P = 0.01$. On removal of the introduced air, the secondary cycle contraction amplitude of the dorsal rumen dropped to a mean value of 9.0 and 7.0 mm Hg during the following two periods of 10 minutes each respectively. These values when compared to the peak mean value of 13 mm Hg during maintained distension were found to be highly significant ($P < 0.001$).

The results obtained at this level of distension when compared with those of insufflation at 0.5 l./min (Figs. 16, 17 and 19) showed differences from both the point of view of frequency of the cyclic activity and the amplitudes of the reticulum and dorsal rumen. Whereas the frequency of secondary cycles and eructation increased significantly during in-:sufflation, no significant change was noticed in the frequency of primary

and secondary cycles at that level of anaesthetic bag distension. The mean reticular amplitudes during insufflation and moderate distension of the 1 l. anaesthetic bag did not show significant differences from the respective resting values, but caudo-dorsal blind sac contraction amplitudes for primary and secondary cycles first showed an increase (Fig. 19) followed by a decrease from the mean peak pressure of 15.5 mm Hg during maintained distension with the anaesthetic bag. During insufflation at 0.5 l./min for 30 minutes the secondary cycle contraction amplitudes were significantly reduced.

The effect of distension of a 4 l. anaesthetic bag in the dorsal rumen with 2.5 l. and 3.5 l. of introduced air is shown in Figs. 20 and 21 respect-:ively. An increase in the frequency of both primary and secondary cycles and amplitudes of the first 6 to 7 dorsal ruminal sac contractions occurred during the period of inflation. The subsequent contractions registered comparatively lesser amplitudes. During the period of maintained distension a decrease in the mean amplitudes of the dorsal ruminal sac contractions and the frequency of the cyclic activity took place. These differences were found to be statistically significant (Tables, Figs. 20 and 21). The mean reticular contraction amplitudes were found to be not significantly affected at the 2.5 l. level of distension of the dorsal rumen, but at 3.5 l. level of distension they were significant-:ly reduced ($P < 0.05$-$0.01$), during the period the distension was maintained. During removal of the introduced air (3.5 l.) from the anaesthetic bag the reticular contraction amplitudes steadily became normal (10 to 16 mm Hg) and as the deflation was complete, the contractions recorded significantly higher amplitudes (17 to 30 mm Hg range).

In one experiment the reticulo-ruminal contents were completely removed and 4 l. of normal saline at 39°C added into the rumen

Fig. 16. The effect of insufflating the rumen with a 95% $O_2$ + 5% $CO_2$ gas mixture at rates of 0.5 l./min for 30 minutes, 1.0 l./min for 10 minutes and 1.5 l./min for 10 minutes through a rumen cannula, on the frequency of primary and secondary cycles and eructation in sheep. The data presented are mean values obtained from three experiments, one each from 3 sheep. Standard deviations are indicated by vertical bars.

Note the increase in the frequency of secondary cycles and eructation during insufflation.

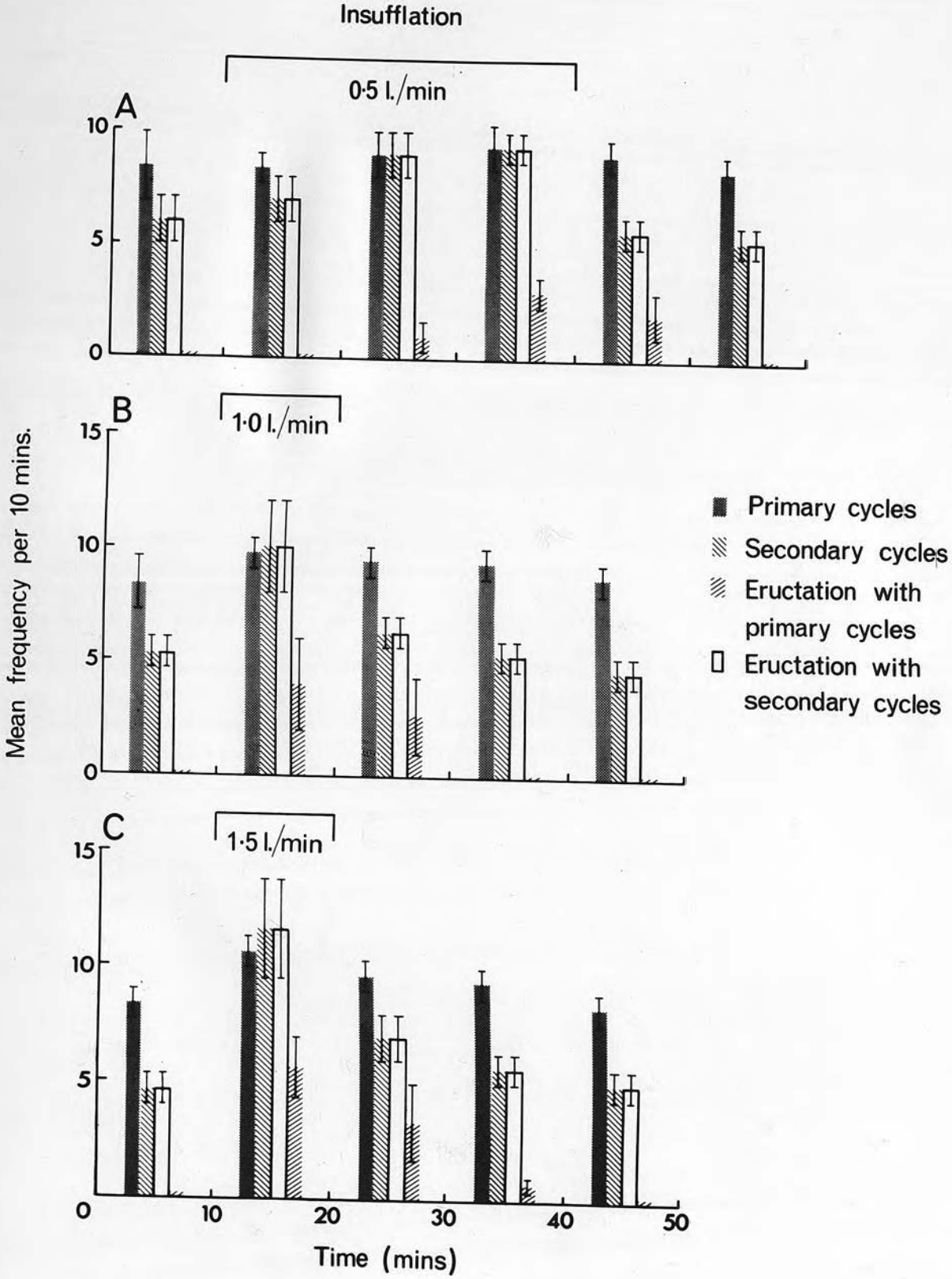

Insufflation
0·5 l./min
A
10
5
0
B
1·0 l./min
15
10
5
0
C
1·5 l./min
15
10
5
0
10
20
30
40
50
Time (mins)
Mean frequency per 10 mins.
Primary cycles
Secondary cycles
Eructation with primary cycles
Eructation with secondary cycles

Fig. 17. The effect of insufflating the rumen with 95% $O_2$ + 5% $CO_2$ gas mixture at the rate of 0.5 l./min on the amplitude of reticulum and caudo-dorsal blind sac contractions during primary and secondary cycles. The data presented here are mean values obtained during each 10 minute interval. Standard deviations are indicated by vertical bars for each measurement.

Letters (a-f) on the X-axis represent mean values obtained during each 10 minute interval.

The reticular amplitudes were not significantly different from each other ($P \geqslant 0.05$) during and before the period of insufflation but when the insufflation was stopped the increase in the reticular mean pressure increment was significant ($P = 0.01$) in the following two periods of 10 minutes each.

The primary cycle contraction amplitudes of the caudo-dorsal blind sac were also not significantly different ($P \geqslant 0.05$) except between (a and e) when value of P was $< 0.001$.

The secondary cycle contraction amplitudes of the caudo-dorsal blind sac significantly decreased ($P < 0.01$) from the resting values during the period of insufflation.

CDBS = Caudo-dorsal blind sac

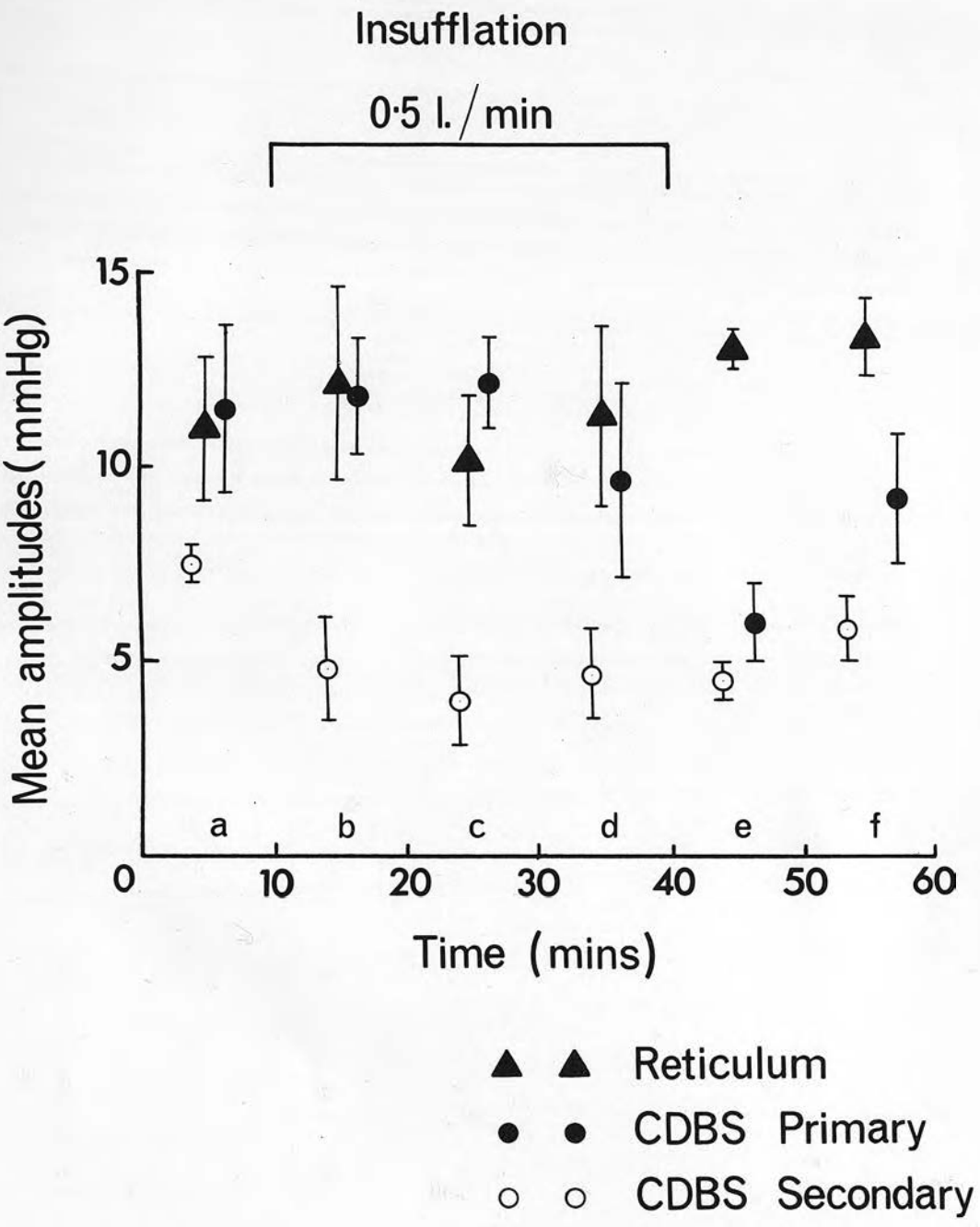

Insufflation
0·5 l./min
15
10
5
0
Mean amplitudes (mmHg)
a
b
c
d
e
f
10
20
30
40
50
60
Time (mins)
Reticulum
CDBS Primary
CDBS Secondary

Fig. 18. The effect of insufflating 95% $O_2$ + 5% $CO_2$ gas mixture for 10 minutes at the rate of 1 l./min, 1.5 l./min and 2.0 l./min on the frequency of primary and secondary cycles and eructation and on the amplitudes of reticular and caudo-dorsal blind sac contractions during resting. The data presented for amplitudes of the contractions represents the mean values obtained for each 10 minute interval. The standard deviation for each measurement is indicated by vertical bars.

Letters (a - g) along the x-axis represent the values for each 10 minutes interval for comparison and significance of differences.

Probability Table

| | Values | a | b | c | d | e | f | g |
|---|---|---|---|---|---|---|---|---|
| Reticulum | a | - | 0.1 | 0.1 | <0.001 | <0.001 | <0.001 | <0.001 |
| | b | - | - | <0.05 | <0.001 | <0.001 | <0.001 | <0.001 |
| | c | - | - | - | 0.001 | <0.001 | <0.001 | <0.001 |
| | d | - | - | - | - | - | <0.001 | - |
| | f | - | - | - | - | - | - | 0.05 |
| Caudo-dorsal blind sac primary cycle | a | - | 0.1 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | b | - | - | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | c | - | - | - | <0.001 | <0.001 | <0.001 | <0.001 |
| | d | - | - | - | 0.01 | 0.1 | 0.1 | >0.1 |
| | e | - | - | - | - | - | - | 0.1 |
| Caudo-dorsal blind sac secondary cycle | a | - | 0.1 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | b | - | - | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | c | - | - | - | 0.1 | >0.05 | >0.05 | >0.05 |
| | d | - | - | - | - | >0.1 | >0.1 | >0.1 |

CDBS = Caudo-dorsal blind sac

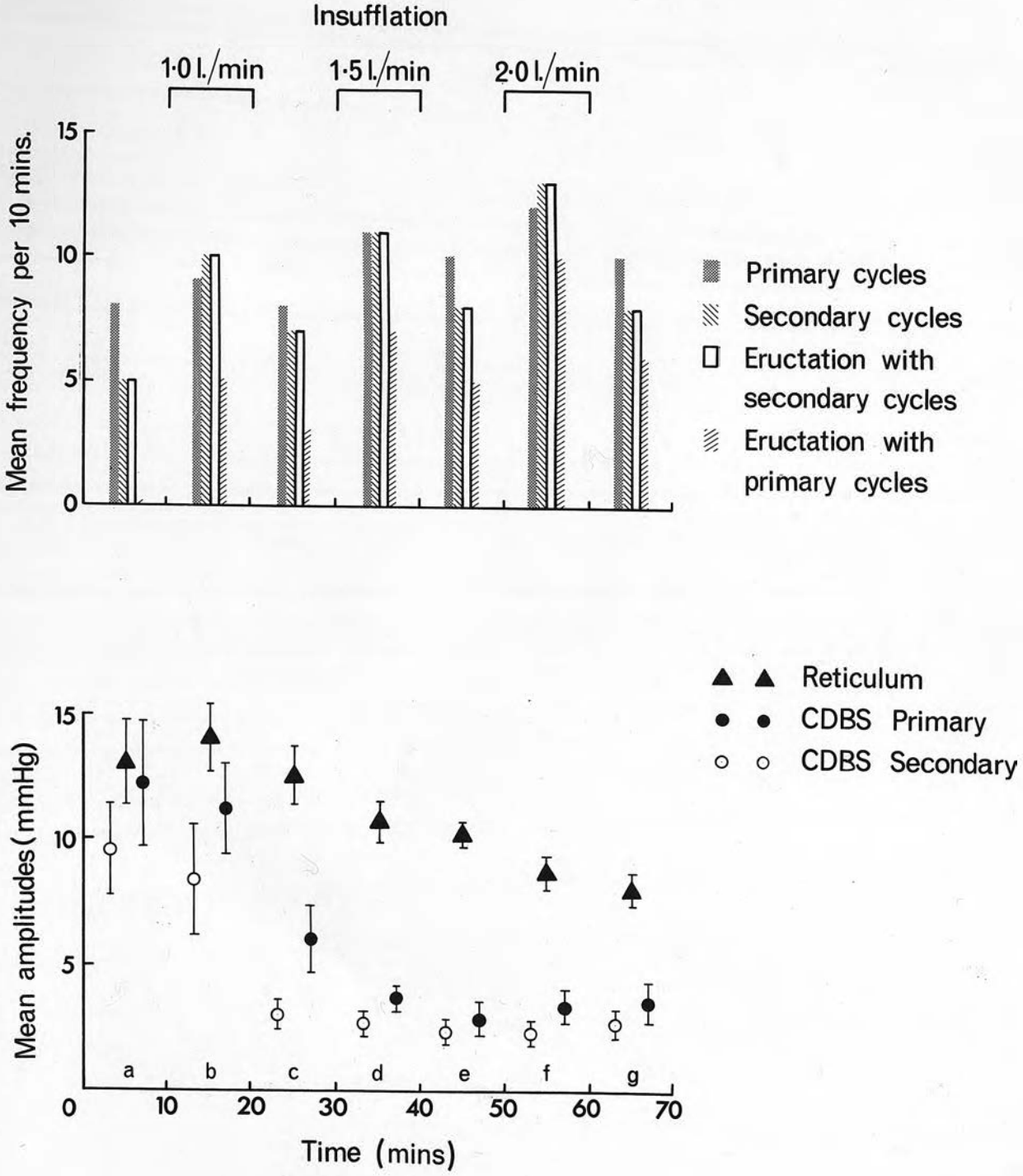

Insufflation
1·0 l./min
1·5 l./min
2·0 l./min
Mean frequency per 10 mins.
15
10
5
0
Primary cycles
Secondary cycles
Eructation with secondary cycles
Eructation with primary cycles
Reticulum
CDBS Primary
CDBS Secondary
Mean amplitudes (mmHg)
15
10
5
0
a
b
c
d
e
f
g
10
20
30
40
50
60
70
Time (mins)

Fig. 19. Effect of distending a 1 l. anaesthetic bag with 800 ml of introduced air in the caudo-dorsal blind sac on the amplitudes of reticulum and caudo-dorsal blind sac. The anaesthetic bag had 600 ml of air initially. The data presented here show mean values obtained from primary and secondary cycle contractions of the respective organ during each 10 minute interval. The standard deviation is indicated by vertical bars for each measurement. The digesta were partly removed and the animal was allowed $\frac{1}{2}$ - 1 hour to recover from the effect of handling before starting the experiment.

Letters (a - f) along the x-axis represent the values for each 10 minute interval for comparison and significance of differences.

(i) The reticular amplitudes were not significantly different from each other ($P \geqslant 0.1$) throughout the experiment.

