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PHYSIOLOGICAL STUDIES ON ERUCTATION IN RUMINANTS.

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INTRODUCTION.

Although the problem of bloat, which is a cause of serious economic losses particularly amongst high-grade dairy cattle, has been investigated all over the world, very little is known about the eructation reflex and factors which may influence it. This is acknowledged by Clark (1948), who states that the mechanism of the eructation reflex is not well understood.

The modern conception of bloat is that it is due to a failure of the eructation mechanism, and not to excess gas formation. It has been shown that ruminants are capable of eructating volumes of gas artificially introduced into the rumen considerably in excess of those normally produced. Clark and Quin (1945) have shown that sheep can eructate CO_2 or air introduced into the rumen at the rate of two litres per minute. According to Cole, Mead and Kleiber (1942) a bovine can eructate various gases, introduced at the rate of seven litres per minute for 30 minutes. To quote from Cole, Huffman, Kleiber, Olson and Schalk (1945): "The evidence points fairly convincingly to the conclusion that excess gas production in the rumen is not the cause of bloat per se. On the contrary, most investigators agree that bloat is due to an upset in the normal mechanism for expelling gas."

It should be borne in mind, however, that eructation is not the only method of expelling gas. Large amounts of CO_2 are absorbed from the rumen, especially during active fermentation, and exhaled with the expired air.

In a comprehensive review on bloat in ruminants Cole *et al.* (1945) have discussed various theories regarding its cause, but it appears that a co-ordinated study of the eructation reflex and the factors influencing it, has not been attempted previously. The object of this paper is to report investigations into these problems.

METHOD.

Eight Merino sheep, two adult goats, and two young grade Friesland bovines each with a permanent ruminal fistula, were used for the experiments. The sheep were numbered from 1 to 8. Sheep No. 7 had a caecal fistula and sheep No. 8 an abomasal fistula in addition to the rumen fistulae.

Due to the difficulty in reproducing natural bloat without the complication of frothing, a slight modification of the method described by Clark (1950) was used. Fig. 1 illustrates the apparatus.

The air in the 20 litre aspirator bottles (A), was displaced by water from the mains and forced into the ruminal mass through a 9-inch gas inlet (B) with a perforated tip, which passed through an air-tight cork in the fistula. Another short tube, passing just through the cork sealing the fistula opening, was connected to a membrane tambour (C), which recorded on a Kymograph the pressure changes in the rumen as a whole and of the left dorsal sac in particular. Air was

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introduced at the rate of approximately one litre per minute in some cases and one litre per three or four minutes in other cases. The entry of each litre of air was recorded by the signal needle (D). The rate of introduction of air did not appear to have any significance; a faster rate of introduction was employed on occasion because of the greater ease of evaluating the efficiency of eructation. In the case of the bovines, air was usually introduced at the rate of approximately three litres per minute.

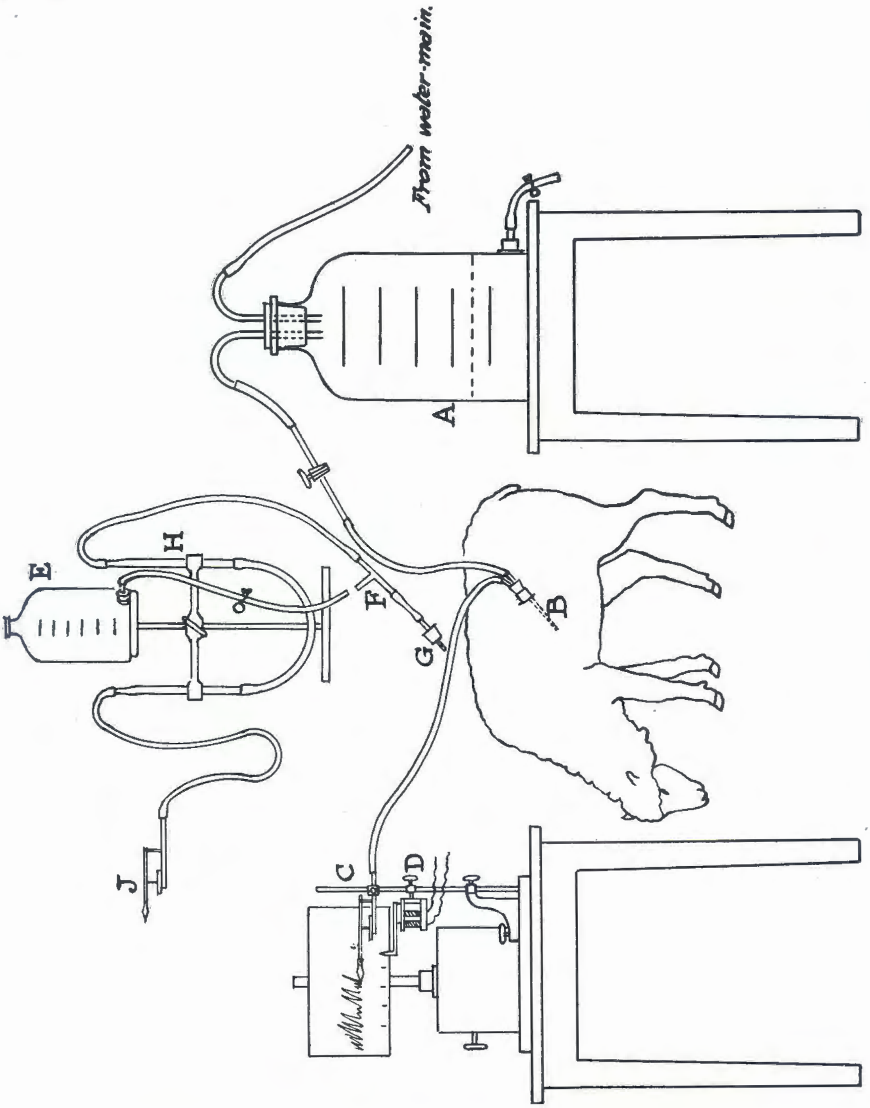


FIG. 1.—Diagram of apparatus used for insufflation of air and recording of intra-ruminal pressure. (For explanation see text.)

In order to eliminate the complication of frothing when bubbling air through the ruminal ingesta a proprietary anti-frothing agent (Cooper and Nephews or I.C.I.) (Clark, 1950) was dosed as a routine prior to the introduction of air into the rumen.

I. The Normal Eructation Reflex.

The Mechanics of the Reflex.

The oesophagus enters the rumino-reticular sac at a level considerably below the dorsal limit of the rumen (Sisson 1938). To quote from Cole *et al.* (1945): "This structural arrangement would appear to offer considerable interference with the freedom of movement of gas to the oesophagus".

The following conditions therefore, are considered essential before eructation can take place Gas, accumulated in the dorsal sac of the rumen, must be moved forward and downwards to reach the cardia. This has been postulated by Amadon (cited by Cole *et al,* 1945) and Clark (1948). The second essential factor is that the cardia must be patent and clear of any obstructing ingesta. Thirdly, the oesophagus must be patent and relaxed for the free passage of gas. It is evident, therefore, that eructation is an active and co-ordinated reflex, mainly involving the ruminal musculature.

(*a*) *Eructation in relation to ruminal motility.*

Most investigators (Wester, 1935; Hoflund, 1940; Dougherty, 1942; Cole, Mead and Regan, 1944; Cole *et al.*, 1945; Clark, 1948; and Evans and Evans, 1949) have associated eructation with active rumen motility, in the absence of which eructation is suspended. The cycle of ruminal contractions has been studied by Czepa and Stigler (1926), Magee (1932) and Phillipson (1939) using an X-ray technique. Wester (cited by Czepa and Stigler, 1926) and Schalk and Amadon (1928) have recorded ruminal motility through permanent ruminal fistulae. The main outcome of these extensive investigations, in relation to the present study, is that ruminal contractions can be divided into two types: (1) A backward moving cycle of contractions, involving a two-stage contraction of the reticulum, immediately followed by a contraction of the left dorsal and right ventral sacs, followed by a pause of varying length; (2) a forward-moving ruminal contraction starting at the posterior dorsal blind sac, followed by another pause of varying length.

Wester (1935) and Hoflund (1940) have reported from their observations that eructation occurs in conjunction with a return movement or antiperistaltic wave which follows the backward rumen contraction.

In order to confirm the observations of Wester and Hoflund on the direction of the two types of ruminal contractions, the following variation of the method described was employed. Two flexible tubes with balloons attached to the ends, were inserted through two holes in the pressure stopper sealing the fistula opening. One balloon was directed to the region of the cardia and the other to the posterior part of the left dorsal sac of the rumen. Each balloon was connected to a recording tambour. The usual gas inlet with its connections was passed through a third opening in the fistula stopper. Air was introduced into the rumen at the rate of one litre per three minutes, in order to be able to recognise the ruminal contraction at which eructation occurs. This can be identified readily as a marked drop in intra-ruminal pressure coinciding with a specific rumen contraction.

By observing the time at which the anterior balloon responded to pressure changes in relation to the response of the posterior balloon, it was found that, with the ordinary contraction, the anterior balloon responded before the posterior, but with the rumen contraction which coincides with eructation, the posterior balloon responded before the anterior. This indicates that the eructation contraction moves from behind forwards with the object of moving the gas bubble in the dorsal sac forward and downwards towards the cardia. The ordinary rumen contraction, essential for the mixing of the ingesta, is a wave in the opposite direction.

Tracings of normal eructation in sheep and cattle are presented in Figs. 2 and 3. Eructation results in a sharp drop in intraruminal pressure and occurs at the height of each eructation contraction, which frequently follows immediately on a backward contraction. Phillipson (1939) has observed that ruminal contractions follow a definite rhythm in relation to reticular contractions and that the rhythm may change from one type to another, without any apparent reason. It is evident from the tracings that not every backward contraction is followed by an eructation

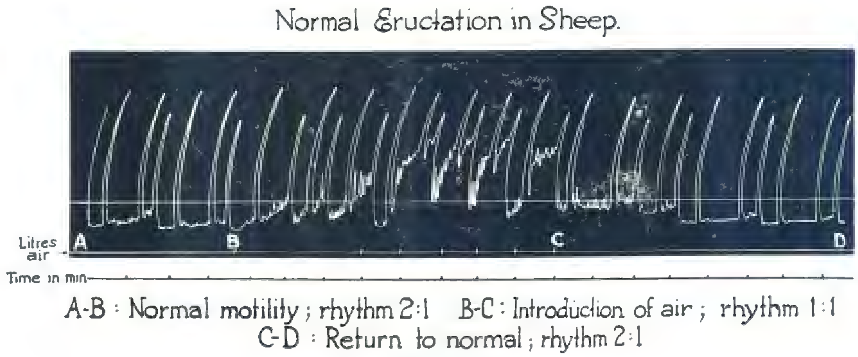


FIG. 2.