Probability Table for caudo-dorsal blind sac amplitudes

| | Values | b | c | d | e | f |
|---|---|---|---|---|---|---|
| Primary cycle contraction | a | 0.01 | <0.001 | <0.001 | >0.05 | >0.1 |
| | b | - | 0.001 | 0.01 | >0.01 | >0.01 |
| | c | - | - | 0.01 | <0.001 | <0.001 |
| | d | - | - | - | <0.01 | <0.001 |
| Secondary cycle contraction | a | <0.05 | 0.002 | >0.1 | >0.1 | <0.05 |
| | b | - | 0.05 | 0.01 | 0.002 | <0.001 |
| | c | - | - | 0.01 | <0.001 | <0.001 |
| | d | - | - | - | >0.1 | 0.01 |

CDBS = Caudo-dorsal blind sac

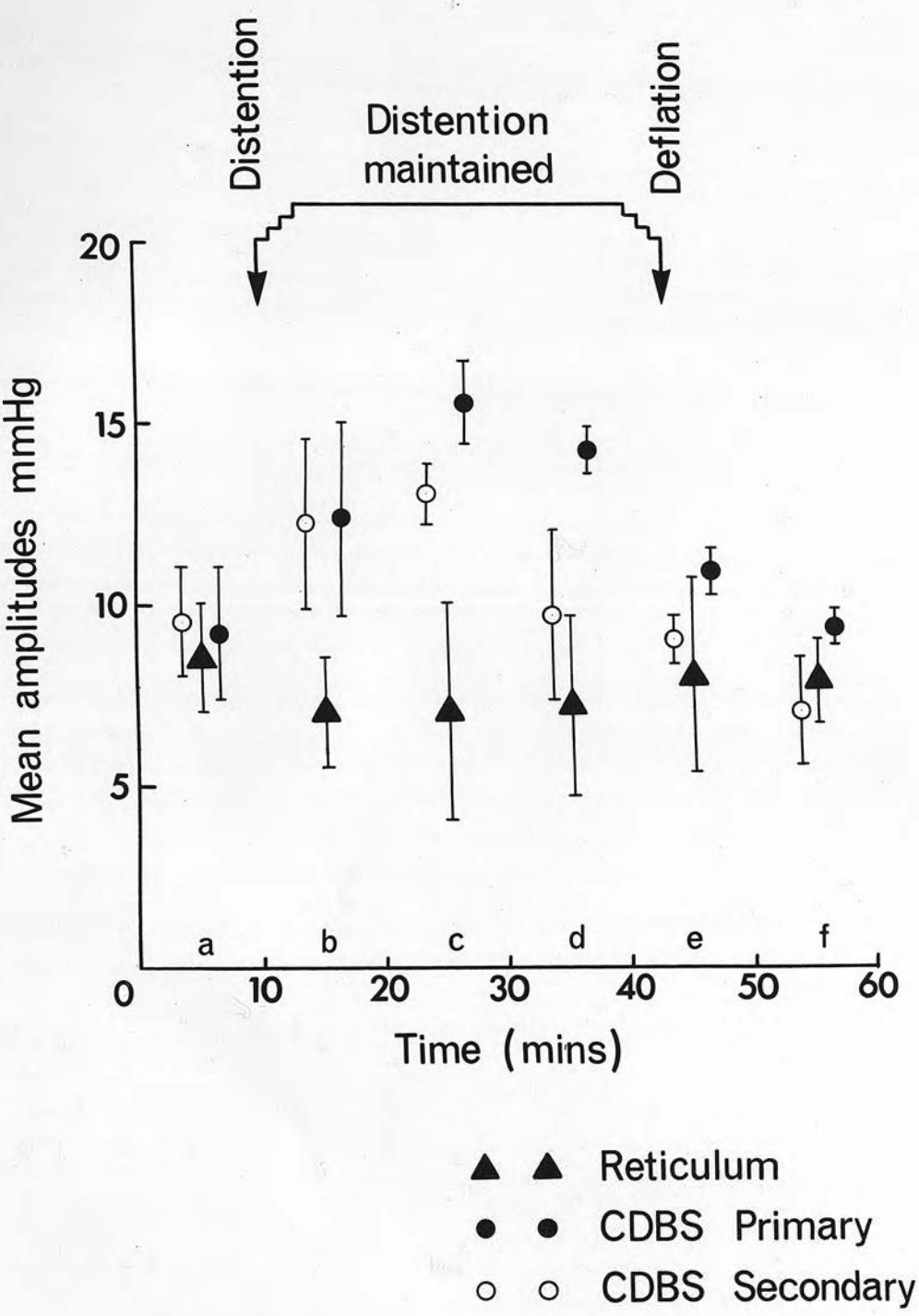

Distention
Distention maintained
Deflation
Mean amplitudes mmHg
20
15
10
5
0
10
20
30
40
50
60
a
b
c
d
e
f
Time (mins)
Reticulum
CDBS Primary
CDBS Secondary

Fig. 20. Effect of distending a 4 l. anaesthetic bag with 2.5 l. of introduced air in the caudo-dorsal blind sac on the amplitude of reticulo-ruminal contractions and the frequency of primary and secondary cycles. The anaesthetic bag had 1 l. of air initially. The data presented here show mean values obtained from primary and secondary cycle contractions of the respective organ during different 10 minute intervals. The standard deviation is indicated by vertical bars for each measurement. The digesta were partly removed and the animal allowed $^{1}/_{2}$ - 1 hour to recover from the effect of handling before starting the experiment.

Letters (b - g) on the x-axis represent the values obtained during each 10 minute interval. Letter (a) represents resting values during 20 minutes.

(i) The reticular contraction amplitudes when statistically tested were not significantly different from each other except between (b and c) and (c and f) at values of $P < 0.05$.

(ii) The significance of differences for caudo-dorsal blind sac amplitudes was as under.

Probability Table

| | Values | b | c | d | e | f | g |
|---|---|---|---|---|---|---|---|
| Caudo-dorsal blind sac primary cycle contractions | a | <0.01 | 0.05 | >0.1 | 0.1 | <0.01 | 0.001 |
| | b | - | >0.1 | 0.01 | <0.05 | <0.001 | <0.001 |
| | c | - | - | <0.1 | 0.05 | <0.001 | <0.001 |
| | d | - | - | - | >0.1 | <0.002 | <0.002 |
| Caudo-dorsal blind sac secondary cycle | a | 0.002 | <0.001 | <0.01 | 0.01 | >0.1 | >0.1 |
| | b | - | >0.1 | >0.01 | <0.05 | 0.001 | 0.001 |
| | c | - | - | 0.05 | 0.05 | <0.002 | 0.002 |
| | d | - | - | - | >0.1 | 0.002 | 0.002 |

CDBS = Caudo-dorsal blind sac

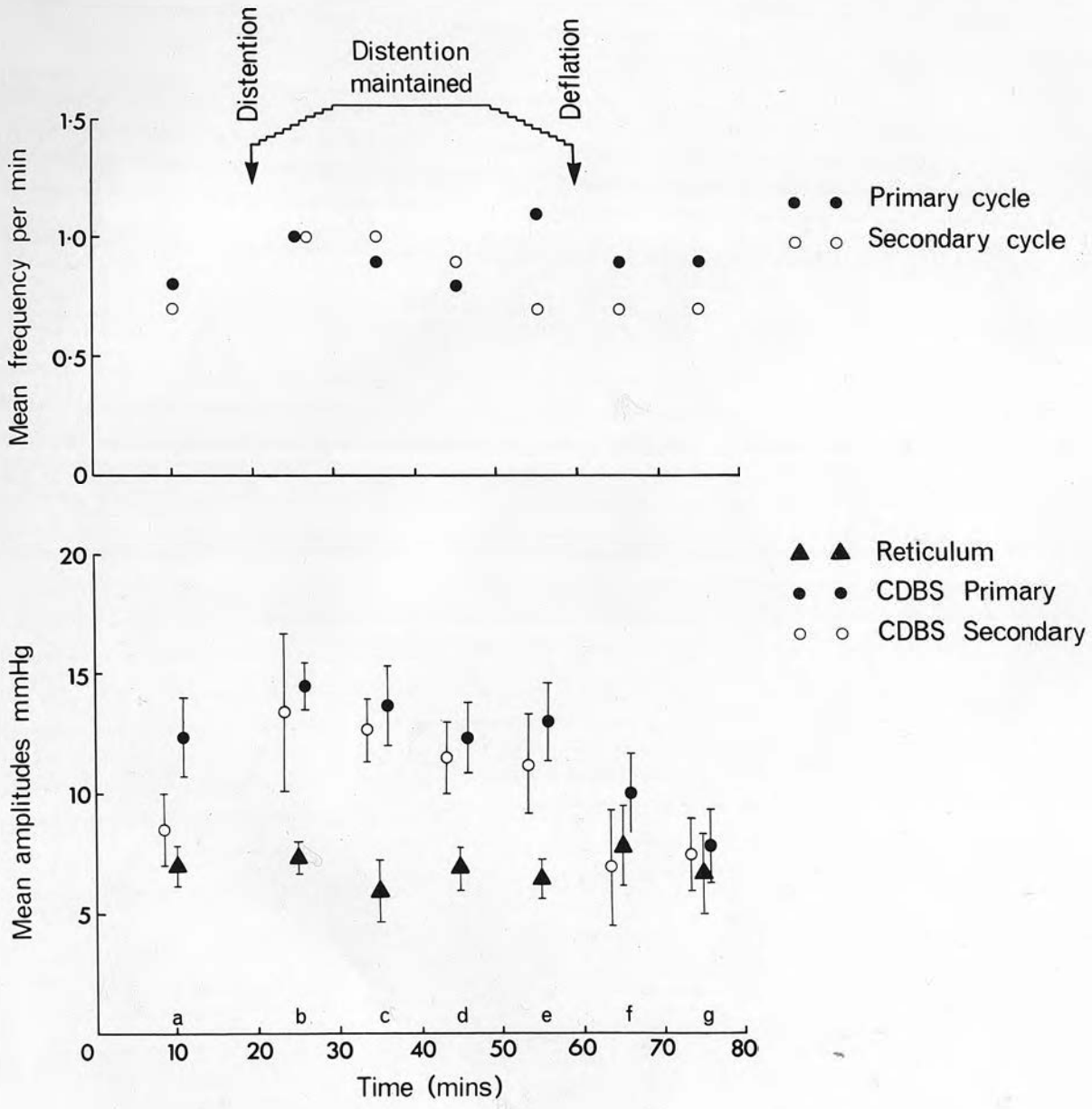

Distention
Distention maintained
Deflation
Mean frequency per min
1·5
1·0
0·5
0
Primary cycle
Secondary cycle
Mean amplitudes mmHg
20
15
10
5
0
Reticulum
CDBS Primary
CDBS Secondary
a
b
c
d
e
f
g
10
20
30
40
50
60
70
80
Time (mins)

Fig. 21. Effect of distending a 4 l. anaesthetic bag with 3.5 l. of air introduced in the dorsal rumen on the amplitude of reticulo-ruminal contractions and the frequency of primary and secondary cycles. The anaesthetic bag had 1 l. of air initially. The data present here show mean values obtained from primary and secondary cycle contractions of the respective organ during different 10 minute intervals. The standard deviation for amplitudes is indicated by vertical bars for each measure-:ment. The digesta were partly removed and the animal was allowed $\frac{1}{2}$ - 1 hour to recover from the effect of handling before starting the experiment.

Letters (b - g) on the x-axis represent values obtained during each 10 minute interval. Letter (a) represents mean resting values during 20 minutes.

Statistical tests for the effect of distension at this level on the amplitude of reticulo-ruminal contractions are shown overleaf.

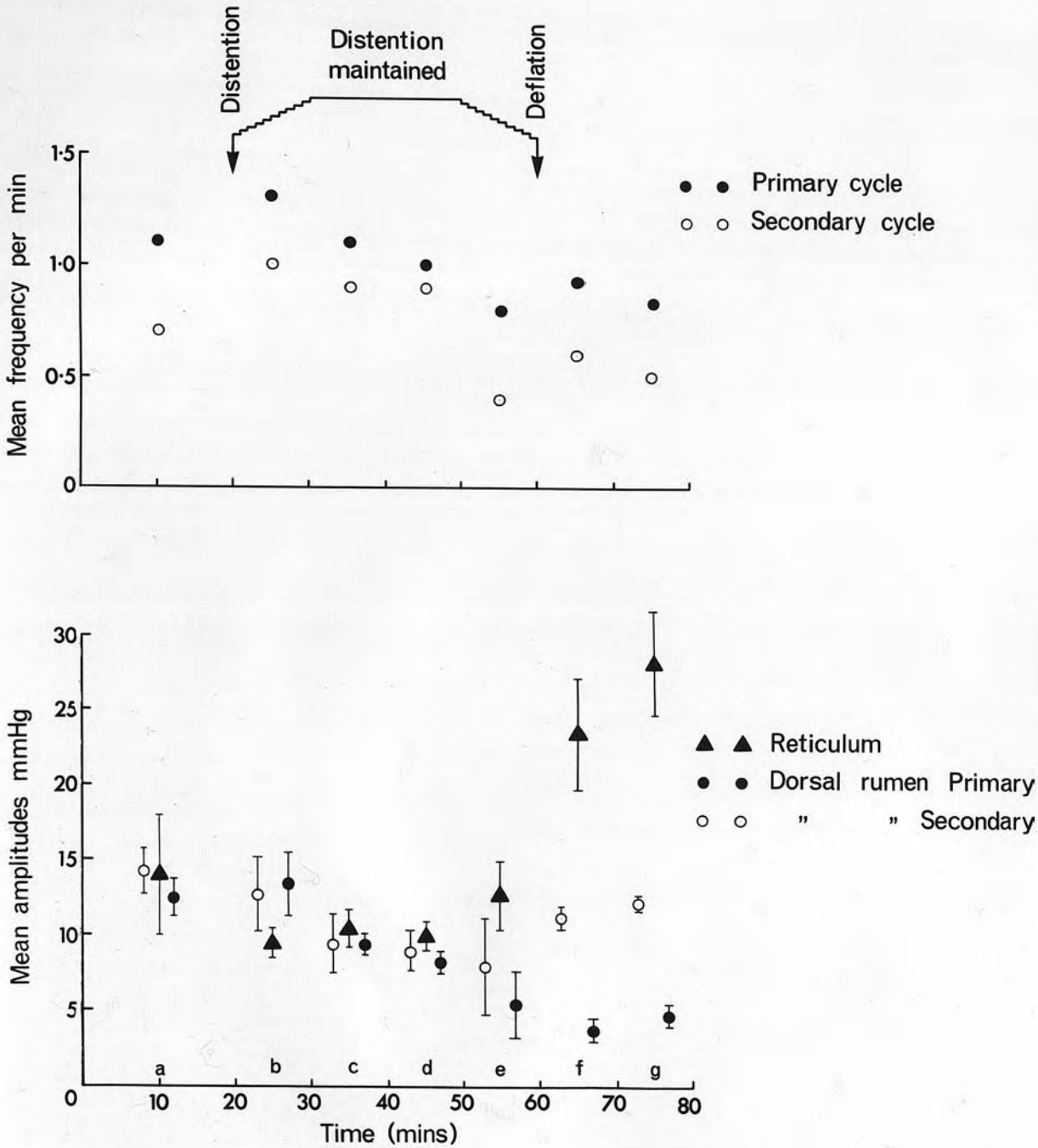

Distention
Distention maintained
Deflation
Mean frequency per min
1·5
1·0
0·5
0
Primary cycle
Secondary cycle
Mean amplitudes mmHg
30
25
20
15
10
5
0
Reticulum
Dorsal rumen Primary
" " Secondary
a
b
c
d
e
f
g
10
20
30
40
50
60
70
80
Time (mins)

Fig. 21. Probability Table

| | Values | a | b | c | d | e | f | g |
|---|---|---|---|---|---|---|---|---|
| Reticulum | a | - | 0.01 | <0.05 | <0.05 | >0.1 | <0.001 | <0.001 |
| | b | - | - | >0.05 | >0.1 | 0.001 | <0.001 | <0.001 |
| | c | - | - | - | >0.1 | <0.01 | <0.001 | <0.001 |
| | d | - | - | - | - | <0.01 | <0.001 | <0.001 |
| | e | - | - | - | - | - | <0.001 | <0.001 |
| Dorsal rumen primary cycle | a | - | >0.05 | <0.01 | <0.001 | <0.001 | <0.001 | <0.001 |
| | b | - | - | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | c | - | - | - | <0.1 | <0.001 | <0.001 | <0.001 |
| | d | - | - | - | - | <0.01 | <0.001 | <0.001 |
| | e | - | - | - | - | - | <0.05 | 0.1 |
| Dorsal rumen secondary cycle | a | - | 0.1 | <0.001 | <0.001 | <0.001 | <0.01 | <0.05 |
| | b | - | - | <0.01 | <0.001 | 0.01 | <0.1 | >0.1 |
| | c | - | - | - | >0.1 | >0.1 | >0.05 | 0.002 |
| | d | - | - | - | - | >0.05 | <0.05 | 0.002 |
| | e | - | - | - | - | - | <0.01 | 0.002 |

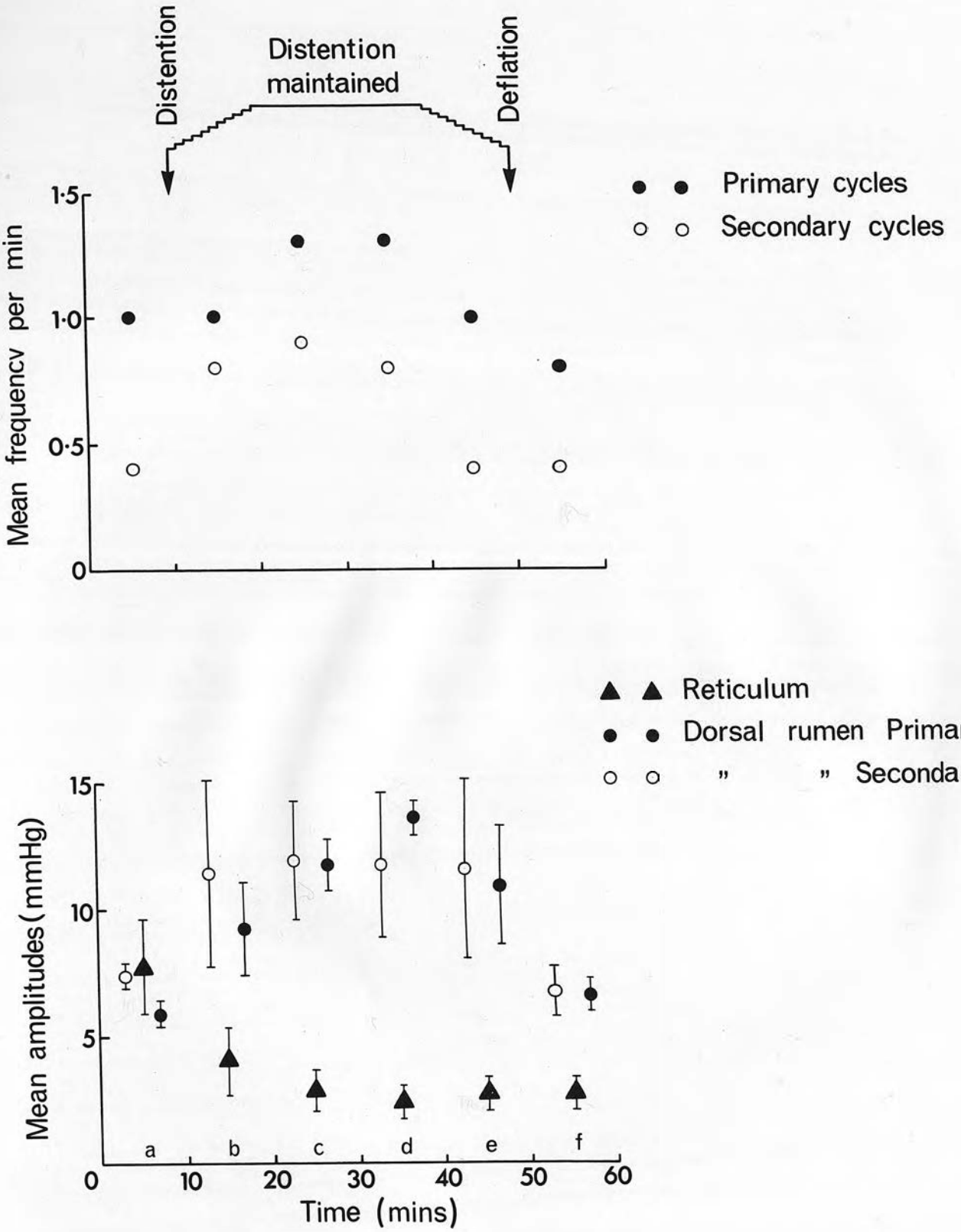
Fig. 22. Effect of distending a 4 litre anaesthetic bag with 2 l. of air introduced into the dorsal sac of rumen of sheep. The anaesthetic bag had 1 l. of air initially. The forestomach contents were totally removed and 4 l. of normal saline at 39°C added through the cannula. The animal was allowed ½ - 1 hour to recover from the effect of handling before starting the experiment. The data presented here show mean values obtained from primary and secondary cycle contractions during each 10 minute interval. The standard deviation is indicated by vertical bars for each experiment.