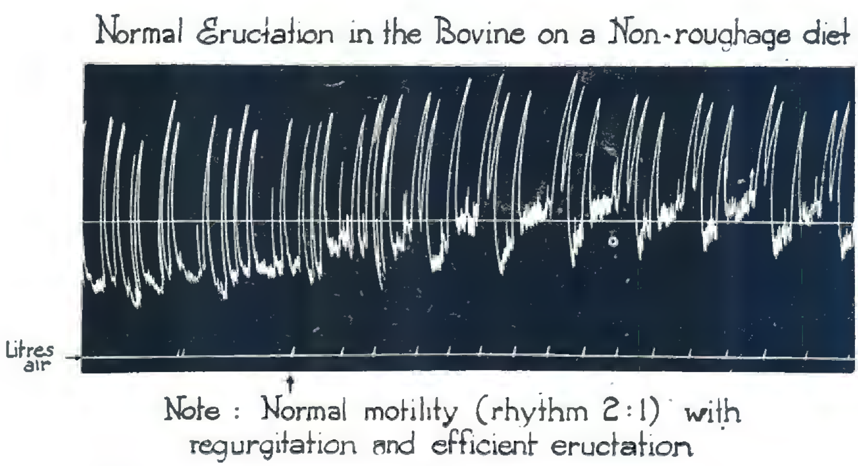


FIG. 3.

movement. These may occur after every backward movement (1:1 rhythm) or after every alternate one 2:1 rhythm). It is also evident from the tracing that this rhythm can change as a result of a pressure stimulus. This will be discussed in the part dealing with the initiation of the reflex. The varying rhythm of ruminal contractions, mentioned by Phillipson, will depend, therefore, on the presence or absence of eructation contractions.

The interval between the backward and forward rumen contractions is variable. In most cases the eructation contraction follows within 10 to 15 seconds of a backward contraction, although intervals of up to 60 seconds were recorded.

(b) The Rôle of the Cardiac Orifice.

Although Cole, *et al.* (1945) have suggested the failure of a hypothetical cardiac sphincter to relax as a possible cause of bloat, there is no anatomical or histological evidence of a true sphincter of the cardiac orifice. Aggazzotti (1910) believed that the orifice was normally relaxed because, when a sheep was placed on its back with the head downwards, some ruminal contents leaked into the mouth at each inspiration. On the other hand, Stigler (1931) palpated the cardia and found it usually closed. In the author's opinion the cardia is kept closed, not so much by the tonic contraction of its own musculature, but more by external pressure exerted by surrounding organs on the orifice itself and on the abdominal portion of the oesophagus. This would explain the partial patency noted by Aggazzotti when the animal was inverted.

In their review Cole *et al.* (1945) state that, in Wester's opinion, the opening of the oesophagus depends on the strength of the ruminal contraction, more particularly on the contraction of the " transverse folds ". It is stated also that Amadon and Detweiler palpated the cardia at the moment of eructation and found it widely dilated and funnel-shaped. They concluded this was due to muscular contraction but the muscles involved are not stated. Active dilatation of the cardia could only be brought about by muscles surrounding the orifice, i.e. rumen musculature.

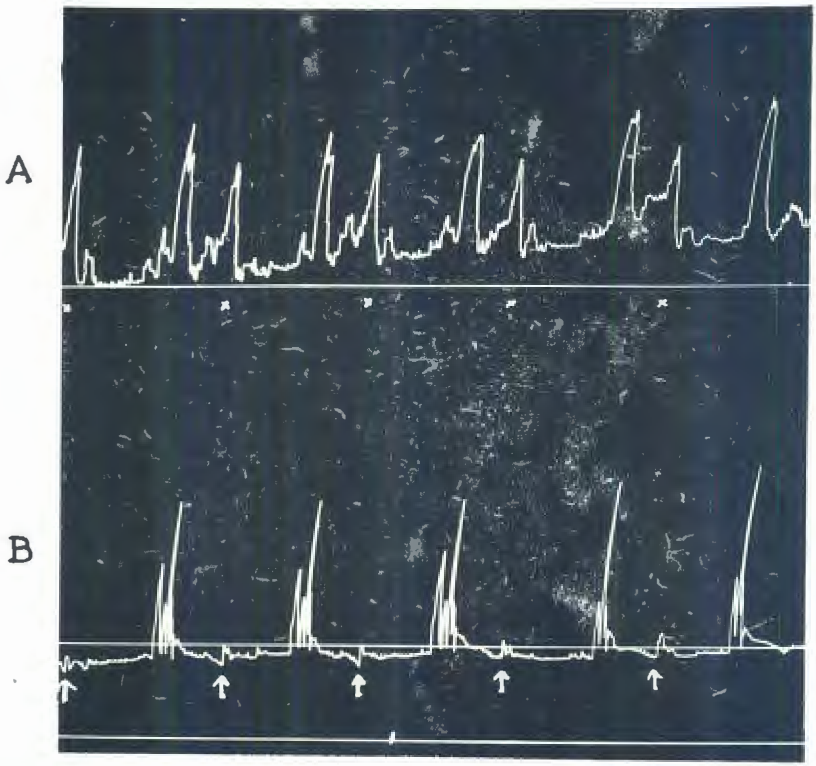
As Wester's original publication is not available, it is difficult to understand what is meant by the " transverse folds ". In the present author's opinion the cardiac orifice is pulled open at the moment of eructation by contraction of the medial and lateral pillars of the rumino-reticular fold. These are described by Sisson (1938) as follows: " The lateral part of the fold fades out an inch or two lateral to and behind the cardia. The medial part of the fold ends just behind the reticular groove and about three inches below the level of the cardia." As will be seen a shortening of these pillars would tend to pull the cardia open to the " funnel shape " described above.

A strong contraction of these pillars of the rumino-reticular fold, with the object of dilating the cardia, is considered an integral part of the forward eructation roll of the rumen and occurs at the moment the free gas is over the cardiac orifice.