Letters (a - f) on the x-axis represent the values obtained during each 10 minute interval for the purpose of comparison.

Statistical tests for the effect of distension at this level on the amplitudes of reticulo-ruminal contractions were as follows:
(i) the reticular and ruminal contraction amplitudes responded differently to the effect of distension with the bag. Whereas the reticular amplitudes were significantly reduced, the ruminal amplitudes were significantly increased. The table shows the significance of results for both primary and secondary cycles.

Probability Table

| | Values | a | b | c | d | e | f |
|---|---|---|---|---|---|---|---|
| Reticulum | a | - | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | b | - | - | <0.05 | <0.01 | 0.05 | 0.05 |
| | c | - | - | - | >0.05 | - | - |
| Dorsal rumen primary cycle | a | - | <0.001 | <0.001 | <0.001 | <0.001 | >0.1 |
| | b | - | - | 0.01 | <0.001 | <0.1 | 0.002 |
| | c | - | - | - | 0.01 | 0.1 | <0.001 |
| Dorsal rumen secondary cycle | a | - | 0.01 | <0.01 | <0.01 | <0.01 | >0.1 |
| | b | - | - | >0.1 | >0.1 | >0.1 | 0.001 |
| | c | - | - | >0.1 | - | >0.1 | <0.01 |


Distention
Distention maintained
Deflation
Primary cycles
Secondary cycles
Mean frequency per min
1·5
1·0
0·5
0
Reticulum
Dorsal rumen Primary
" " Secondary
Mean amplitudes (mmHg)
15
10
5
0
a
b
c
d
e
f
10
20
30
40
50
60
Time (mins)

through the cannula. The animal was allowed $\frac{1}{2}$-1 hour to recover from the effects of handling. Figure 22 shows the effect of distending a 4 l. anaesthetic bag in the dorsal rumen with 2 l. of introduced air. The bag had 1 l. of air initially. In the absence of normal reticulo-ruminal contents, the reticular contraction amplitudes were significantly reduced ($P < 0.001$) while that of the dorsal rumen were significantly increased ($P < 0.001$) for primary and secondary cycles throughout the period of distension. The reduction in the reticular amplitudes and increase in the dorsal ruminal sac contraction amplitudes was gradual. Also, the frequency of both primary and secondary cycles increased. The secondary cycles responded more quickly than the primary cycles to the effect of anaesthetic bag distension in the rumen devoid of its normal contents.

The effect of evacuating ruminal gases on the cyclic activity of reticulo-rumen and eructation

The ruminal gases from three cannulated sheep were evacuated with a vacuum pump connected to a stiff polythene tube (I.D. 5 mm) bearing perforations in the part passed into the top of the dorsal sac of rumen through the rubber bung. The cannula was made leak-proof. To avoid the fluid rumen contents passing to the pump during suction, trap bottles were inserted by thick rubber tube connections between the pump and the rumen. One arm of a metallic Y-piece was connected to the tube coming from the rumen. A rubber tube with a clip was connected to the other arm of the Y-piece so that the suction of the pump could be regulated at 8 to 10 mm Hg. This was enough to prevent belching in the normal animal if the polythene tube did not get plugged with rumen contents. The occurrence of an eructation during the period of evacuation of rumen gases was regarded as due to plugging of the polythene tube with rumen contents and hence these observations were not counted in the data presented. The experiments were carried out between 10.00 a.m. and

Table 8. Mean intervals (secs) ± S.D. between successive primary cycles and between successive secondary cycles with and without evacuating ruminal gases while not eating or ruminating (i.e. resting) and in a standing position.

| Sheep | Activity and position | Control, primary cycles: No. of observations | Control, primary cycles: Intervals (secs) | Gas evacuated primary cycles: No. of observations | Gas evacuated primary cycles: Intervals (secs) | P |
|---|---|---|---|---|---|---|
| I | Resting<br>Standing | 9 | 54.27 ± 5.5 | 7 | 69.22 ± 6.5 | <0.01 |
| III | Resting<br>Standing | 10 | 56.50 ± 7.6 | 6 | 63.20 ± 4.0 | 0.01 |
| V | Resting<br>Standing | 7 | 88.86 ± 10.5 | 5 | 115.20 ± 17.0 | 0.01 |

| Sheep | Activity and position | Control, secondary cycles: No. of observations | Control, secondary cycles: Intervals (secs) | Gas evacuated secondary cycles: No. of observations | Gas evacuated secondary cycles: Intervals (secs) | P |
|---|---|---|---|---|---|---|
| I | Resting<br>Standing | 9 | 80.57 ± 26.2 | 7 | 161.33 ± 37.5 | <0.01 |
| III | Resting<br>Standing | 10 | 101.89 ± 23.5 | 6 | 147.00 ± 33.0 | 0.01 |
| V | Resting<br>Standing | 7 | 107.33 ± 26.8 | 5 | 189.00 ± 87.5 | <0.05 |

Each observation period lasted 10 minutes. Measurements were made from peak to peak of successive caudo-dorsal blind sac contractions for primary cycles and for secondary cycles. Removing the ruminal gases significantly reduces the frequencies of both the primary and secondary cycles.

7.00 p.m. Each observation consisted of not less than 10 minutes of an uninterrupted resting activity with the longest being 56 minutes. Observations were interrupted by periods of rumination activity which were not counted. The pooling of data has been done from observations of the same day or different days in the same sheep. The intervals between successive primary and secondary cycles were measured from peak to peak of the dorsal ruminal sac contractions in each experiment.

The intervals in seconds between successive primary and successive secondary cycles before and during the period the gases were evacuated are shown in Table 8, and the effect of removing ruminal gases on the amplitude of reticular and dorsal ruminal sac contractions for both the cycles during the longest uninterrupted period of 50 minutes is shown in Fig. 23. The intervals between successive primary and secondary cycles were significantly increased ($P < 0.01$) while eructation did not take place. Before the gases were removed, each secondary cycle was accompanied by an eructation. When the pump was disconnected, one or two secondary cycles were unaccompanied by an eructation presumably because of the volume of gases in the rumen was very small. The intervals between successive primary and secondary cycles and the frequency of eructation were found to become normal within 15 to 20 minutes of disconnecting the pump.

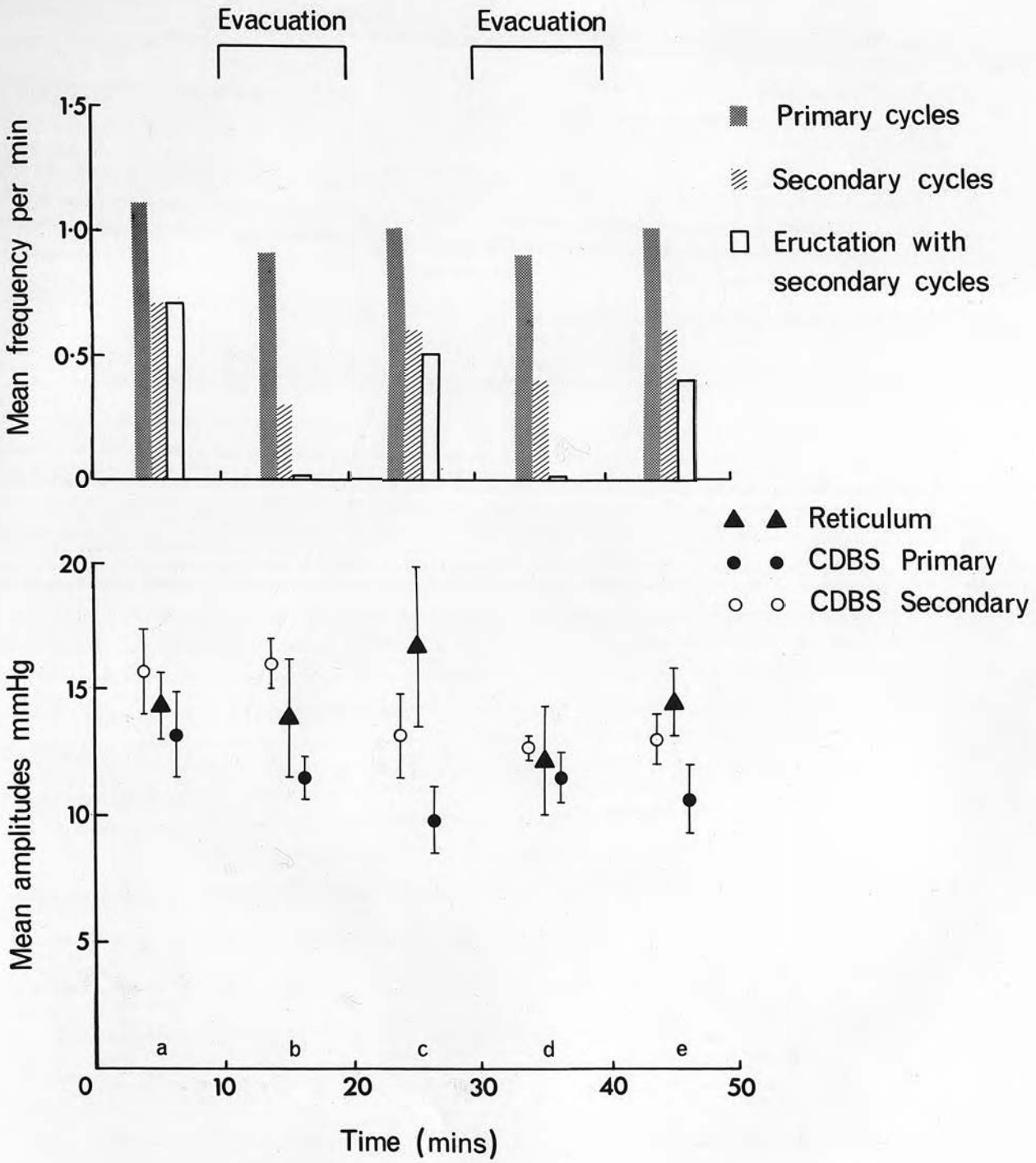
Although the amplitudes of reticulo-ruminal contractions for both primary and secondary cycles were not significantly affected during the first trial, in the second trial they were significantly reduced ($P \leq 0.01$) in both the compartments as compared to the control values. These experiments suggested that the ruminal gas pressure was an important stimulus for the normal frequency of the cyclic activity and eructation and the force of the contractions of the reticulo-rumen.

Fig. 23. The effect of evacuating rumen gases with a vacuum pump on the frequency and amplitudes of reticular and caudo-dorsal blind sac contrac-:tions for primary and secondary cycles. During evacuation, eructation was absent, otherwise it was closely associated with secondary cycles. The data presented are mean values obtained from reticulo-ruminal contractions for primary and secondary cycles during each 10 minute interval. The standard deviation for amplitudes is indicated by vertical bars in each measurement.

Letters (a - e) on the x-axis denote the values for each 10 minute interval for comparison between different amplitude values. The probabilities are shown in the table below.

| | Values | a | b | c | d | e |
|---|---|---|---|---|---|---|
| Reticulum | a | - | 0.1 | 0.05 | 0.01 | 0.1 |
| | b | - | - | 0.05 | 0.1 | 0.1 |
| | c | - | - | - | 0.002 | 0.05 |
| | d | - | - | - | - | <0.01 |
| Caudo-dorsal blind sac, primary cycle | a | - | <0.05 | 0.001 | 0.01 | <0.01 |
| | b | - | - | <0.01 | >0.1 | 0.1 |
| | c | - | - | - | 0.01 | 0.1 |
| | d | - | - | - | - | 0.1 |
| Caudo-dorsal blind sac, secondary cycle | a | - | 0.1 | <0.05 | 0.01 | 0.01 |
| | b | - | - | <0.05 | 0.002 | <0.01 |
| | c | - | - | - | >0.1 | >0.1 |
| | d | - | - | - | - | >0.1 |

CDBS = Caudo-dorsal blind sac


Evacuation
Evacuation
Mean frequency per min
1·5
1·0
0·5
0
Primary cycles
Secondary cycles
Eructation with secondary cycles
Reticulum
CDBS Primary
CDBS Secondary
Mean amplitudes mmHg
20
15
10
5
a
b
c
d
e
0
10
20
30
40
50
Time (mins)

The effect of altering the ruminal pH by the addition of acid or alkali solutions on the reticulo-ruminal motility and eructation

These experiments were carried out on two sheep each fitted with one large mid-dorsal sac cannula (3.7 cm I.D.). The digesta were removed from the forestomach through the cannula, the sacs were washed with tap water at 39°C and 2 to 3 l. of normal saline at the same temperature introduced into the rumen. The animal was allowed $\frac{1}{2}$-1 hour to recover from the effects of handling.

A wide-bore stiff polythene tube open at both ends was passed through the rubber bung to hang in the ventral rumen. This tube was used for the addition of test solutions. Manometric recordings on a Devices 8-channel hot-wire pen-recorder through strain-gauge pressure transducers were made from oesophagus, reticulum, caudo-dorsal blind sac and ventral rumen. The glass reference electrode system and the temperature compensator were introduced into the rumen for recording the pH of its contents whenever required during an experiment.

If, during an experiment, the rumen was found to be full of liquid contents (indicated by oesophageal contractions) some of them were aspirated through the wide-bore polythene tube using a vacuum pump. At the end of each experiment, the liquid contents from the rumen were aspirated and some of the contents removed in the morning were put back. In addition, some ruminal contents from another healthy cannulated sheep were also added. Experiments were done once each fortnight on a sheep to allow time for recovery from the effects of total removal of digesta for these experiments.

The intervals between successive primary and secondary cycles were measured from peak to peak of the caudo-dorsal blind sac contractions. The amplitudes of the contractions of different compartments were

measured from the base-line pressure to the peak of the contraction. The solutions were added into the rumen in quantities varying between 200 ml. to 1 l. at a time and when the ruminal pH became too high or too low, the contractions of the reticulo-rumen disappeared for periods between 10 to 60 minutes. They returned on the addition of opposite solutions within varying intervals when the pH was in the normal range. These periods have been considered separately.

The reticulo-ruminal motility and eructation were recorded for periods varying between $\frac{1}{2}$-$1\frac{1}{2}$ hours before the introduction of any acid or alkali solution. In spite of the absence of normal reticulo-ruminal con-:tents, eructation was found to take place with every secondary cycle con-:traction of the caudo-dorsal blind sac. In both the sheep, the reticular contraction amplitudes were exceptionally high during these experiments while those of the caudo-dorsal blind sac were within normal range for a normally fed sheep. The reticular contractions were biphasic throughout and the absence of normal forestomach contents did not change the pattern of movements which continued for periods not less than 4 to 12 hours or more, after which the experiment was abandoned. In two instances attempts at rumination for 5 to 12 minutes were also observed.

The effect of adding 0.205 N HCl pH 0.74 at 39°C into the rumen

In one experiment 0.205 N HCl pH 0.74 at 39°C was added into the rumen in quantities between 200 to 500 ml. at intervals of not less than 10 minutes. The effects on the amplitudes of reticular and caudo-dorsal blind sac contractions and the intervals in seconds between successive primary and successive secondary cycles are represented in Fig. 24. They were measured for 132 minutes. Except for the first addition of 200 ml. of the acid solution, the reticular contraction amplitudes registered a progressive, highly significant reduction ($P < 0.001$) in their mean

values throughout the subsequent additions of the acid. The caudo-dorsal blind sac contraction amplitudes showed an increase on the first four additions of the acid at 200 ml. at a time. The increase was highly significant ($P < 0.001$) at pH range 6.1-6.5 for primary cycles. The mean values for secondary cycles were significantly reduced at the first 200 ml. after which they registered a significant increase ($P = 0.01$) at pH range 6.1-6.5. Further addition of 200 ml. of 0.205 N HCl resulted in progressive decrease in the mean amplitudes of the caudo-dorsal blind sac contractions for both the cycles. This decrease was highly significant ($P < 0.001$) at pH range 4.6-5.0 or less for primary cycles and significant ($P = 0.01$) at the same pH range for secondary cycles. The intervals in seconds between successive primary cycles did not show significant differences ($P > 0.1$) from the control values till the pH range decreased to 5.6-6.0 or less after which the increase in intervals was highly signifi-:cant ($P \leq 0.001$). The increase in the intervals between successive secondary cycles was highly significant ($P = 0.002$-$0.001$) after the pH range decreased to 6.1-6.5 or less).