From clinical observations Clark (1950) postulated that excess ruminal pressure interfered mechanically with the act of eructation. Nichols (1951) found that, when gas was introduced into a rumen already overloaded with fluid, belching took place for a time and then failed. He remarks that further investigations into the motility of the rumen under such conditions are required. The present author considers that the overloading interferes with the efficiency of eructation (*vide infra*) and that the rising pressure ultimately causes mechanical closure of the cardia. Tracings made from animals with excessive ruminal pressure when eructation failed have shown clearly that the eructation contractions of the rumen were still powerful and regular. Similarly clinical examination of animals with acute bloat has proved the rumen to be highly active. Wester (cited by Cole, *et al.* 1945) noted that there is hypermotility of the rumen in the early stages of acute bloat.

During numerous insufflation experiments it has been noted that, under a given set of conditions, eructation efficiency is inversely proportional to intraruminal pressure. A study of the anatomical relations of the cardiac region suggests an explanation of this interference. It is suggested that, with a high intraruminal pressure, the anterior dorsal sac bulges over and presses on the cardiac orifice and abdominal portion of the oesophagus, thus causing a mechanical closure. This pressure will be counteracted by the pull of the ruminal folds described above. The efficiency of the cardiac dilatation will depend therefore on the relation between intraruminal pressure and the strength of the ruminal contractions.

The Rôle of the Reticulum in the Eructation reflex



A : Ruminal Motility . x = eructation contraction
B : Reticular Motility . ↑ = dilatation of reticulum coinciding with eructation

FIG. 4.

(c) The Rôle of the Reticulum in the Eructation Reflex.

The importance of the reticulum in the complex eructation reflex has not been fully assessed. It has been mentioned that the second requisite for eructation is that the cardia must be freed from obstructing ingesta. In a normally full rumen the level of ingesta lies above the cardiac orifice. For efficient eructation to take place some mechanism must come into play which lowers the level of fluid in the anterior rumen below that of the cardia. Amadon (cited by Cole, *et al.* 1945) has reported that the dilatation of the reticulum which accompanies ruminal contraction, lowers the fluid level in the anterior rumen, so that the free passage of gas from the cardiac orifice is not obstructed. The present author is in full agreement with this view. The simultaneous recordings from the rumen and reticulum shown in Figure 4 clearly illustrate the dilatation of the reticulum coinciding with each eructation.

For further confirmation of this hypothesis, sheep No. 13 was deprived of a functioning reticulum by surgical invagination and suturing of the organ to obliterate the lumen. Before the operation eructation and ruminal motility were found to be normal on a full rumen after feeding. The degree of rumen filling was determined roughly by the removal of $3\frac{1}{2}$ litres of fluid rumen contents.

Food and water consumption was very low after the operation and the rumen obviously was relatively empty when recordings were taken on the sixth post-operative day. The degree of rumen filling was determined roughly by the removal of $2\frac{1}{2}$ litres of fluid and eructation efficiency was then found to be normal. Replacement of the $2\frac{1}{2}$ litres ruminal contents reduced the efficiency of eructation slightly, but the addition of a further one litre of water interfered markedly with the reflex. It would appear that, at approximately the same degree of rumen filling ($3\frac{1}{2}$ litres), eructation efficiency was reduced markedly in the absence of a functional reticulum.

Elevation of the hindquarters also appeared to have an abnormal effect. Raising the hindquarters 15° resulted in marked interference with eructation efficiency, whereas normal sheep with approximately the same degree of rumen filling show no effect on 15° elevation. The effects of posture will be discussed later.

The Initiation of the Reflex.

According to Cole *et al.* (1945) eructation is a reflex rather than a voluntary act because involuntary muscles are involved in the process. Being considered a reflex, one must necessarily think in terms of a reflex arc, consisting of receptors, nerves, the co-ordinating centre and the efferent motor nerves, which have been shown to be the vagi. [Ellenberger (cited by Cole *et al.*, 1945), Mangold and Klein (1927) and Hoflund (1940).]

From his observation that eructation could occur in an animal with an open ruminal fistula Wester concluded that an increase in intra-ruminal pressure is not essential to initiate the reflex. Stålfors (1926), however, believed that gas pressure is an important stimulus for the reflex and postulated that pressure may be exerted in certain parts of the rumen in spite of an open fistula.

Hoflund (1940) observed that the eructation contractions became irregular and less frequent on starvation, but during active fermentation after feeding they became regular with extra eructations at intervals.

Dougherty (1942) showed that by increasing intraruminal pressure by the insufflation of various gases, especially oxygen, ruminal motility was stimulated markedly even after total paralysis by atrophine. Nichols (1951) also reported that insufflation of the rumen increased belching.

During experiments with the artificial introduction of air into sheep it has been observed constantly that an increase in intraruminal pressure stimulates eructation contractions. After a period of fasting a ruminal rhythm of two to four backward contractions to every one forward eructation contraction was observed frequently. The introduction of air under these conditions markedly changed the rhythm of ruminal contractions bringing about more regular eructation movements, often with interposed additional eructations.

A rhythm of 2:1 to 4:1 often has been observed to change to a rhythm of 1:1 or even 1:2 on introduction of air. The same effect is produced by feeding. An animal exhibiting a rhythm of 2:1 before feeding will show a rhythm of 1:1 and 1:2 after feeding, i.e. during active fermentation. This is most pronounced after feeding green lucerne or lucerne hay, feeds which are known to produce large amounts of gas.

Bovines are capable of dealing with far greater amounts of gas at a faster rate than sheep. It has been found that bovines usually exhibit a 2:1 rhythm, even during air insufflation. This rhythm has been noted to change in some cases, to 1:1 if intraruminal pressure rose above atmospheric pressure.