Further addition of 250 ml. of 0.205 N HCl at 39°C 25 minutes after the last addition of the acid shown in Fig. 24, resulted in complete inhibi-:tion of primary cycle contractions of the reticulo-rumen for 6 minutes. Then four contractions appeared within four minutes, after which they were inhibited for another 30 minutes. The pH range decreased from 3.6 -4.0 to 2.5-3.5 with this addition of the acid. The primary cycle con-:tractions of the reticulo-rumen reappeared 17 minutes after the addition of 250 ml. of 0.18 N KOH pH 12.4 at 39°C when the ruminal pH changed from 2.5-3.5 range to 6.1-6.5. They gradually increased in force and frequency and became near but significantly lower ($P < 0.002$) than the con-:trol values within the next 60 minutes. The mean amplitudes of reticular contractions were 28.7 mm Hg (S.D. $\pm$6.2) while that of the caudo-dorsal blind sac contractions were 7.0 mm Hg (S.D. $\pm$ 3.6) for primary cycles

and 5.5 mm Hg (S.D. ± 2.4) for secondary cycles. The mean intervals between successive primary cycles were 70 sec (S.D. ± 5.6) and between secondary cycles 85.5 sec (S.D. ± 12.0) during the period of recovery. They were significantly longer ($P < 0.01$) than the control values. Throughout the period of primary cycle inhibition as a result of adding 0.205 N HCl pH 0.74 at 39°C into the rumen, the secondary cycle con-:tractions of the caudo-dorsal blind sac followed by a contraction of the ventral ruminal sac continued occurring at mean intervals of 170 sec (S.D. ± 66.0). They had mean amplitudes of 3.0 mm Hg (S.D. ± 0.7). Each secondary cycle contraction was accompanied by an eructation (Fig. 26). The increase in the intervals between successive scondary cycles and decrease in the mean amplitudes of caudo-dorsal blind sac contractions at pH range 2.5 to 3.5 was highly significant ($P < 0.001$) when compared with the control values.

The addition of 0.205 N HCl at 39°C in 1 l. quantity immediately inhibited the primary cycle contractions of the reticulo-rumen. In one instance they disappeared for 55 minutes. The pH range decreased from 6.6 - 7.0 to 2.5 - 3.5 during this period. They reappeared 10 minutes after 0.5 l. of 0.18 N $Na_2CO_3$ solution pH 10.1 at 39°C was added. When recovery began the intraruminal pH was 5.9. For the next 38 minutes the amplitudes of the reticulo-rumen contractions were not significantly different from the control values but the intervals between successive primary cycles significantly increased ($P < 0.001$).

During the period of primary cycle disappearance, the secondary cycles continued to take place though at reduced frequency and amplitude. When 0.18 N $Na_2CO_3$ solution was added, five secondary cycles each accompanied by an eructation occurred within ten minutes before a primary cycle contraction of the reticulum and caudo-dorsal blind sac appeared (Fig. 27).

The effect of adding 0.205 N acetic acid pH 2.7 at 39°C into the rumen

The addition of 0.205 N acetic acid pH 2.7 at 39°C into the rumen in 0.5 l. quantities at intervals of not less than 10 to 15 minutes progressively decreased the amplitudes of reticular contractions (Fig. 25). The decrease was highly significant ($P < 0.001$). The primary cycle contraction amplitudes of the caudo-dorsal blind sac showed a progressive highly significant increase ($P < 0.001$) until the pH was in the range 5.1-5.5. Further additions of 0.205 N acetic acid at 39°C lowered the pH range to 4.1-4.5 and the amplitudes of the caudo-dorsal blind sac registered progressive decrease which was highly significant ($P < 0.001$) when compared to the values obtained at 5.1-5.5 pH range.

The secondary cycle contraction amplitudes of the caudo-dorsal blind sac showed comparatively less variation with changes in the intraruminal pH by the addition of 0.205 N acetic acid. The increase in their amplitudes was significant ($P < 0.05$) at 5.1-5.5 pH range, below which the mean amplitudes were significantly decreased ($P < 0.05$).

The intervals between successive primary and successive secondary cycles were differently affected by changes in the intraruminal pH due to the addition of acetic acid solution. They increased significantly ($P = 0.05$-$0.01$) between successive primary cycles below the pH range 6.1-6.5 but between successive secondary cycles there was a significant decrease ($P < 0.002$) until the pH range dropped below 4.6-5.0 by serial additions of the acid solution.

Further addition of 0.5 l. of 0.205 N acetic acid in these two experiments completely inhibited the primary cycle contractions of the reticulo-rumen for 15 and 50 minutes but the secondary cycle contractions continued taking place at a mean interval of 102 sec during the 15 minute period of inhibition and 480 sec during the 50 minute period of inhibition

Table 9. The effect of adding 1 l. 0.205 N. Acetic acid pH 2.7 at 39°C into the rumen, on the amplitudes (mm Hg) of reticulo-ruminal contractions and the intervals (secs) between successive primary and secondary cycles. The control values are mean values ± S.D. obtained over 32 minutes. The + acid values represent mean values ± S.D. obtained over 30 minutes immediately after the addition of acetic acid.

| | | Amplitudes (mm Hg) | | Intervals (sec) | pH |
|---|---|---|---|---|---|
| | | Reticulum | Caudo-dorsal blind sac | | |
| Primary cycle | control | 43.81 ± 4.01 | 5.40 ± 1.10 | 62.60 ± 6.339 | 5.6 - 6.0 |
| | + acid | 28.42 ± 3.72 | 3.87 ± 0.95 | 71.54 ± 13.750 | 5.1 - 5.5 |
| Secondary cycle | control | - | 3.79 ± 0.718 | 61.42 ± 11.084 | 5.6 - 6.0 |
| | + acid | - | 3.62 ± 0.711 | 70.92 ± 16.981 | 5.1 - 5.5 |

After adding acetic acid the contractions did not cease in contrast to HCl, but were significantly reduced both in frequency and amplitude.

of primary cycles.

Each secondary cycle contraction of the caudo-dorsal blind sac was accompanied by an eructation during the 0.205 N acetic acid trials at 0.5 l. each time. During the period of complete inhibition of primary cycles for 15 minutes in the first experiment, four out of seven secondary cycle contractions of the caudo-dorsal blind sac were not accompanied by an eructation, while during the next 50 minute period of inhibition in the second experiment, each secondary cycle was accompanied by an eructation.

In another experiment 0.205 N acetic acid pH 2.7 at 39°C was added into the rumen in 1 l. quantity at a time and the effect studied for 30 minutes. The pH changed from 5.6-6.0 to 5.1-5.5 range. The values so obtained have been represented in Table 9. The reticular contraction amplitudes were highly significantly reduced ($P < 0.001$) while those of the caudo-dorsal blind sac were not affected ($P > 0.05$) in both primary and secondary cycles. The intervals between successive primary and secondary cycles were found to be significantly increased ($P = 0.01$-$0.002$). Each secondary cycle was accompanied by an eructation before and after the addition of acetic acid.

The addition of one more litre of 0.205 N acetic acid pH 2.7 at 39°C, 30 minutes after the first 1 l. completely inhibited the primary cycle contractions of the reticulo-rumen for 22 minutes. The pH changed from 5.1-5.5 to 4.6-5.0 range. When recovery began the pH was 4.8. During the period of primary cycle inhibition, the secondary cycles continued taking place at a mean interval of 78.6 sec (S.D. $\pm$ 29.5) between the successive contractions of the caudo-dorsal blind sac. They registered a mean amplitude of 3.0 mm Hg (S.D. $\pm$ 0.4). Each secondary cycle was accompanied by an eructation (Figs. 28 and 29).

Table 10. The effect of altering ruminal pH by the addition of 0.5 - 1 l. of 0.18 N. $Na_2CO_3$ solution pH 10.1 at 39°C into the rumen on the amplitudes of reticulo-ruminal contractions and intervals between successive primary and secondary cycles. The data presented are mean values ± S.D. from three experiments on different days.

The control values were obtained over a period of not less than 30 minutes.

The values after the addition of 0.5 - 1 l. $Na_2CO_3$ solution were measured for 15 - 20 minutes.

| Expt. No. | Primary cycles | Amplitudes (mm Hg) Reticulum | Amplitudes (mm Hg) Caudo-dorsal blind sac | Intervals (secs) | pH |
|---|---|---|---|---|---|
| 1 | control | 24.83 ± 3.60 | 2.85 ± 0.69 | 75.86 ± 21.04 | 7.1 - 7.5 |
| | + $Na_2CO_3$ | 18.86 ± 2.79 | 2.14 ± 0.37 | 108.29 ± 28.17 | 8.1 - 8.5 |
| 2 | control | 33.44 ± 3.74 | 7.82 ± 2.94 | 73.33 ± 7.60 | 7.1 - 7.5 |
| | + $Na_2CO_3$ | 20.40 ± 4.77 | 2.50 ± 0.57 | 292.80 ± 35.98 | 8.1 - 8.5 |
| 3 | control | 33.00 ± 2.82 | 3.17 ± 0.98 | 148.95 ± 50.92 | 6.6 - 7.0 |
| | + $Na_2CO_3$ | 29.17 ± 3.54 | 2.33 ± 0.51 | 233.00 ± 72.34 | 7.6 - 8.0 |

| Expt. No. | Secondary cycles | Amplitudes (mm Hg) Caudo-dorsal blind sac | Intervals (secs) | pH |
|---|---|---|---|---|
| 1 | control | 2.91 ± 0.628 | 75.89 ± 22.50 | 7.1 - 7.5 |
| | + $Na_2CO_3$ | 2.62 ± 0.506 | 105.60 ± 41.35 | 8.1 - 8.5 |
| 2 | control | 5.69 ± 1.494 | 100.23 ± 34.10 | 7.1 - 7.5 |
| | + $Na_2CO_3$ | 3.62 ± 1.193 | 104.85 ± 52.37 | 8.1 - 8.5 |
| | control | 3.72 ± 1.344 | 121.98 ± 71.71 | 6.6 - 7.0 |
| | + $Na_2CO_3$ | 3.42 ± 1.165 | 121.00 ± 75.151 | 7.6 - 8.0 |

The addition of $Na_2CO_3$ depressed the amplitudes of reticular contrac-:tions and the frequency of primary cycles.

The effect of adding 0.18 N $Na_2CO_3$ solution pH 10.1 at 39°C into the rumen

The 0.18 N $Na_2CO_3$ solution pH 10.1 at 39°C was usually added into the rumen after the effect of acid solution had been studied for some time. The ruminal pH was adjusted to the control range (i.e. pH range at the time of the start of the experiment) and a pattern of motility obtained for not less than 30 minutes before the addition of $Na_2CO_3$ solution. The solution was added in 0.5-1 l. quantity. The values so obtained from three experiments are represented in Table 10. The addition of $Na_2CO_3$ solution significantly reduced ($P < 0.01$-$0.002$) the reticular contraction amplitudes while those of the caudo-dorsal blind sac contractions registered significantly lower ($P < 0.002$) amplitudes only in one experiment. In other experiments the differences were not significant ($P > 0.1$-$0.05$) for both primary and secondary cycles. The intervals between successive primary cycles increased highly significantly ($P < 0.001$), while between successive secondary cycles they were not significantly different from the control values except in one instance. After the addition of 0.5-1 l. of the $Na_2CO_3$ solution primary cycles disappeared for 3 to 5 minutes during which period one or two secondary cycles each accompanied by an eructation took place.

Fig. 24. Effect of altering ruminal pH by the sudden addition of 200 - 500 ml of 0.205 N. HCl pH 0.74 on the frequency and amplitudes of reticular and caudo-dorsal blind sac contractions for primary and secondary cycles. The data presented are mean values of measurements after each addition of the acid, obtained over a period of not less than 10 minutes in each case. The control values were obtained over a period of 82 minutes. The volume of acid after each addition in the rumen is shown on the x-axis. The standard deviation for the amplitudes of reticulo-ruminal contractions have been shown by vertical bars for each measurement. Values at point O are control values.

Letters (a - i) along the x-axis represent the values obtained for each pH change for comparison of results and their significance.

(i) Except for the increase between (a and b) which was significant ($P < 0.01$) the reticular contraction amplitudes were highly significantly reduced ($P < 0.001$) after each addition of 0.205 N. HCl.

The table overleaf shows the significance of differences of caudo-dorsal blind sac contraction amplitudes and intervals between successive primary and secondary cycles.

CDBS = Caudo-dorsal blind sac

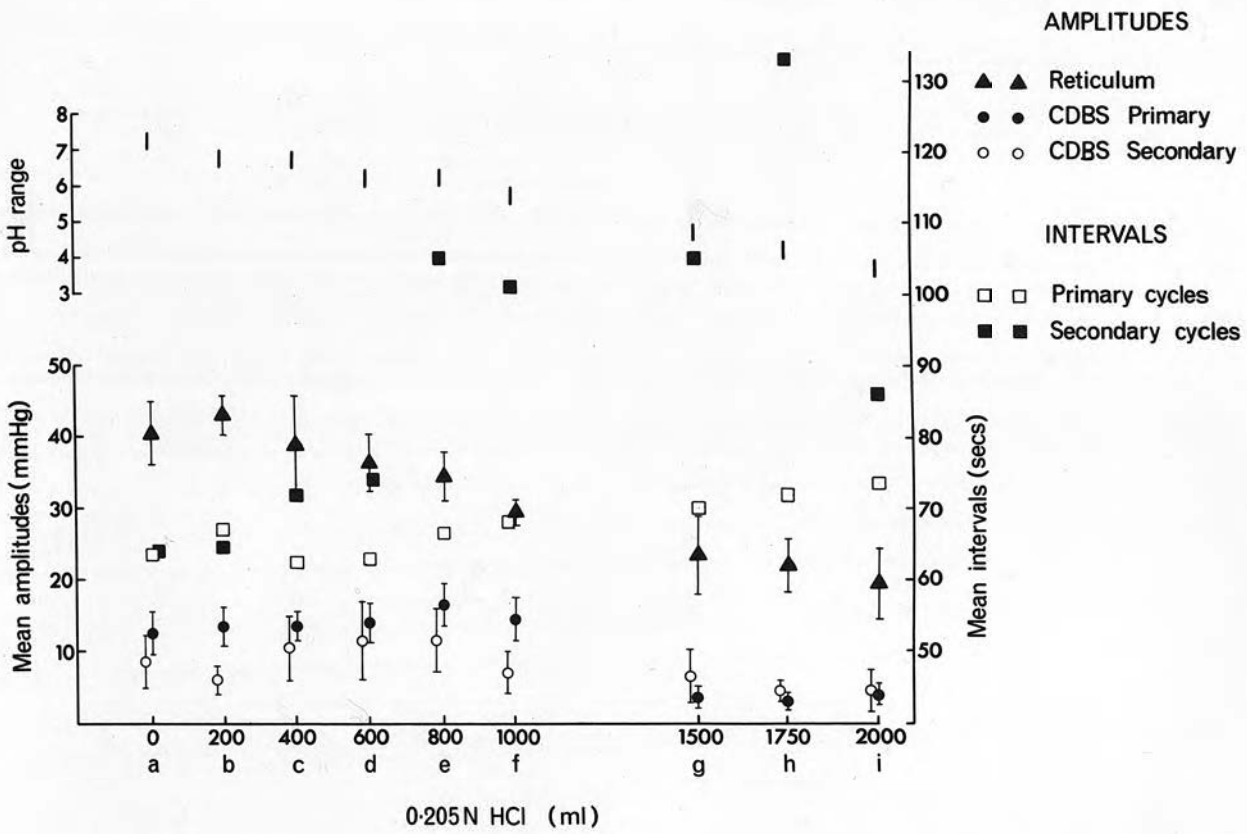

AMPLITUDES
Reticulum
CDBS Primary
CDBS Secondary
INTERVALS
Primary cycles
Secondary cycles
pH range
Mean amplitudes (mmHg)
Mean intervals (secs)
0·205N HCl (ml)
0
200
400
600
800
1000
1500
1750
2000
a
b
c
d
e
f
g
h
i

Fig. 24.

Probability Table for amplitudes

| | Values | b | c | d | e | f | g | h | i |
|---|---|---|---|---|---|---|---|---|---|
| Caudo-dorsal blind sac primary cycle | a | >0.1 | >0.1 | >0.1 | <0.001 | 0.1 | 0.001 | 0.001 | 0.001 |
| | e | - | - | - | - | <0.1 | <0.001 | <0.001 | <0.001 |
| Caudo-dorsal blind sac secondary cycle | a | 0.001 | 0.01 | 0.01 | <0.01 | 0.1 | 0.1 | <0.01 | 0.002 |
| | e | - | - | - | - | <0.001 | <0.002 | 0.001 | <0.001 |

Probability Table for intervals

| | Values | b | c | d | e | f | g | h | i |
|---|---|---|---|---|---|---|---|---|---|
| Primary cycles | a | >0.1 | >0.1 | >0.1 | 0.1 | <0.05 | 0.001 | <0.001 | <0.001 |
| | d | - | - | - | <0.05 | <0.05 | 0.01 | <0.001 | <0.001 |
| Secondary cycles | a | >0.1 | 0.01 | 0.002 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

Fig. 25. The effect of altering the ruminal pH by the addition of 0.205 N. acetic acid pH 2.7 at 39°C into the rumen on the amplitudes of reticulo-ruminal contractions and the intervals between successive primary and secondary cycles. The acid solution was added 0.5 l. at a time. Point 0 on the x-axis is the point representing control values before the addition of any acid. The data presented here are mean values obtained over a period of not less than 10 minutes for each measurement. The standard deviation for amplitude measurements are indicated by vertical bars in each case. The results were obtained from 2 experiments on the same sheep.

Letters (a - e) along the x-axis represent the values for each pH range or the addition of acid for comparison.

(i) The intervals between successive primary cycles increased significantly ($P < 0.05 - 0.01$) at c, d and e from the control values.

(ii) The intervals between successive secondary cycles decreased significantly ($P = 0.01 - 0.002$) at b, c and d and then increased highly significantly ($P < 0.001$) at e from the control values.

CDBS = Caudo-dorsal blind sac

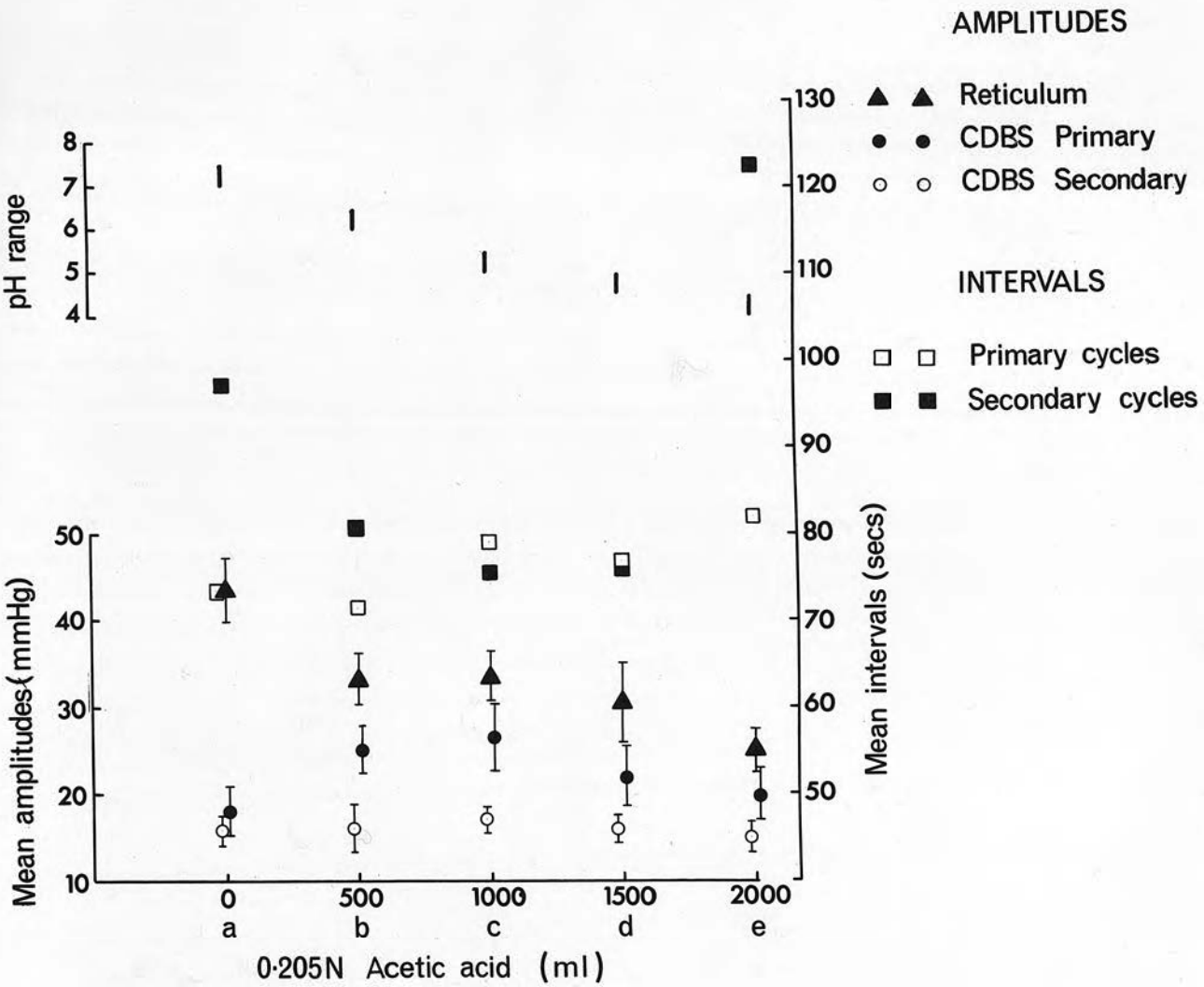

AMPLITUDES
Reticulum
CDBS Primary
CDBS Secondary
INTERVALS
Primary cycles
Secondary cycles
pH range
8
7
6
5
4
Mean amplitudes (mmHg)
50
40
30
20
10
Mean intervals (secs)
130
120
110
100
90
80
70
60
50
0
500
1000
1500
2000
a
b
c
d
e
0·205N Acetic acid (ml)

Fig. 25. Probability Table for amplitudes

| | Values | a | b | c | d | e |
|---|---|---|---|---|---|---|
| Reticulum | a | - | <0.001 | <0.001 | <0.001 | <0.001 |
| | b | - | - | >0.1 | >0.1 | <0.001 |
| | c | - | - | - | 0.1 | <0.001 |
| | d | - | - | - | - | 0.001 |
| Caudo-dorsal blind sac primary cycle | a | - | <0.001 | 0.001 | 0.002 | <0.01 |
| | b | - | - | >0.1 | <0.01 | 0.001 |
| | c | - | - | - | <0.001 | <0.001 |
| | d | - | - | - | - | 0.01 |
| Caudo-dorsal blind sac secondary cycle | a | - | >0.05 | <0.05 | >0.05 | >0.05 |
| | b | - | - | - | - | - |
| | c | - | - | - | - | <0.05 |
| | d | - | - | - | - | - |

Fig. 26. Hot-wire recorder tracing showing the disappearance of primary cycle contractions of the reticulo-rumen following the addition of graded volumes (200-500 ml.) of 0.205 N HCl, pH 0.74, into the rumen. At the arrow 250 ml. of 0.18 N KOH solution pH 12.4 was added into the rumen and the pH range changed from 2.5-3.5 to 6.1-6.5. The balloons were placed in (from above downward) the oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac.

Note the continued occurrence of secondary cycle contractions of the rumen (indicated by "S " under the caudo-dorsal blind sac record) and eructation (indicated by small dots under the oesophageal record) during the period of primary cycle inhibition. Also note the gradual recovery of primary cycle contractions of the reticulo-rumen 17 minutes after the addition of potassium hydroxide solution.

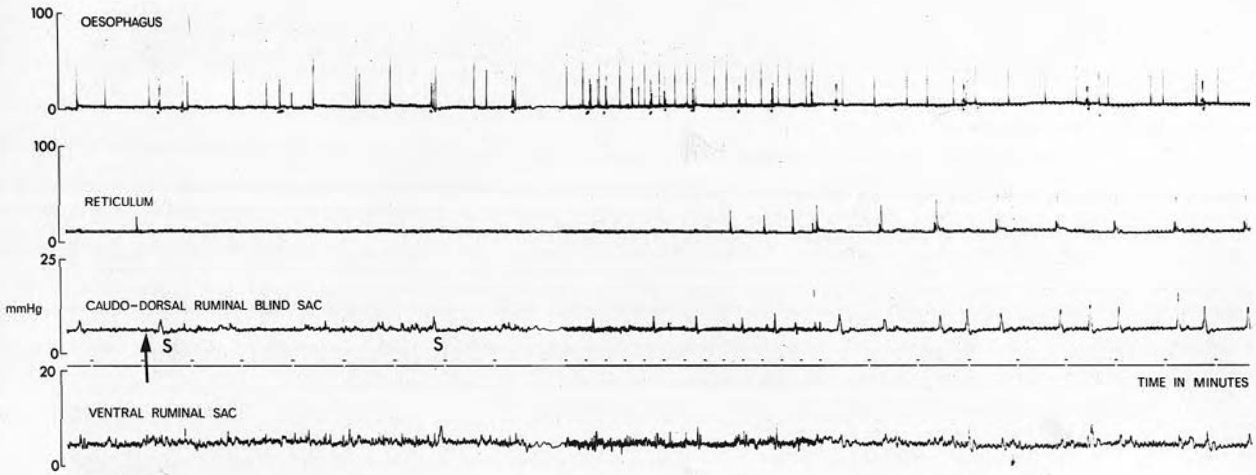

100
OESOPHAGUS
0
100
RETICULUM
0
25
mmHg
CAUDO-DORSAL RUMINAL BLIND SAC
0
S
S
20
TIME IN MINUTES
VENTRAL RUMINAL SAC
0

Fig. 27. Hot-wire recorder tracing showing the absence of primary cycle contractions of the reticulo-rumen following the addition of 1 l. of 0.205 N HCl, pH 0.74, into the rumen. At the point, indicated by the arrow, 250 ml. of 0.18 N $Na_2CO_3$ solution pH 10.1 were added into the rumen and the primary cycle contractions reappeared 10 minutes later. The pH range changed from 2.5-3.5 to 6.1-6.5. Balloons were placed in (from above downward) the oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac. The oesophageal balloon was passed intranasally.

Note the continued occurrence of secondary cycle contract-:ions of the rumen and eructation (indicated by letter "E" under the oesophageal record) during the period, the primary cycles were absent. The frequency of both the secondary cycles and eructation increased following the addition of $Na_2CO_3$ solution.

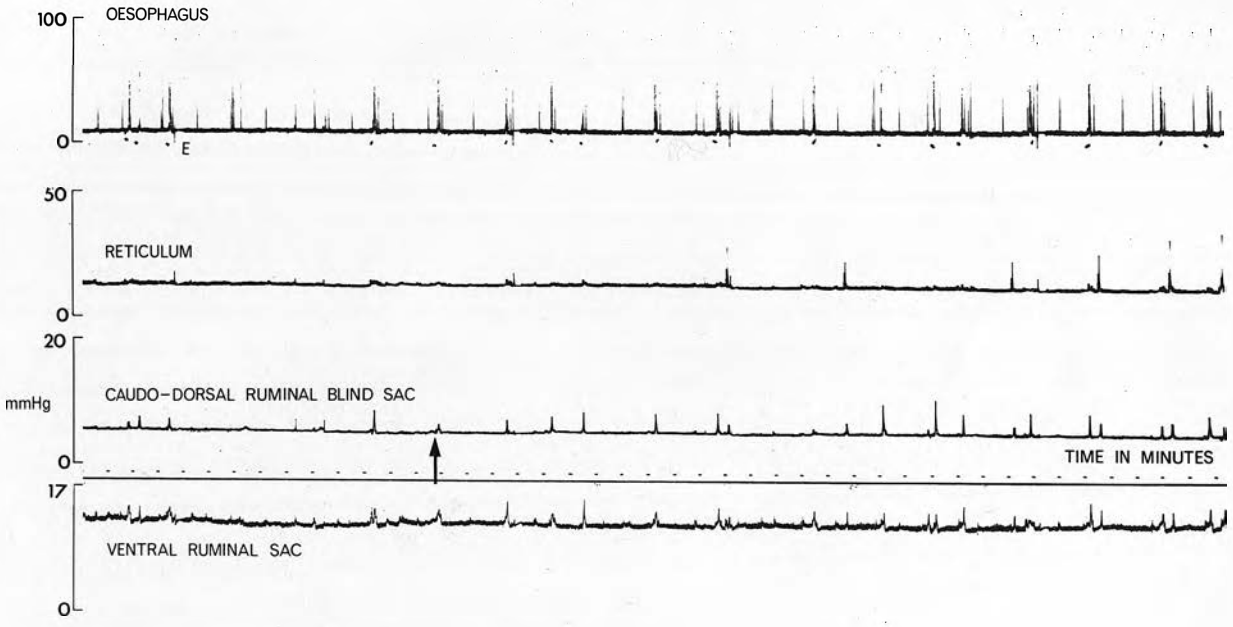

100
OESOPHAGUS
0
E
50
RETICULUM
0
20
mmHg
CAUDO-DORSAL RUMINAL BLIND SAC
0
TIME IN MINUTES
17
VENTRAL RUMINAL SAC
0

Fig. 28. Hot-wire recorder tracing showing the effect of adding (at the arrow) into the rumen 1 l. of 0.205 N acetic acid pH 2.7 on the reticulo-ruminal motility and eructation. The pH range changed from 5.6-6.0 to 5.1-5.5. Balloons were placed in (from above downward) the oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac. The oesophageal balloon was passed intra-:nasally.

Note the decrease in the amplitude of reticular contract-:ions and the frequency of primary and secondary cycles. The eructation is indicated by the letter 'E' under the oesophageal record.

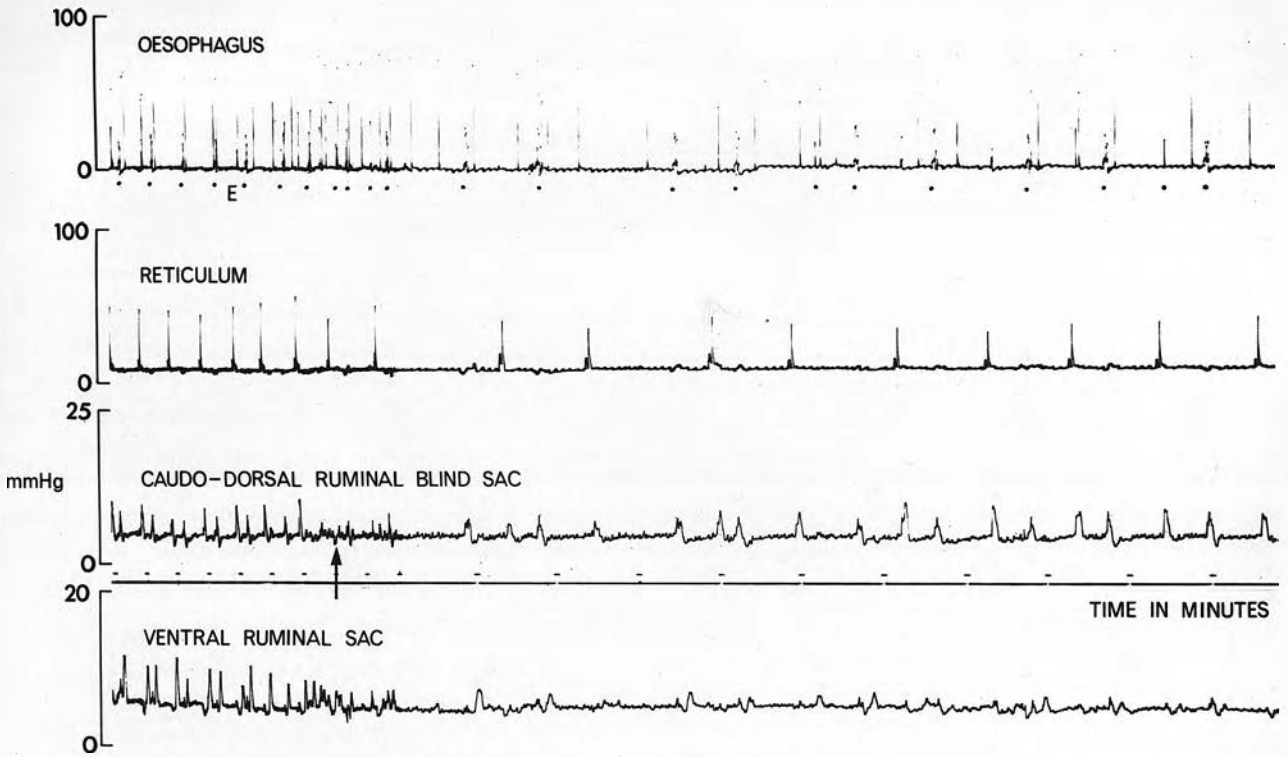
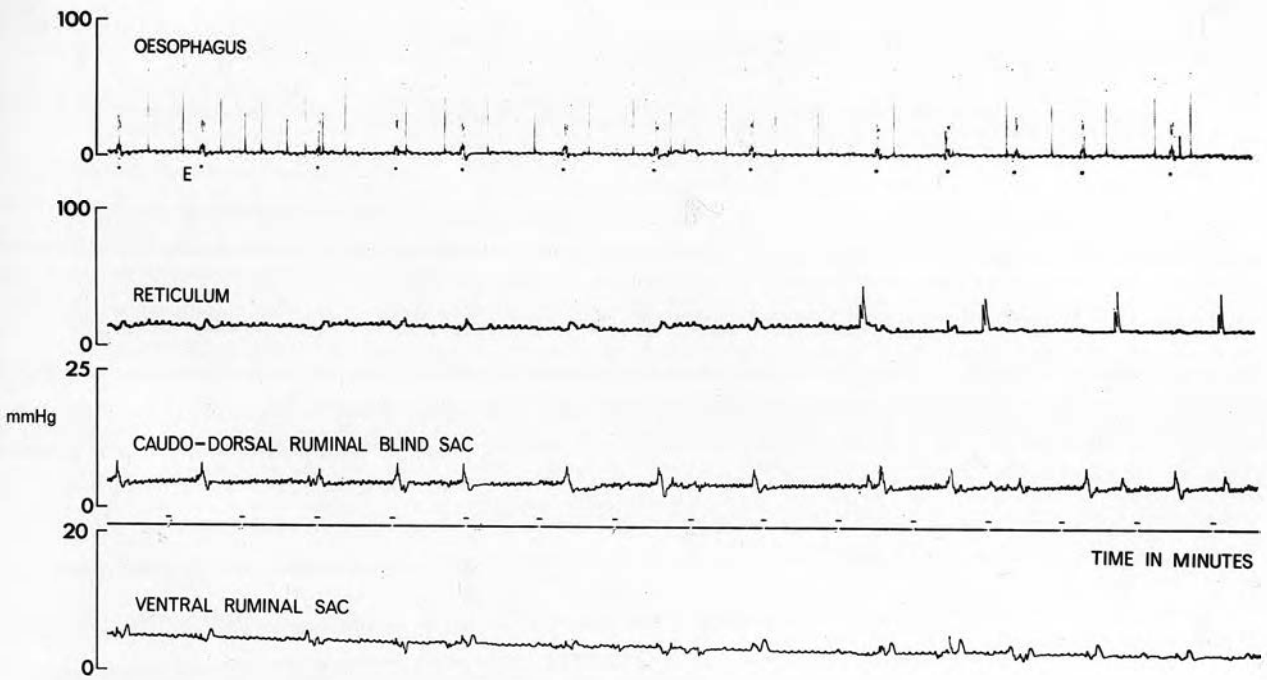

100
OESOPHAGUS
0
E
100
RETICULUM
0
25
mmHg
CAUDO-DORSAL RUMINAL BLIND SAC
0
20
TIME IN MINUTES
VENTRAL RUMINAL SAC
0

Fig. 29. Hot-wire recorder tracing showing the absence of primary cycle contractions of the reticulo-rumen following the addition of one more litre of 0.205 N acetic acid pH 2.7 into the rumen, thirty minutes after that shown in Fig. 28. The pH range changed from 5.1-5.5 to 4.6-5.0. When recovery began, the pH was 4.8. Balloons were placed in (from above downward) the oesophagus, reticulum, caudo-dorsal blind sac and ventral ruminal sac. The oesophageal balloon was passed intranasally.

Note the continued occurrence of secondary cycle contract-:ions of the rumen and eructation (indicated by letter 'E' under the oesophageal record) during the period, the primary cycle contractions of the reticulo-rumen were absent. They reappeared after twenty-two minutes.


100
OESOPHAGUS
0
E
100
RETICULUM
0
25
mmHg
CAUDO-DORSAL RUMINAL BLIND SAC
0
20
TIME IN MINUTES
VENTRAL RUMINAL SAC
0

# DISCUSSION

## Methods

### Visual inspection and manual exploration

Visual inspection and manual exploration of the internal surfaces of the reticulo-rumen, because of its drawbacks of not providing a permanent record and its being subjective rather than objective, was used only for ascertaining the movements of the ingesta and for obtaining a general idea of the involvement of different regions of the forestomach in primary and secondary cycle contractions.

### Pressure recording

The limitations of pressure recording as a measure of gut motility have been recognized for some time by investigators, e.g. Reid & Cornwall, (1959); Sellers & Stevens, (1966) and Quigley, (1955). The limitations are - recording of events from a wide area in the lumen of an organ, the problem of transmitted pressures, forming of a cavity within a cavity and the effects resulting from direct contact of the gut wall with a sensing device (e.g. a balloon).