In experiments on sheep to be described later, a total paralysis of the rumen was induced by dosing either sodium carbonate or potassium cyanide. Introduction of air into the rumen caused an increase in intraruminal pressure which stimulated the eructation reflex so that forward eructation contractions reappeared rhythmically although backward rumen contractions remained inhibited. The frequency of these eructation contractions was observed to be markedly increased especially if eructation was inefficient with consequent sustained high intraruminal pressure.

The tracing presented in Fig. 2 shows the change of rhythm from 2:1 before insufflation (A to B) to 1:1 during insufflation (B to C) with return to the original 2:1 rhythm after the introduction of air was stopped (C to D).

The contention of Stålfors (1926) that pressure in any part of the rumen may initiate the reflex in turn suggested that receptors in the posterior dorsal blind sac where the forward eructation contraction has its origin might be more sensitive to pressure stimuli than those elsewhere in the rumen. Observations on the effect of posture of the animal have strengthened this theory. A ruminal rhythm of 2:1 changed to 1:1 during air insufflation with the animal standing level. With the forequarters raised it remained at 2:1 in spite of air insufflation. In this position pressure was being exerted mainly in the anterior dorsal part of the rumen. With the hindquarters raised pressure was exerted mainly on the posterior sac and the rhythm changed to 1:1 with frequent extra eructation contractions. (The tracings presented in Fig. 6 illustrate these results.)

It would appear therefore that an increase in intraruminal pressure, especially in the posterior dorsal blind sac, is the main stimulus for the eructation reflex. The increased rate of ruminal contractions caused by oxygen insufflation, reported by Dougherty (1940), was presumably caused by an increase in the rate of eructation contractions.

Mead, Cole and Regan (1944) advanced the theory that the presence of coarse irritating material in the rumen provided the stimulus for the eructation reflex and that the absence of such material leads to defective eructation and bloat. Cole, Mead and Regan (1943) also reported the existence of some correlation between rumination and eructation and postulated that both acts were apparently initiated by the same stimulus. Although the "physical deficiency" theory of the cause of bloat is supported by considerable evidence from clinical trials, these authors have failed to prove that the eructation reflex itself is stimulated by coarse roughage or that it is inhibited by the absence of such material. Their suggestion that turpentine relieves bloat by stimulating eructation due to its irritant action cannot be accepted. The administration of turpentine has no stimulating action on the eructation reflex, but, as shown by Clark (1948), the beneficial effect of this drug is due to the breaking of the froth by its action upon surface tension.

In order to test the " physical deficiency " theory one of the bovines was placed on a ration consisting solely of freshly cut tops of young lucerne. Despite the absence of coarse material in this feed there was no adverse effect on the efficiency of eructation. The tracing shown in Fig. 3 was made after the animal had been on the purely succulent diet for one month. As will be seen eructation was entirely efficient. Ruminal motility and rumination persisted throughout. By chance the animal was actually ruminating during the experiment recorded in Fig. 3. Regurgitation took place immediately preceding a backward ruminal movement and was accompanied by a sudden sharp rise in intraruminal pressure presumably caused by the extra contraction of the reticulum known to accompany regurgitation.

During the insufflation experiments on sheep it has been found frequently that the experimental animals were able to ruminate normally even though they lacked an inefficient eructation mechanism. This has been observed on various occasions both when inefficiency of eructation was associated with the degree of ruminal filling and during total paralysis of the rumen due to the administration of atropine.

These observations indicate that there is no common stimulus for, or correlation between, the two totally different acts of regurgitation and eructation. Rumination may occur independently of ruminal or reticular contractions, whereas eructation is entirely dependent on active ruminal and reticular motility. The presence or absence of coarse roughage in the rumen does not appear to affect the eructation reflex nor apparently is it the stimulus for its initiation. As stated previously pressure by gas is considered by the present author to be the main stimulus for the eructation reflex.

Individual Variations amongst Animals.

It is well-known that individual animals in a herd may bloat repeatedly whilst others, kept under similar conditions, are affected less frequently. In an outbreak of bloat on lucerne pasture, one rarely finds all the animals affected. This individual difference in susceptibility has been observed by Cole, Mead and Regan (1943) and Clark (1950). Knapp, Baker and Phillips (1943) have described variations in the occurrence of bloat in the steer progeny of beef bulls and suggest that these variations are due to a difference in the level of nervous reaction amongst the different animals. They have found a significant difference in the number of steers showing excessive bloat among the progeny of different bulls and also a highly significant difference amongst progeny groups.

Mead, Cole and Regan (1944) suggested that individual differences are due to a change in rumen activity brought about by feeding concentrates.

During the series of experiments on the eructation reflex, the eight sheep used as experimental animals showed marked differences in their ability to eructate. Some sheep consistently showed low-grade efficiency while others were very efficient throughout. A third group could be classified as medium.

This individual variation may be explained satisfactorily by assuming a difference in the level of nervous reaction of each animal. As the stimulus for eructation appears to be gas pressure, any given pressure would thus produce a varied response in eructation contractions depending on the threshold of nervous action. These variations would apply also to the effective opening of the cardia by the contraction of the pillars of the rumino-reticular fold in conjunction with the eructation contraction. Further, the efficiency of eructation is dependent on reticular activity clearing the cardia so that any variation in effective reticular activity could also account for individual differences in susceptibility.

As the whole eructation reflex depends on innate nervous and muscular reactions it is probable that defects in the mechanism may be hereditary. The work of Knapp and his associates quoted above is evidence of the acceptability of this assertion. Acute bloat is merely an expression of the failure of the eructating ability of the individual animal under the prevailing circumstances. While it is necessary to continue in an endeavour to determine the factors which render eructation more difficult, a natural corollary is to breed cattle with a physiologically efficient reflex.

II. Factors Affecting the Eructation Reflex.

A. Mechanical.

(1) *Obstruction of the Oesophagus.*

Any obstruction of the oesophagus will interfere with the eructation of gas. As such conditions are well-known and have no direct effect on the reflex as such, they will not be discussed in this paper.

(2) *Frothy Bloat.*

Wester (1935) devided bloat into two types. In the one, free gas is present in the dorsal sac of the rumen whereas, in the other, the gas is entrapped throughout the ingesta as a froth thus preventing eructation. Quin (1943) discussed the question of frothing and suggested saponins in the plant to be the cause. Clark (1948, 1950) advocated the use of agents affecting the surface tension to free the gas. Quin, Austin and Ratcliff (1949) described successful clinical trials with such preparations.

The absence of free gas in frothy bloat interferes purely mechanically with both the eructation and the absorption of gas. Further research into the basic cause of frothing is an urgent requirement.

(3) *The Degree of Filling of the Rumen and Posture.*

As described above the fundamental requisite for eructation is the movement of the free gas forwards and downwards to the cardia. This is accomplished by both the forward wave of contraction of the rumen and the relaxation of the reticulum. As the amount of fluid present in the rumen will determine the distance between the free gas and the cardia, the degree of filling obviously will play an important rôle in eructation. Elevation of the fore- or hindquarters also influences the relative positions of the free gas and the cardia as demonstrated in Fig. 5.

Although Quin (1943) could not demonstrate any effect on the eructation of artificially introduced gas by filling the rumen and elevating the hindquarters, Dougherty (1940) has shown that by pumping water into the rumen and elevating the hindquarters of the animal so that the fluid level is well above the cardia, belching of introduced air is markedly impeded.

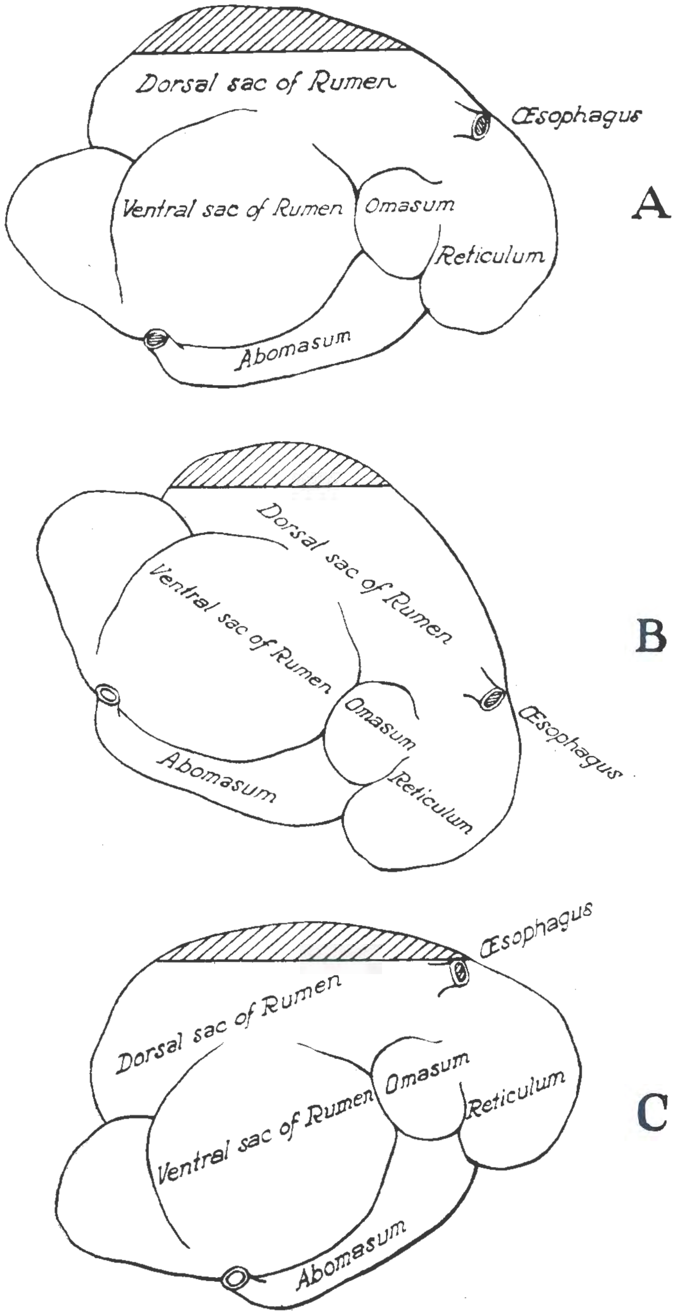


FIG. 5.—Diagram showing the effects of posture on the relative positions of the free gas and the cardia.

A. Animal standing level. B. Hindquarters raised.
C. Forequarters raised.

The following relevant experiment, of which tracings are presented in Fig. 6, was conducted. Air was introduced at the rate of one litre per three minutes into one of the experimental sheep three hours after feeding on a ration of 500 grams lucerne hay and grass hay *ad lib.* with water constantly available. The rumen was regarded as normally full at the start of the experiment.

A recording of normal efficient eructation was made. This is shown in the top tracing. Two litres of water were then added to the rumen, the effect being shown in the second tracing. Eructation efficiency was affected as can be seen from the rise in pressure and protracted recovery after air insufflation was stopped. The effect of 28° elevation of the forequarters is shown in the third tracing. It is evident that, in spite of an unaltered degree of rumen filling, eructation efficiency was improved markedly. The initial ruminal pressure though slightly higher as a result of elevation of the forequarters was not increased by air insufflation. The drop in intraruminal pressure coinciding with eructation contractions is well illustrated. The bottom tracing shows the effect of 28° elevation of the hindquarters. Eructation efficiency was markedly reduced compared with the animal standing on the level.