Most of the results reported here were obtained by recording reticulo-ruminal motility from slightly inflated balloons introduced into the lumen of these organs. Because of the disadvantages mentioned above, the extent of changes in the forestomach motility in different cycles could not be appreciated in finer details.

Hence a new technique of recording forestomach motility was developed

which consisted in surgically implanting the sensitive portions of the microcannulae (p. 25) at discrete locations into the smooth muscle layers of different reticulo-ruminal compartments for obtaining some of the results reported in this work. By this technique it was not only possible to record contractions from discrete locations in the reticulo-ruminal wall but also to avoid the problem of transmitted pressures from one compartment to the other. The changes in motility found to occur in those locations have provided clues as to the over-all pattern of the changes in motility of the forestomach and to their origin, e.g. the involvement of caudo-ventral blind sac in the secondary cycles and the fall in pressure in the ventral ruminal sac simultaneous with the start of the first reticular contraction during the primary cycle on all occasions in four sheep.

The sheep used for this technique showed no apparent discomfort due to the implantation of microcannulae in the wall of the forestomach and ate normally. Useful records can be obtained for a week after the operation which is a sufficient period to establish the pattern of motility of the stomach in an animal.

Reid & Titchen, (1959; 1965) developed the technique of partial exteriorization of different regions of the reticulo-rumen for systematic studies of the motility of these compartments. This technique, no doubt, enabled the authors to obtain a better definition of the relationships between the motility of the forestomach compartments but had the disadvantage that it is only possible to record from the left side of the reticulo-rumen.

Results

The cyclic activity and patterns of reticulo-ruminal contractions described here, occurred consistently in all the animals. Characteristic sequence of the movements of ingesta (Fig. 3) and the involvement of different structures within the reticulo-rumen during primary and secondary cycles were generally similar to those reported by Schalk & Amadon, (1928), Reid & Cornwall, (1959) in cattle and Phillipson, (1939) in sheep, and Dziuk & McCauley, (1965) in cattle, sheep and goats. The movements of the ingesta more or less conformed to the direction of contractions of the reticulo-ruminal wall for primary and secondary cycles.

The form of the ruminal contractions differs in primary and secondary cycles. Wester, (1926) reported the presence of two types of ruminal contractions. This was confirmed by Weiss, (1953) who described the primary cycle contractions as 'backward moving rumen contractions' and the secondary cycles as 'forward moving rumen contractions'. He stated that the ruminal contractions following those of the reticulum progressively involved the cranial and caudal regions of the dorsal rumen, while those dorsal ruminal sac contractions not associated with the reticulum started in the caudal regions and successively involved the cranial regions of the organ. The present studies confirm the contention of Weiss, (1953). The temporal relationships of primary cycle contraction peaks in discrete locations of the ruminal sacs were measured from the peak of the second reticular contraction (Table 6). The cranial and caudo-dorsal blind sac contraction peaks were separated from each other by about two seconds. This is similar to that reported by Reid, (1960) in sheep and Dziuk & McCauley, (1965) in sheep and goats. An interval of

5 to 10 seconds between the contraction peaks of cranial and caudo-dorsal blind sacs was recorded by the latter authors, in cattle.

In the secondary cycles the caudo-dorsal blind sac started its contrac-:tion 1.2-2.4 sec before the dorso-lateral wall of the cranial sac. The two compartments were 16-18 cm apart and reached the peak of their contrac-:tions at the same time. These values are very near to those (1 sec) obtained by Reid & Titchen, (1965) from points 10-12 cm apart in the dorsal rumen.

In a series of publications, Reid, (1960), Reid & Titchen, (1965), and Titchen & Reid, (1965) have reported that a secondary cycle is initiated in the caudo-ventral blind sac 1-7 sec before it appears in the caudo-dorsal blind sac. The results obtained by the microcannula technique from different discrete locations of the caudo-ventral blind sac indicate that the organ presents a variable behaviour. It may start contracting before, at the same time or after a secondary cycle contraction of the caudo-dorsal blind sac has appeared (Figs. 12 and 14). In those preparations (Table 7) in which the microcannula was inserted in the dorsal or caudal wall of the caudo-ventral blind sac, the secondary cycle contractions usually appeared earlier in the caudo-ventral blind sac than in the caudo-dorsal blind sac. In those preparations having a microcannula inserted in the lateral or ventral wall 5-6 cm from the caudal end of the caudo-ventral blind sac, caudo-ventral and caudo-dorsal blind sacs of the rumen usually started contracting at the same time (Table 7). It can be stated that a secondary cycle having been initiated in the caudal wall of the caudo-ventral blind sac progressively involves the rest of the compartment together with the caudo-dorsal blind sac and dorsal rumen. At the end of each caudo-ventral blind sac contraction for secondary cycles, a contraction of the ventral ruminal sac took place in the form reported by Titchen & Reid,

(1965).

The ventral wall of the cranial sac did not show any activity as determined by manual exploration or by the balloon recording technique, (Figs. 7 and 8). A microcannula was not inserted in that location because of its anatomical situation. There is evidence (Dougherty et al. 1960) that in sheep the rumino-reticular fold contracts during a secondary cycle to form an effective barrier to the forward movements of ingesta into the reticulum, thus keeping the cardia free of ingesta for facilitating the expulsion of gases. Dziuk & Sellers, (1955b), Reid & Cornwall, (1959) and Lucas & Dougherty, (1964) working on cattle, indicated that only the cranial pillar contracted during a secondary cycle. The last named authors discerned little or no movement of the rumino-reticular fold. Dziuk & Sellers, (1955b) and Dziuk & McCauley, (1965) found that the ventral wall of the cranial sac did not show any activity in a secondary cycle in cattle, sheep and goats. It appears that the part of the cranial sac between the reticulo-ruminal fold and the cranial pillar remains quiescent.

The fall in pressure in the ventral ruminal sac that occurs with the start of the first reticular contraction for a primary cycle (Figs. 12 and 14) has not been reported previously in the literature. It could be due to the ventral ruminal sac either undergoing a relaxation or to some other unknown effect.

Phillipson, (1939) observed two or four rumen contractions to each biphasic reticular contraction. These were, in fact, one contraction each of dorsal and ventral ruminal sacs for each primary and secondary cycle respectively. Phillipson & Reid, (1960) and Dziuk & McCauley, (1965) described the variable sequence of pressure changes in the rumen of cattle. The measurements made in the present studies for sheep also

showed four major patterns of pressure changes in the dorsal and ventral rumen between successive reticular contractions (Table 2). The values obtained in sheep, except for slight variations, were very near to those reported by Phillipson & Reid, (1960). The dorsal rumen always contract-:ed during each primary cycle and the ventral rumen nearly always con-:tracted during the secondary cycle. The ruminal pressure sequences for primary and secondary cycles were more variable during resting and ruminating than during eating when the cyclic activity of the forestomach becomes more regular (Phillipson & Reid, 1960; Reid, 1963).

## The normal reticulo-ruminal motility and eructation

### (a) During resting

The reticulo-ruminal cyclic motility and eructation varied with the changes in the activity of the animal. The results obtained for normal amplitudes of reticulo-ruminal contractions and the frequency of primary and secondary cycles and eructation during resting in the present experi-:ments, are in general agreement with those in sheep and goats, reported by Phillipson, (1939) Weiss, (1953) Reid, (1963) and of Dziuk & McCauley, (1965). The variations found in the same animal over a five day period (Figs. 9 and 10) in the frequency of primary and secondary cycles and eructation and the amplitudes of reticulo-ruminal contractions could be due to a number of factors, such as the amount of food eaten in one meal, the frequency of meals taken previously, the quantity and nature of the food residues in the forestomach and the metabolic state of its contents (Reid, 1963). Reid & Cornwall, (1959) found that the frequency of fore-:stomach movements in cattle fell off rapidly in the first 15 minutes after feeding and then tended to decrease slowly over the course of several hours. The frequency and amplitudes of the reticulo-ruminal contractions are also dependent upon the time of recording after the morning meal.

According to Felinski, Rotenberg & Baranow-Baranowski (1959) the con-:tractions of the rumen in adult sheep, recorded as pressure increments, using a balloon and Marey tambours, showed fluctuations in amplitudes and frequency at different times of the day; the frequency was highest between 11.00 a.m. and 1.00 p.m. and lowest between 5.00 to 7.00 p.m. The sheep were fed at 7.00 a.m., 3.00 p.m. and 7.00 p.m. Since the measurements reported in present investigations were obtained over different intervals on different days between 11.00 a.m. and 5.00 p.m., the variations in the frequency of cyclic activity and amplitudes of reticulo-ruminal contractions may be partly accountable to diurnal variations and the effects of feeding.

(b) During rumination

The mean frequency results for primary and secondary cycles and eructation and the amplitude of reticulo-ruminal contractions during rumination were similar to those reported for sheep and goats by Phillipson, (1939) Dziuk & McCauley (1965) and McCauley & Dziuk, (1965).

The increase in the frequency of cyclic activity and eructation from the resting to ruminating state was significant ($P \leq 0.05-0.01$) in the present studies. The results obtained by other workers for the frequency of primary and secondary cycles during rumination in cattle are different from those for small ruminants and American bison (Dziuk, 1965). Schalk & Amadon, (1928) found that the rate of primary cycle contractions of the forestomach decreased from 60 cycles per hour during resting to 50 cycles per hour during rumination. Balch, (1952) showed that the rate of reticular contractions was slower during rumination (1 per minute) than during resting (1.2 per minute) and Reid & Cornwall, (1959) did not find any difference in the reticulo-ruminal activity during resting and rumina-:tion in cattle. These workers obtained their measurements on standing

cattle which were maintained on normal diets containing long hay, thus avoiding the fluctuations due to change in position or physical condition of the diet. Since the position of the animals and the physical condition of the ration were similar for the measurements obtained by different workers in different ruminants during rumination there seems to exist certain species difference between cattle and other ruminants.

In sheep, the increase in the frequency of secondary cycles and of eructation during rumination corresponded to that of the primary cycles, and the ratio between the primary and secondary cycles during resting and rumination tended to be similar (Figs. 4 and 5). No gas collection measurements were made during resting or rumination in the present experiments, so the increase in eructation frequency when an animal changed from resting to ruminating activity, may have resulted from an increase in gas accomulation in the dorsal ruminal sac, although recent observations by B.F. Leek (personal communication) show that the frequency changes occur even when the intraruminal pressure is maintained at a constant level. Conversely, the observations of Dougherty & Cook, (1962) who collected eructated gases in cattle through a face mask and an endo-tracheal catheter, indicate that a correlation exists between the ruminal gases eructated and the activity of the animal. The volume of eructated gases was slightly more during rumination than during resting. Similarily McCauley & Dziuk, (1965) collected ruminal gases in goats from the gas pocket of the dorsal rumen by inserting an aspirating tube through a rumen fistula and found the rates of gas accumulation were significantly higher during rumination than during rest. They were reduced below resting rates during ruminal stasis induced by intramuscular administra-:tion of atropine in doses of 0.1 to 0.15 mg/kg body weight. They found that abrupt increases in the rate of gas accumulation occurred with the

onset of rumination after a period of rest, the return of ruminal movements after a period of atony and other movements of the body. From these observations it was concluded that the increase in eructation frequency and the rate of gas accumulation was due to the release of gas bubbles, lodged within the reticulo-ruminal contents in different locations, by any agitation. In the light of these observations by McCauley & Dziuk, (1965) it can be suggested that the significant increase in the frequency of primary cycles (the 'mixing cycles' of Reid & Cornwall, 1959) during rumination is partly responsible for the increased gas accumulation in the dorsal rumen. In addition, the small size of the food particles brought about by remastica-:tion and reswallowing provides a greater surface area for microbial fermentation (Annison & Lewis, 1962) and increased saliva secretion during the rumination (Ash & Kay, 1959) with resultant ruminal gas production, are other possible sources of increased gas accumulation and eructation.

(c) <u>During feeding</u>

The increase in the frequency of primary and secondary cycles and eructation and the amplitudes of reticulo-ruminal contractions during feeding, (Figs. 6 and 11) was in agreement with that reported by Wester, (1926); Schalk & Amadon, (1928); Reid & Cornwall, (1959) in cattle; Phillipson, (1939); Reid, (1963); Titchen & Reid, (1965) in sheep; Dziuk & McCauley, (1965) in cattle, sheep and goats. The frequency of the cyclic activity of the forestomach and eructation during feeding has been found to be greater in white-tailed deer (Dziuk et al. 1963) and American bison (Dziuk, 1965) than in cattle, sheep or goats.

It was found that not only the reticulo-ruminal contractions for primary and secondary cycles registered an increase in frequency and amplitudes but also the eructation contractions of the oesophagus (recorded

from the lower third of its cervical part) showed an increase in their amplitudes (recorded manometrically). These excitatory changes during feeding have been interpreted by Reid, (1963) and Titchen & Reid, (1965) to be of reflex nature. Reid, (1963) stated that the afferent input to the motor centres will be altered as a result of sensory stimulation induced by the acts of mastication, deglutition and by the arrival of newly ingested food into the forestomach which already contains ingesta from the previous meals. Weiss, (1953) reported that feeding increases intra-ruminal pressure by increasing fermentation. Two of the kinds of stimuli likely to be involved, tactile stimulation and stretch of the walls of the reticulo-rumen, are known to be capable of inducing changes in the reticulo-ruminal motility (Ash & Kay, 1959; Reid, 1963, in conscious sheep, and Iggo, 1956; Titchen, 1958 in decerebrate sheep). Thus the increase in the frequency of primary and secondary cycles and eructation during feed-:ing may partly be due to mechanical stimulation of the nerve endings of the trigeminal nerve in the mouth and pharynx (Borgatti & Matscher, 1958), and partly due to a combined effect of tactile, tension and stretch stimuli afforded by the newly arrived food in the forestomach. As soon as feed-:ing stops there is a rapid drop in the frequency of cyclic activity which returns to resting values within 5 to 10 min, though the amplitude of each contraction in different compartments may still be greater than before feeding.

The type of food ingested influences the forestomach motility and eructation (Colvin, Cupps & Cole, 1958). The frequency of the cyclic activity of the forestomach and eructation was greater when alfalfa tops and oat hay were fed than when only hay was fed. Schalk & Amadon, (1928) stated that when animals were maintained on grain alone or other concentrate rations for prolonged periods gastric motility, eructation and rumination were depressed. Stevens & Sellers, (1959) found that the

characteristics of the forestomach contents affected the frequency of cyclic activity and the amplitudes of reticulo-ruminal contractions. Complete removal of forestomach contents decreased the rates of primary and secondary cycles. Replacement of normal contents by an equal weight of completely fluid rumen contents had a similar effect on the primary and secondary cycles and eructation. Recently, Colvin & Daniels (1965) commenting on the requirement of scabrous material for normal tactile stimuli and efficient digestion in the ruminant stomach indicated that oat-hay in 1/4 or 3/32 inch dimensions significantly depressed ($P=0.05-0.01$) the forestomach motility and eructation which took 4 to 6 weeks to return to the long hay pattern and frequency.

Though the 'change of food' experiments were not performed during the present work, from the foregoing it can be stated that tactile stimulation and stretch of the walls of reticulo-rumen are efficacious forms of stimula-:tion which can bring about changes in the force and frequency of primary and secondary cycle contractions of the reticulo-rumen, all of which are features of the changes in motility during feeding.

The effect of insufflation on reticulo-ruminal motility and eructation

Gaseous distension of the rumen with 95% $O_2$ + 5% $CO_2$ gas mixture at low or high rates was found to be excitatory to the frequency of both primary and secondary cycles and eructation. However, the increase in the frequency was more for the secondary cycle contractions of the rumen and eructation than it was for the primary cycles (Fig. 16). Eructation took place not only with each normal secondary or an extra secondary cycle contraction of the dorsal rumen but also with a few primary cycle contrac-:tions during and after the insufflation was stopped. Eructation with a primary cycle took place when 2-3 l. or more of the gas mixture had been introduced into the rumen. It was also found that with increased volume

of the intra-ruminal gases, an extra secondary cycle accompanied by an eructation was brought into play or else eructation took place with a prim-:ary cycle contraction of the dorsal rumen or with both. An increase in the frequency of secondary cycles and eructation due to increased intra-ruminal pressure during insufflation has been reported by Weiss, (1953), Stevens & Sellers, (1959) and Reid & Titchen,(1965). Weiss, (1953) stated that the presence or absence of coarse roughage in the rumen did not appear to affect the eructation reflex and that pressure by gas was the main stimulus for the eructation reflex. This was later confirmed by Stevens & Sellers, (1959) who performed a series of insufflation experiments with different gases in the presence, absence or by the replacement of normal reticulo-ruminal contents and found that the stimulus responsible for eructation reflex was pressure or tension rather than chemical or tactile. Though 'change of food' or 'change of ingesta' experiments were not per-:formed during the present investigations the results obtained during insufflation experiments are consistent with the above results because 10 to 15 minutes after the insufflation was stopped, the frequency of secondary cycles and eructation returned to pre-insufflation values. Dougherty et al. (1958) surgically removed most of the rumen from decerebrate sheep and then clamped off and insufflated the remaining pocket of reticulum, cardia, and cranial dorsal rumen; the eructation continued as before suggesting that an important number of receptors was also located in these areas and they were stimulated by pressure or distension. They also demonstrated the presence of an eructation inhibition reflex by the submersion of the cardia with ingesta or fluid. This reflex was found to be absent after the topical application of a local anaesthetic (Butacaine sulphate) to the area around the cardia.

An increase in the number of contractions of the caudal wall of the caudo-ventral blind sac for primary and secondary cycles during distension

with gas mixture in microcannulated preparations in the present work indicate that the distension sensitive receptors in the rumen reflexly accelerate the reticulo-ruminal motility and modify the form of the caudo-ventral blind sac contractions.

Distension of the rumen with 95% $O_2$ + 5% $CO_2$ gas mixture at the rates above 0.5 l./min used in these experiments was usually found to inhibit the amplitudes of reticulo-ruminal contractions for both primary and secondary cycles except for the first two or three contractions. Distension of the rumen at 0.5 l./min for 30 minutes did not affect the reticular contraction amplitudes but gave a mixed response to primary cycle contractions of the dorsal rumen. They registered slightly increased values for variable periods of 15 to 20 minutes after which the amplitudes were considerably reduced. Secondary cycle contraction amplitudes were significantly decreased throughout. The inhibitory response of the reticulo-ruminal contraction amplitudes was probably dependent upon the degree of filling of the rumen. There is evidence that distension of rumen to 15 to 20 mm Hg of ruminal pressure in anaesthetized sheep (Kay & Phillipson, 1959), is inhibitory to salivary secretion. Reid & Titchen (1965) using decerebrate preparations, found that increasing intra-ruminal pressure up to 8-12 cm water by insufflating a 40% $CH_4$ + 60% $CO_2$ gas mixture at the rate of 150 to 250 ml./min, caused a slight increase in the force of secondary cycle contractions of the rumen. Above these pressures the force of the contractions declined. Comline & Titchen (1961) also using decerebrate sheep indicated that distending the reticular balloon with water proved an efficacious form of stimulation for reticular contractions. The responses to stretch were fairly prolonged (up to 150 minutes) during which time the contractions first gradually increased in force and frequency and then declined in both parameters until they ceased.

Distension of the rumen with varying degrees of inflation of an anaesthetic bag during the present work gave complex responses depending upon the experimental conditions. Unfortunately the inhibitory effect of anaesthetic bag distension was observed for short durations and hence cannot be assessed for a general conclusion. However, moderate distension of the rumen with a 1 l. anaesthetic bag did not affect the cyclic frequency but increased the amplitudes of ruminal contractions for both primary and secondary cycles. This increase was followed by a decrease in amplitudes during maintained distension. Distension of a 4 l. anaesthetic bag with 2.5 l. of introduced air, showed first an increase followed by a decrease in both the frequency and amplitudes of ruminal contractions for primary and secondary cycles during maintained distension. Distension of the bag with 3.5 l. of air showed more pronounced inhibitory effects after initial stimulation. The excitatory and inhibitory effects of bag distension appeared to be more on the frequency of primary cycles than on the secondary cycles. These results when compared with those obtained during insufflation of different volumes of 95% $O_2$ + 5% $CO_2$ indicate that the primary and secondary cycle contraction frequencies of the dorsal rumen respond differently to the two forms of distension. While the primary cycles are more sensitive to distension by an anaesthetic bag the secondary cycles respond more to distension by free gas. Reid, (1963) stated that distension of the reticulum with a balloon in conscious sheep was excitatory to primary cycles but inhibitory to secondary cycles which might disappear completely. On the other hand distension of the rumen was excitatory to secondary cycles and probably inhibitory to primary cycles. A more generalised stimulus of distending the stomach with gas resulted in a mixture of these effects. Leek, (1966) using anaesthetized sheep for recording single unit activity from the left cervical vagus showed that distension of the reticular balloon up to 1000 ml. was excitatory to the rate

and amplitude of reticular contractions and to the efferent discharge. Further distension caused initially a reduction in the amplitude of reticular contractions and the efferent discharge, followed by a reduction in the rate of reticular contractions. He concluded that there existed a low thres-:hold (i.e. 300 ml. air in the reticular balloon) above which there was excitation, and a high threshold of reticular tension (1000 ml. of air in the reticular balloon) above which inhibition occurred.

There is evidence that primary and secondary cycle contractions of the reticulo-rumen are also reflexly influenced by distension stimuli from other parts of the stomach and the lower alimentary tract. Phillipson, (1939) and Weiss, (1953) showed that distension of the abomasum with warm saline or by the insertion and inflation of a balloon reduced the frequency and force of reticular contractions and markedly influenced the character and rhythm of ruminal motility. Primary cycle contractions of the rumen were inhibited while secondary cycle contractions remained unaffected. This inhibition of the reticulo-ruminal motility was proportional to the degree of distension of the abomasum. Severe distension caused com-:plete inhibition of primary cycle contractions while secondary cycle contractions each accompanied by an eructation continued to occur. However, the occurrence of eructation was dependent upon the degree of filling of the rumen and the immersion of the cardia due to increased abomasal volume. When the abomasum had been distended with saline, drainage was followed by an almost immediate recovery. The effects of caecal distension were found to be similar to those of the abomasal dis-:tension.

The decrease in the frequency of primary and secondary cycles during the evacuation of ruminal gases in sheep, (Fig. 23 and Table 8) is in keeping with that reported by McCauley & Dziuk, (1965) in goats. The

decrease was comparatively more significant in the secondary cycles than in the primary cycles which is another indication that ruminal gas pressure is an effective stimulus for the normal frequency of secondary cycles and eructation. Conversely, these observations confirmed the previous ones obtained during insufflation of 95% $O_2$ + 5% $CO_2$ gas mixture as well as those of Weiss, (1953) and Stevens & Sellers, (1959) which showed that increased intraruminal gas pressure markedly increased the secondary cycles relative to the primary cycles.

The effect on reticulo-ruminal motility of altering ruminal pH by the addition of acid or alkali solutions into the rumen

These experiments show that the effect of altering ruminal pH by the addition of acid or alkali solutions into the rumen is dissimilar for primary and secondary cycle contractions of the rumen. Whereas the primary cycle contractions of the reticulo-rumen disappeared for 10 to 60 minutes at low intraruminal pH ranges (2.5-3.5 due to HCl solution and 4.1-4.5 due to the addition of acetic acid solution) the secondary cycle contractions of the rumen each accompanied by an eructation, continued to occur, though with reduced force and frequency. If during the acid inhibition (due to HCl or acetic acid) 0.18 N $Na_2CO_3$ solution in 200 to 250 ml. quantities was added, the frequency of secondary cycle contractions of the rumen and eructation always increased (Fig. 27). This was thought to be due to the chemical reactions:

(i) $2\,HCl + Na_2CO_3 \longrightarrow 2\,NaCl + H_2O + CO_2$

or

(ii) $2\,CH_3COOH + Na_2CO_3 \longrightarrow 2\,CH_3COONa + H_2O + CO_2$

and evolution of $CO_2$ gas. In order to check the excitatory effect of $CO_2$ production, 0.18 N KOH solution pH 12.4 at 39°C in 200 to 250 ml.

quantities was added in some experiments during the acid inhibition and it was found that the frequencies of secondary cycle contractions and of eructations were unchanged. This is another indication that gaseous dis-:tension is an effective stimulus for secondary cycle contractions of the rumen and eructation.

These observations differ from those of Ash, (1956) who found that (0.1-0.2 M) solutions of acetate, propionate and butyrate buffers in the pH range 3.6-4.0 caused complete inhibition of reticulo-ruminal contract-:ions (the secondary cycle contractions of the rumen were not mentioned) for 30-90 minutes within 3 minutes of the introduction of volatile fatty acids solutions. Inhibition of reticulo-ruminal contractions also occurred after acidification of the forestomach walls with acetic, propionic or butyric acid vapour, whereas a stream of air, $CO_2$ or oxygen either did not cause inhibition or else inhibition was of very short duration (Ash, 1959). He also stated that 100-200 mM lactate solutions, at pH 3.6-4.0, 167 mM HCl - sodium phosphate at pH 4.0, 167 mM HCl - glycine at pH 2.9 and 167 mM citric acid - disodium hydrogen phosphate at pH 3.7-4.1 did not cause any appreciable inhibitory effects on the reticulo-ruminal motility. This led him to suggest that the pH value at which inhibition of the forestomach contractions occurred depended to a large extent upon the molecular structure and concentration of the acid. During the present experiments 1-2 l. of 0.205 N HCl pH 0.74 or 0.205 N acetic acid solution pH 2.7 when poured into the rumen caused complete inhibition of the primary cycle contractions at the intra-ruminal pH range of 2.5-3.5 due to HCl and 4.1-4.5 due to acetic acid. It is possible that the inhibitory effect of the HCl solution used during the present experiments was due to comparatively higher concentration than HCl buffers used by Ash (1959). This receives support from the same author's observation that a 200 mM solution is more inhibitory than a 50 mM solution of acetic acid.

Clark & Lombard, (1951) found that the rumen contractions of sheep were depressed in amplitude or completely inhibited by the introduction of alkali into the rumen, similar responses were obtained when alkali was injected intravenously. Weiss, (1953) gave graded doses of sodium car-:bonate through a rumen fistula in sheep and found that whereas primary cycles were reduced in both force and frequency or were completely inhibited, the secondary cycle contractions of the rumen accompanied by an eructation remained unaffected. Larger doses, however, inhibited both for several hours even when the pH of the rumen contents had return-:ed to normal. Under such conditions, he found, that the secondary cycle contractions of the rumen tended to reappear when the intra-ruminal pressure was raised by insufflation of air. During the present experi-:ments the addition of 0.18 N $Na_2CO_3$ solution into the rumen reduced the frequency of primary cycles while the secondary cycles did not show much difference from the control values under the experimental con-:ditions. The amplitudes of reticular contractions fell while those of ruminal contraction were not affected except in one experiment. These results differ from those of Ash, (1959) who found slight inhibition of reticular contractions 30 minutes after the addition of 0.5 N $Na_2CO_3$ solution in one experiment. He concluded that there was no direct effect of an alkaline pH of the forestomach contents on the reticulo-ruminal contractions. It is possible that the difference might be due to the experimental conditions, because the solution used in the present experiments was of comparatively lower concentration than that used by Ash, (1959).

Clark & Lombard (1951) concluded from their experiments that inhibition of ruminal movements during alkalosis resulted from acid-base changes in the blood and was of central origin. Phillipson, (1955) however, did not agree with this hypothesis but suggested that the

inhibition might be due to sensory nerve endings in the epithelium of the rumen. So far there is no available evidence which could suggest the presence of alkali sensitive pH receptors in the epithelium of reticulo-rumen and account for the reflex inhibitory response of the forestomach movements for primary cycles. Iggo, (1957) found receptors which responded to alkaline solutions at pH 8 or above in the mucous membrane of cat stomach, which led Ash, (1959) to suggest the possibility of their presence in sheep stomach, but failed to produce any supporting evidence. Subject to their presence in the forestomach of sheep, he indicated that either the alkali-sensitive receptors do not affect the motility, or the keratinized epithelium is impermeable to the solutions used, (0.1 M sodium phosphate pH 7.9-8.1 and 0.1 M glycine - NaOH - NaCl pH 9.2-10.1 and 0.5 M $Na_2CO_3$ pH 9.0) or their threshold is higher than pH 10.1.

The presence of acid-sensitive receptors responding at pH 3.0 of the test solution (0.01 N HCl) was demonstrated by Iggo, (1957) in the stomach of cat. Iggo, (1966) stated that acid-sensitive receptors, in addition to providing the afferent limb for reflexes regulating gastric acid secretion and motility, may also mediate the gastric sensations associated with gastric hyperacidity in man. In the forestomach of sheep no gastric secretions are produced but the pH of the rumen contents is usually main-:tained between 5.5-7.3 which depends principally on the balance achieved between production and absorption of volatile fatty acids and buffering power of the rumen contents. Primary cycle contractions of the fore-stomach are inhibited at low pH values of the rumen contents (Ash, 1956; 1959; Ash & Kay, 1959; Scarisbrick, 1954). This inhibition is not of central origin as shown by Clark & Lombard, (1951) and Ash, (1959) and there is no electrophysiological work available which could demonstrate the presence of acid-sensitive receptors in the forestomach. However, there is evidence (Ash, 1959) which indicates the presence of acid-

sensitive receptors exerting an inhibitory influence on the motility of the forestomach (primary cycles) at low pH values produced by pouring fatty acid solutions into the rumen. He suggested that the receptors are stimulated not so much by the pH of the rumen contents as by the concen-:tration of the un-ionized volatile fatty acids. In order that the receptors should be stimulated by either acids or alkalis, the test solution must gain access to the nerve endings, so that the local pH is increased or decreased to the threshold of the receptor. Stimulation will depend upon three main factors, namely (1) the relationship of the receptor to the surface exposed to the solution; (2) the penetrating ability of the solution through the epithelium; (3) the hydrogen ion concentration of the test solution.

From the results of the present experiments and from those of Weiss, (1953) it is concluded that the secondary cycle contractions of the rumen are not sensitive to the pH changes in the rumen contents. The decrease in their frequency and force may be related to an over-all inhibi-:tion of the primary cycle contractions of the reticulo-rumen and the reduced gas accumulation at very low or high pH values of the forestomach contents.

Though the reflex effects of pH changes in other parts of the stomach were not studied during the present experiments, there is evidence, (Ash, 1959) that lowering the abomasal pH in conscious sheep with 100 ml. of 160-200 mM acetic, butyric or lactic acid reflexly stimulates the force and frequency of reticular contractions within 90-120 sec. This response persisted for 25-50 minutes after which there was a gradual decrease in the amplitude and frequency of the contractions. Similar results were obtained, using hydrochloric acid, by Titchen (1953; 1958 a) and Iggo & Leek (1966) in decerebrate and anaesthetized sheep respectively. The response gradually decreased with time due to increasing pH of the

abomasal contents. Ehrlein & Hill (1967) have stated that the reticular motility is diminished by increasing the abomasal pH.

A valuable extension of the investigations reported in this thesis would be the study of the relative effect of other volatile fatty acids on the primary and secondary cycle contractions of the reticulo-rumen from within the organs and from other parts of the ruminant stomach. The determination of the definite location of the eructation reflex centre in the brain stem needs also to be explored.

## CONCLUSIONS

1. Eructation is principally associated with secondary cycle contractions of the ruminant forestomach.

2. Eructation occurs at the peak of the secondary cycle contraction of the dorsal ruminal sac.

3. Secondary cycle contractions of the rumen differ from those of the primary cycles as follows:

   (a) The reticulum and ventral wall of the cranial sac are not involved.

   (b) The contractions originate at a different site and move cranially.

   (c) Their frequencies and amplitudes are usually different from those of the primary cycle contractions of the rumen.

4. The response of the secondary cycle contractions of the dorsal rumen differs from that of the primary cycle contractions according to the type and degree of distension. Moderate or severe distension with free gas always enhances the frequency of secondary cycles and eructation. The primary cycles are less affected. Distension with an anesthetic bag increases the frequency of primary cycles more than that of the secondary cycles and eructation. Inhibitory effects on the amplitudes of forestomach contractions due to extreme distension with free gas are more pronounced on the secondary cycle contractions. Extreme distension with an anaesthetic bag is more inhibitory for primary cycle contractions.

5. Reduced intraruminal pressure due to evacuation of ruminal gases significantly depresses the secondary cycle contractions of the rumen. The primary cycle contractions are less affected.

6. Secondary cycle contractions and eructation, in contrast to primary cycle contractions of the reticulo-rumen, are not markedly affected by changes in pH of the rumen contents.

7. The primary and secondary cycle contractions of the reticulo-rumen are under independent nervous control.

8. Eructation is regulated through its dependence on the presence of secondary cycle contractions of the rumen, whose frequency and amplitudes are determined by the degree and type of distension of the rumen.

## SUMMARY

1. A new technique of recording reticulo-ruminal movements was developed. It consisted of surgical implantation of micro-:cannulae in discrete locations of the reticulo-ruminal wall, thus avoiding the imprecision of classical manometric methods and the problem of transmitted pressures from one compartment to the other.

2. The involvement of different regions of the reticulo-rumen in primary and secondary cycle contractions is described.

3. The primary cycle contractions started with a biphasic contraction of the reticulum and progressively involved the cranial, the middle and caudal regions of the dorsal rumen, followed usually by a con-:traction of the ventral rumen.

4. The secondary cycle contractions usually originated in the caudal wall of the caudo-ventral blind sac and progressively involved first the caudal and then the cranial regions of the dorsal rumen, followed nearly always by a contraction of the ventral ruminal sac.

5. Eructation was principally associated with the secondary cycle contraction of the dorsal rumen and took place when the contraction had reached its peak. Eructation taking place with a primary cycle contraction was rare.

6. The frequency and the amplitudes of reticulo-ruminal contractions

for primary and secondary cycles and the frequency of eructation varied with the activity of the animal, i.e. resting, ruminating or eating. Except for the amplitudes of reticular contractions which were significantly reduced ($P < 0.001$), during rumination, the rest of the parameters showed significant increase ($P = 0.01$-$0.001$), both during rumination and eating.

7. Gaseous distension was always more excitatory to the frequency of secondary cycle contractions of the rumen and eructation than the primary cycle contractions which were not affected at moderate distension. Higher distension affected both; even then the second-:ary cycles and eructation increased more than the primary cycles.

8. The excitatory effects of an anaesthetic bag distension in the caudo-dorsal blind sac were more pronounced for the primary cycle con-:tractions than for the secondary cycle contractions of the fore-:stomach.

9. Moderate distension for prolonged periods or severe distension of the dorsal rumen for short periods with free gas, depressed the amplitudes of secondary cycle contractions of the caudo-dorsal blind sac more than that of the primary cycle contractions. Inhibitory effect due to extreme distension of the anaesthetic bag was more pronounced on the latter contractions than on the former.

10. Evacuation of ruminal gases significantly depressed the frequency of secondary cycle contractions of the rumen. Eructation was absent. The primary cycle contractions were affected less than the secondary cycles.

11. Both high and low intraruminal pH depressed or completely abolished the primary cycle contractions of the reticulo-rumen. The secondary cycle contractions continued occurring, though with reduced force and frequency. They were accompanied by an eructation.

# APPENDIX

The experiments described in this thesis involved the calculations of a series of mean values and standard deviations and some statistical test to assess the significance of differences between various sets of data obtained at different times. Student's 't' test was applied to find the significance of differences between two sets of data. The mathematics required by this analysis was performed on an Atlas computer from a programme written in Atlas autocode. The programme was designed by Mr. B.F. Leek, of the Department of Veterinary Physiology, Royal (Dick) School of Veterinary Studies, Edinburgh. Sets of data were punched on to tape and each set was given a code number e.g. * 1, * 2, * 3, * 4 and so on, and terminated by the symbol -1. For the students 't' test the autocode was * -3. Blocks of data, after being punched onto tape, were statistically tested for students 't' test as follows:

```
*  -3    1    2
*  -3    1    3
*  -3    1    4
*  -3    2    3
*  -3    3    4        and so on
```

A copy of the programme is included.

```
*** A
JOB
VPY 001/00000007/LEEK
COMPILER AA
```

```
%BEGIN
%REAL X, MIN, MAX, Q, P, S, T
%INTEGER N, H, A, B, C, I
%INTEGERARRAY TITLE (1:30)
%INTEGERARRAY NA (1:30)
%ARRAY PA(1:30)
%ARRAY VA(1:30)
%ROUTINESPEC TL
%ROUTINESPEC TP
%ROUTINESPEC TST
%ROUTINESPEC VP
%ROUTINESPEC VR
%CAPTION ~ MEAN␣␣␣␣␣␣MIN␣␣␣␣␣
%CAPTION MAX ␣␣␣␣S.D.␣␣␣␣S.E.␣␣␣␣␣NO.
15: N = 0; P = 0; Q = 0; MIN = 10    6; MAX = 0
TL
READ (A)
%IF A = -3 %THEN ->44
%IF A ≠ -3 %THEN  ->55
44:TST
-> 15
55:VR
->15
%ROUTINE TL
H = 1
13: READ SYMBOL (I)
%IF I = '~' %THEN  ->  13
%IF I = -2   %THEN %STOP
TITLE (H) = I
```

```
H = H+1
-> 13 %UNLESS I = '*'
%END
%ROUTINE TP
H = 1
33: PRINT SYMBOL (TITLE (H))
H = H + 1
-> 33 %UNLESS TITLE (H) = '*'
%END
%ROUTINE TST
READ (B)
READ (C)
S = SQ RT ((VA(B) + VA (C)) / (NA(B) + NA(C) -2))
T = ((PA(B)/NA(B)) - (PA(C)/NA(C)))/(S * SQ RT ((1/NA (B))+(1/NA (C))))
NEWLINE
SPACES (24)
%CAPTION SERIES ␣␣
PRINT (B, 2, 0)
SPACE
PRINT (C, 2, 0)
SPACES (3)
TP
%CAPTION ␣T =␣
PRINT (T, 3, 3)
SPACE
%CAPTION DEG FREE
SPACE
PRINT (NA(B) + NA(C) -2, 3, 0)
%END
```

```
%ROUTINE VP
VA(A) = Q - ((P↑2)/N)
NA(A) = N
PA(A) = P
NEWLINE
PRINT (P/N, 3, 2)
SPACE
PRINT (MIN, 3, 2)
SPACE
PRINT (MAX, 3, 2)
SPACE
PRINT (SQ RT (VA(A)/(N-1)), 2, 3)
SPACE
PRINT ((SQ RT (VA(A)/(N-1)))/(SQ RT (N)), 2, 3)
SPACE
PRINT (N, 3, 0)
SPACES (3)
TP
PRINT (A, 2, 0)
%END
%ROUTINE VR
20: READ (X)
%IF X = -2 %THEN %STOP
%IF X = -1 %THEN -> 22
N = N+1
Q = Q+(X↑2)
P = P+X
%IF X < MIN %THEN MIN = X
```

```
%IF X > MAX %THEN MAX = X
-> 20
22: VP
%END
%ENDOFPROGRAM
```

## BIBLIOGRAPHY

ANDERSSON, B., KITCHELL, R. & PERSSON, N. (1959). A study of central regulation of rumination and reticulo-ruminal motility. Acta physiol. scand. 46, 319-338.