The effect of the degree of filling of the rumen on eructation and rumination was shown clearly by the following observations. On a particular occasion one of the experimental sheep showed complete inability to eructate introduced air despite the presence of normal ruminal motility. During this period the animal was ruminating regularly. After removal of three litres of ingesta from the rumen rumination ceased but eructation was found to be entirely efficient. Replacement of the ingesta caused resumption of rumination while inefficient eructation reoccurred.

Exactly similar results were obtained from one of the bovines as illustrated in Fig. 7.

In view of the fact that the degree of filling of the rumen had been shown to play such an important part in the efficiency of eructation, it was decided to investigate the influence of water and food intake on the pathogenesis of bloat.

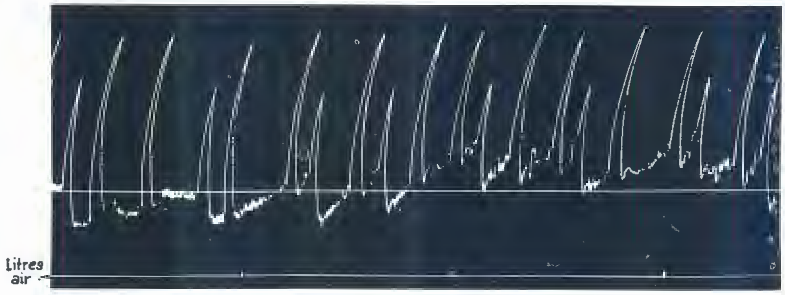
In one trial all six experimental sheep were deprived of water for 24 hours but were given lucerne hay *ad lib.* up to the time of recording. The eructation efficiency of each animal was determined after which both water and food were made available for a period of two hours, the consumption being recorded. The ability of the animals to eructate introduced air was again tested. The efficiency of the reflex was found to have decreased in all six cases, the degree of decrease being proportional to the combined food and water intake.

In several trials, groups of normal cattle and sheep were deprived of water for 24 hours. Half of the animals were then offered water *ad lib.* before the whole group were turned out onto lucerne pasture. The incidence and severity of bloat was considerably higher amongst the watered groups than amongst the controls.

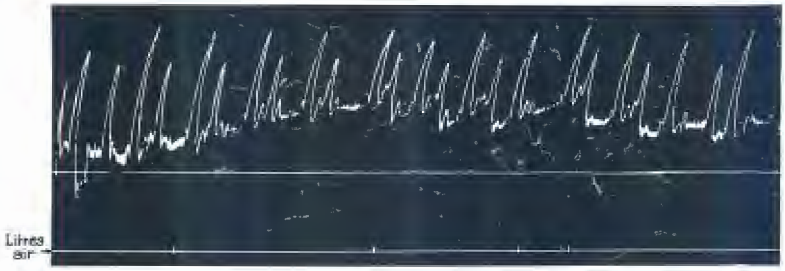
These results indicate that the time of watering might play an important rôle in the pathogenesis of spontaneous bloat.

Watering immediately before pasturing therefore may render the animals more susceptible to bloat, especially if water has not been available for some time previously. The well-known association between rapid greedy feeding and hoven also, may be attributable to overloading, although, as pointed out be Mead *et al.* (1944), the incidence of bloat cannot always be correlated with the ingestion of feed.

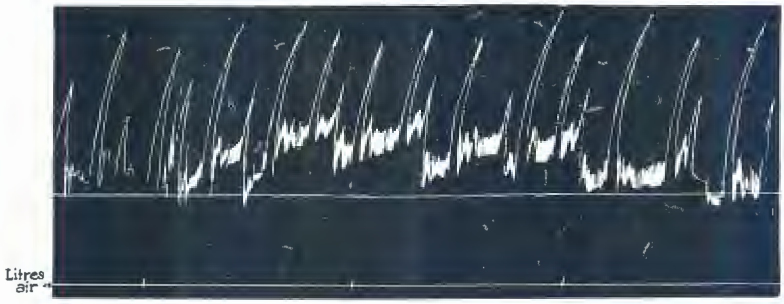
The Effect of Rumen Filling and Posture on Eructation Efficiency in Sheep.



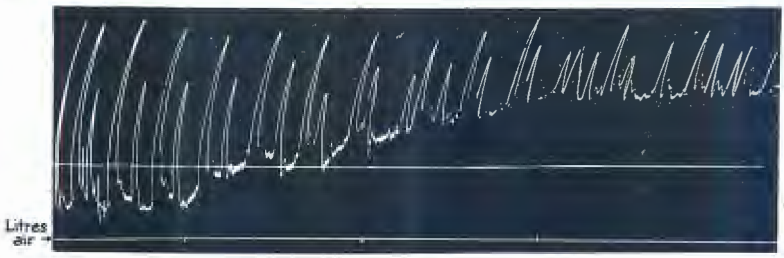
Normal Efficient Eructation.



Interference with Eructation by the addition of 2 litres water to the rumen.