ANNISON, E.F. & LEWIS, D. (1959). Metabolism in the rumen. London : Methuen & Co. Ltd., New York : John Wiley & Sons Inc.

ALEXANDER, F. & MOODIE, E.W. (1960). The recording of rumen movements in the intact cow, and the effects of certain drugs. Res. vet. Sci. I, 248-254.

ASH, R.W. (1956). Inhibition of reticulo-rumen contractions by acid. J. Physiol. 133, 75-76P.

ASH, R.W. (1959). Inhibition and excitation of reticulo-ruminal contract-:ions following the introduction of acids into the rumen and abomasum. J. Physiol. 147, 58-73.

ASH, R.W. & KAY, R.N.B. (1959). Stimulation and inhibition of reticulum contractions, rumination and parotid secretion from the forestomach of conscious sheep. J. Physiol. 149, 43-57.

BALCH, C.C. (1952). Factors affecting the utilization of food by dairy cows. 6. The rate of contraction of the reticulum. Brit. J. Nutr. 6, 366-375.

BALCH, C.C., KELLY, A. & HEIM, G. (1951). Factors affecting the utilization of food by dairy cows. 4. The action of the reticulo-omasal orifice. Brit. J. Nutr. 5, 207-216.

BELL, F.R. & LAWN, A.M. (1955). Localization of regions in the medulla oblongata of sheep associated with rumination. J. Physiol. 128, 577-592.

BENZIE, D. & Phillipson, A.T. (1957). The alimentary tract of the ruminant. Edinburgh & London : Oliver & Boyd.

BORGATTI, G. & Matscher, R. (1958). Voies et signification du réflexe oral du réseau. Arch. ital. Biol. 96, 38-57.

CLARK, C.H. (1953). The nervous control of rumination and reticulo-ruminal motility. Amer. J. Vet. Res. 14, 376-384.

CLARK, R. & LOMBARD, W.A. (1951). Studies on the alimentary tract of merino sheep in South Africa. The effect of the pH of the ruminal contents on ruminal motility. Onderstepoort J. Vet. Res. 25, 79-92.

COLE, H.H., HUFFMAN, C.F., KLEIBER, M., OLSON, T.M. & SCHALK, A.F. (1945). A review of bloat in ruminants. J. Anim. Sci. 4, 181-236.

COLE, H.H., MEAD, S.W. & KLEIBER, M. (1942). Bloat in cattle. Univ. Calif. Coll. Agri. Bull. 662, 3-22.

COLVIN, H.W. Jr., CUPPS, P.T. & COLE, H.H. (1958). Dietary influ-:ences on eructation and related ruminal phenomena in cattle. J. Dairy Sci. 41, 1565-1579.

COLVIN, H.W. & DANIELS, L.B. (1965). Rumen motility as influenced by physical form of oat hay. J. Dairy Sci. 48, 935-941.

COLVIN, H.W. Jr., WHEAT, J.D., RHODE, E.A. & BODA, J.M. (1957). Technique for measuring eructated gas in cattle. J. Dairy Sci. 40, 492-502.

COMLINE, R.S. & KAY, R.N.B. (1955). Reflex secretion of the parotid gland in sheep. J. Physiol. 129, 55-56P.

COMLINE, R.S. & TITCHEN, D.A. (1957). Reflex contractions of the reticulum and rumen and parotid salivary secretion. J. Physiol. 139, 24P.

COMLINE, R.S. & TITCHEN, D.A. (1961). Nervous control of the rumin-:ant stomach. In Digestive Physiology and Nutrition of the Ruminant. ed. D. Lewis. p. 10-22. London : Butterworths.

CZEPA, A. & Stigler, R. (1926). Der Wiederkäuermagen in Röntgenbild. 1. Mitteilung. Pflüger's Arch Ges. Physiol. 212, 300-356.

DOUGHERTY, R.W. (1955). Permanent stomach and intestinal fistulas in ruminants: some modifications and simplifications. Cornell Vet. 45, 331-357.

DOUGHERTY, R.W. (1961). The physiology of eructation in ruminants. In Digestive Physiology and Nutrition of the Ruminant. ed. D. Lewis, pp. 79-87. London : Butterworths.

DOUGHERTY, R.W. & COOK, H.M. (1962). Routes of eructated gas expulsion in cattle. A quantitative study. Amer. J. Vet. Res. 23, 997-1000.

DOUGHERTY, R.W. & HABEL, R.E. (1955). The cranial oesophageal sphincter, its action and its relation to eructation in sheep as deter-:mined by cinefluorography. Cornell Vet. 45, 459-464.

DOUGHERTY, R.W., HABEL, R.E. & BOND, H.E. (1958). Oesophageal innervation and the eructation reflex in sheep. Amer. J. Vet. Res. 19, 115-128.

DOUGHERTY, R.W., HILL, K.J., CAMPETI, F., McCLURE, R.C. & HABEL, R.E. (1962). Studies of pharyngeal and laryngeal activity during eructation in ruminants. Amer. J. Vet. Res. 23, 213-219.

DOUGHERTY, R.W. & MEREDITH, C.D. (1955). Cinefluorographic studies of the ruminant stomach and of eructation. Amer. J. Vet. Res. 16, 96-100.

DOUGHERTY, R.W., MULLENAX, C.H. & ALLISON, M.J. (1966). Physiological phenomena associated with eructation in ruminants. In Physiology of Digestion in the Ruminant. ed. R.W. Dougherty, et al. pp. 159-170.

DOUGHERTY, R.W., STEWART, W.E., NOLD, M., LINDAHL, I., CAMPETI, F. & HILL, K.J. (1960). Eructation in insufflated sheep and its relation to the rapid blood gas changes. 5th Conference on Rumen Function, Maryland, U.S.A. pp. 13-37.

DOUGHERTY, R.W., STEWART, W.E., NOLD, M.M., LINDAHL, I.D., MULLENAX, C.H. & LEEK, B.F. (1962). Pulmonary absorption of eructated gas in ruminants. Amer. J. Vet. Res. 23, 205-212.

DUKES, H.H. (1955). The Physiology of Domestic Animals. 7th edn. London: Bailliere, Tindall & Cox.

DUNCAN, D.L. (1953). The effects of vagotomy and splanchnotomy on gastric motility in the sheep. J. Physiol. 119, 157-169.

DUNCAN, D.L. & PHILLIPSON, A.T. (1951). The development of motor responses in the stomach of the foetal sheep. J. exp. Biol. 28, 32-40.

DZIUK, H.E. (1965). Eructation, regurgitation and reticulo-ruminal contraction in the American bison. Amer. J. Physiol. 208, 343-346.

DZIUK, H.E., FASHINGBAUER, B.A. & IDSTROM, J.M. (1963). Rumino-reticular pressure patterns in fistulated white-tailed deer. Amer. J. Vet. Res. 24, 772-783.

DZIUK, H.E. & McCAULEY, E.H. (1965). Comparison of rumino-reticular motility patterns in cattle, sheep and goats. Amer. J. Physiol. 209, 324-328.

DZIUK, H.E., & SELLERS, A.R. (1955 a). Physiological studies of the vagal nerve supply to the bovine stomach. 1. Comparison of re-:sponses in milk-fed and roughage-fed calves, using a chronic intra-thoracic vagal electrode technique. Amer. J. Vet. Res. 16, 411-417.

DZIUK, H.E. & SELLERS, A.F. (1955 b). Physiological studies of the vagal nerve supply to the bovine stomach. 2. Studies on the eructa-:tion mechanism in adult cattle. Amer. J. Vet. Res. 16, 499-504.

EHRLEIN, H.J. & HILL, H. (1967). The influence of abomasal and duodenal contents on the motility of the stomach in goats. 18th World Veterinary Congress, Paris. p. 732.

FELINSKI, L., ROTENBERG, S. & BARANOW - BARONOWSKI, St. (1959). Dobowe wahania w motoryce zwacza u owiec. Acta physiol. Pol. 10, 365.

FLATT, W.P., WARNER, R.G. & LOOSLI, J.K. (1959). Evaluation of several techniques used in the study of developing rumen function. Cornell Univ. Memoir 361, 1-30.

HABEL, R.E. (1956). A study of the innervation of the ruminant stomach. Cornell Vet. 46, 555-628.

HABEL, R.E. (1965). Anatomical and physiological nomenclature of the ruminant stomach. In Physiology of Digestion in the Ruminant. ed. R.W. Dougherty et al. pp. 15-23.

HOWARD, B.R. (1966). The central nervous regulation of ruminant gastric activity. Ph.D. Thesis. University of Edinburgh.

HUNGATE, R.E., FLETCHER, D.W., DOUGHERTY, R.W. & BARRENTINE, B.F. (1955). Microbial activity in the bovine rumen, its measure-:ment and relation to bloat. Appl. Microbiol. 3, 161-173.

IGGO, A. (1951). Spontaneous and reflexly elicited contractions of reticulum and rumen in decerebrate sheep. J. Physiol. 115, 74-75P.

IGGO, A. (1956). Central nervous control of gastric movements in sheep and goats. J. Physiol. 131, 248-256.

IGGO, A. (1957). Gastric mucosal chemoreceptors with vagal afferent fibres in the cat. Quart. J. exp. Physiol. 42, 398-409.

IGGO, A. (1966). Physiology of visceral afferent systems. Acta neuroveg. 28, 121-134.

IGGO, A. & LEEK, B.F. (1966). Reflex regulation of gastric activity. Acta neuroveg. 28, 353-359.

KAY, R.N.B. & HOBSON, P.N. (1963). Reviews of the progress of dairy science. 1. The physiology of the rumen. 2. Rumen microbiology. J. Dairy Res. 30, 261-313.

KAY, R.N.B. & PHILLIPSON, A.T. (1959). The effects of distension of the oesophagus and rumen upon salivary secretion. Proc. 16th Int. Vet. Congr., Madrid.

KINGWELL, R.G., OPPERMANN, R.A., NELSON, W.O. & BROWN, R.E. (1959). Factors affecting the composition of rumen gas. J. Dairy Sci. 42, 912-913.

LAMBERT, P.S. (1948). The development of the stomach in the ruminant. Vet. J. 104, 302-310.

LEEK, B.F. (1963). Single unit activity in cervical vagal efferent axons associated with reticulo-ruminal movements. J. Physiol. 169, 5-6P.

LEEK, B.F. (1966). The reflex regulation of reticulo-ruminal movements. World Congress on Animal Feeding, Madrid. Pt. 2, 19-24.

LUCAS, K. & DOUGHERTY, R.W. (1964). An electromagnetic induction technic as applied to the study of ruminoreticular motility in the bovine animal. Cornell Vet. 54, 535-540.

MARSCHALL, A. (1910). Cited by Habel 1956.

McANALLY, R.A. & PHILLIPSON, A.T. (1944). Digestion in the ruminant. Biol. Rev. 19, 41-54.

McARTHUR, J.M. & MILTIMORE, J.E. (1961). Rumen gas analysis by gas - solid chromatography. Canad. J. Anim. Sci. 41, 187-196.

McCAULEY, E.H. & DZIUK, H.E. (1965). Correlation of motility and gas collection from goat rumen. Amer. J. Physiol. 209, 1152-1154.

MAGEE, H.E. (1932). Observations on digestion in the ruminant. J. exp. Biol. 9, 409-426.

MANGOLD, E. & KLEIN, W. (1927). Bewegungen und Innervation des Wiederkäuermagens. Georg Thieme, Leipzig.

OHGA, A., OTA, Y. & NAKAZATO, Y. (1965). The movement of the stomach of sheep with special reference to the omasal movement. Jap. J. vet. Sci. 27, 151-160.

PHILLIPSON, A.T. (1939). The movements of the pouches of the stomach of sheep. Q. J. exp. Physiol. 29, 395-415.

PHILLIPSON, A.T. (1955). Rumen dysfunction. Adv. Vet. Sci. 2, 212-261.

PHILLIPSON, A.T. & INNES, J.R.M. (1939). Permanent stomach fistulae in ruminants. Quart. J. exp. Physiol. 29, 333-341.

PHILLIPSON, A.T. & REID, C.S.W. (1960). The incidence of pressure waves in the rumen of cattle. Proc. Nutr. Soc. 19, xxvii

QUIGLEY, J.P. (1955). Digestive tract. Intralumen pressures with special reference to gastro-intestinal propulsion and gastric evacuation. In Medical Physics. ed. O. Glasser, Chicago. Year Book 1955, 1, 310.

QUIN, J.I., VAN der WATH, J.G. & MYBURGH, S. (1938). Studies on the alimentary tract of merino sheep in South Africa. 5. The motility of the rumen under various conditions. Onderstepoort J. Vet. Sci. and Anim. Indust. 11, 361-382.

REID, C.S.W. (1960). Eructation and rumen movements in sheep. J. Physiol. 153, 39-40P.

REID, C.S.W. (1963). Diet and the motility of the forestomachs of the sheep. Proc. N.Z. Soc. Anim. Prod. 23, 169-188.

REID, C.S.W. & CORNWALL, J.B. (1959). The mechanical activity of the reticulo-rumen of cattle. Proc. N.Z. Soc. Anim. Prod. 19, 23-35.

REID, C.S.W. & TITCHEN, D.A. (1959). Activity of the partially exteriorized reticulum and rumen in conscious sheep. J. Physiol. 149, 14-15P.

REID, C.S.W. & TITCHEN, D.A. (1965). Reflex stimulation of move-:ments of the rumen in decerebrate sheep. J. Physiol. 181, 432-448.

SALMIN, I.P. (1960). Mechano-receptors in the compound stomach and regulation of periodic rumination. J. Physiol. Sechenova, 46, 1148-1158.

SCARISBRICK, R. (1954). Acid indigestion in sheep fed on mangolds. Vet. Rec. 66, 131-132.

SCHALK, A.F. & AMADON, R.S. (1928). The physiology of the ruminant stomach, study of the dynamic factors. N. Dak. agric coll. Exp. Stn. Bull. 216, 1-64.

SELLERS, A.F. & STEVENS, C.E. (1966). Motor functions of the ruminant forestomach. Physiol. Rev. 46, 634-661.

SEREN, E., MOLINARI, P. & BRAMBILLA, E. (1965). Contribution to the knowledge of a reticular contraction during rumination in cattle. Festschrift der Wiener Tierärztlichen Monatsschrift. 52, 455-460.

SISSON, S. & GROSSMAN, J.D. (1953). The Anatomy of Domestic Animals. Philadelphia & London: W.B. Saunders Co.

STEVENS, C.E. & SELLERS, A.F. (1959). Studies of the reflex control of the ruminant stomach with special reference to the eructation reflex. Amer. J. Vet. Res. 20, 461-482.

STEVENS, C.E. & SELLERS, A.F. (1960). Pressure events in bovine oesophagus and reticulo-rumen associated with eructation, deglutition and regurgitation. Amer. J. Physiol. 199, 598-602.

TAMATE, H., McGILLIARD, A.D., JACOBSON, N.L. & GETTY, R. (1962). Effect of various dietaries on the anatomical development of the stomach in the calf. J. Dairy Sci. 45, 408-420.

TITCHEN, D.A. (1953). Reflex contractions of the reticulum. J. Physiol. 122, 32P.

TITCHEN, D.A. (1958 a). Reflex stimulation and inhibition of reticulum contractions in the ruminant stomach. J. Physiol. 141, 1-21.

TITCHEN, D.A. (1958b). Partial exteriorization of the reticulum in sheep. J. Physiol. 143, 35P.

TITCHEN, D.A. & REID, C.S.W. (1965). The reflex control of the motility of the ruminant stomach. In Physiology of Digestion in the Ruminant. ed. R.W. Dougherty et al. pp. 69-77. London: Butterworths.

WALKER, D.M. & WALKER, G.J. (1961). The development of the digestive system of the young animal. 5. The development of the rumen function in the young lamb. J. agric. Sci. 57, 271-278.

WALLACE, L.R. (1948). The growth of lambs before and after birth in relation to the level of nutrition. J. agric. Sci. 38, 242-302.

WARDROP, I.D. & COOMBE, J.B. (1960). The post natal growth of the visceral organs of the lamb. The growth of the visceral organs of the grazing lamb from birth to 16 weeks of age. J. agric. Sci. 54, 140.

WASHBURN, L.E. & BRODY, S. (1937). Cited Dukes, H.H. The Physiology of Domestic Animals, 7th edn.

WEISS, K.E. (1953). Physiological studies on eructation in ruminants. Onderstepoort J. vet. Res. 26, 251-283.

WESTER, J. (1926). Die Physiologie und Pathologie der Vormägen beim Rinde. Berlin: Schoetz.

WILLIAMS, E.I. (1955). A study of reticulo-ruminal motility in adult cattle in relation to bloat and traumatic gastritis. A study of reticulo-ruminal motility in adult cattle with reference to the eructation of ruminal gases and bloat. Vet. Rec. 67, 907-911.