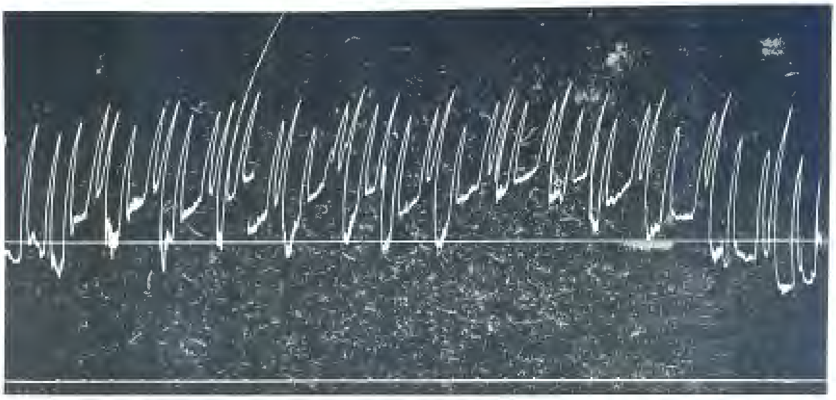
Eructation Efficiency improved by raising forequarters.



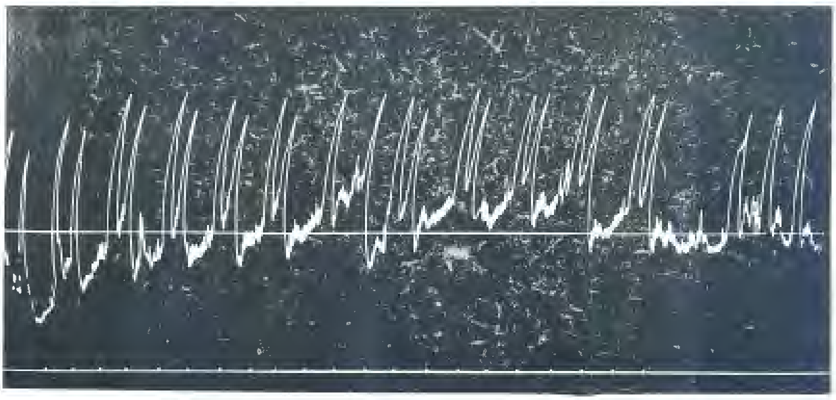
Eructation Efficiency markedly reduced by raising hindquarters.

FIG. 6.

The Effect of Volume of Ingesta on Eructation Efficiency in the Bovine.



Normal Eructation (2-1 Rhythm)



Increased Efficiency (1-1 Rhythm) after removal of 8 litres ingesta.

FIG. 7a.

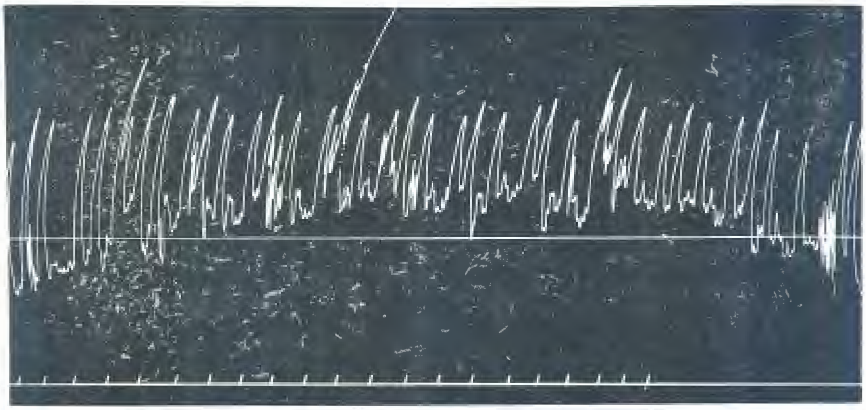
B. The Effect of Alkalosis.

Clark and Lombard (1951) showed that the administration of alkali, either *per os* or by intravenous injection caused ruminal paralysis. This effect was shown to be of central origin and presumably due to alkalosis. Consequently it was decided to investigate the effect of alkalosis on the eructation reflex.

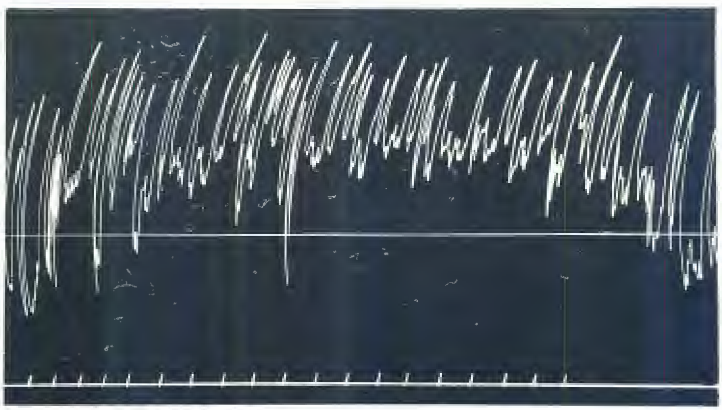
By giving graded doses of sodium carbonate per ruminal fistula it was found that the two types of ruminal movement were not affected equally. The backward moving contraction was reduced in strength first and could even be entirely inhibited, while the eructation contraction still persisted at almost normal strength. Under such conditions, however, the animals were found to be particularly susceptible to overfilling, probably due to paralysis of the reticulum. Even when the eructation contractions were completely inhibited by large doses, they tended to reappear when the intra-ruminal pressure was raised by air insufflation.

In their work Clark and Lombard showed that after dosing alkali ruminal paralysis persisted for several hours after the pH of the ruminal ingesta had returned to normal. They postulated that this was due to a continued alteration in the acid-base ratio of the blood. Similarly it was found that the decreased efficiency of eructation persisted despite a natural readjustment of the pH of the ingesta. In order to prove that this was due to a residual alkalosis, the CO_2-combining power of the blood was followed throughout the experiment. As

The Effect of Volume of Ingesta on Eructation Efficiency in the Bovine.



Decreased Efficiency after introduction of 12 litres water

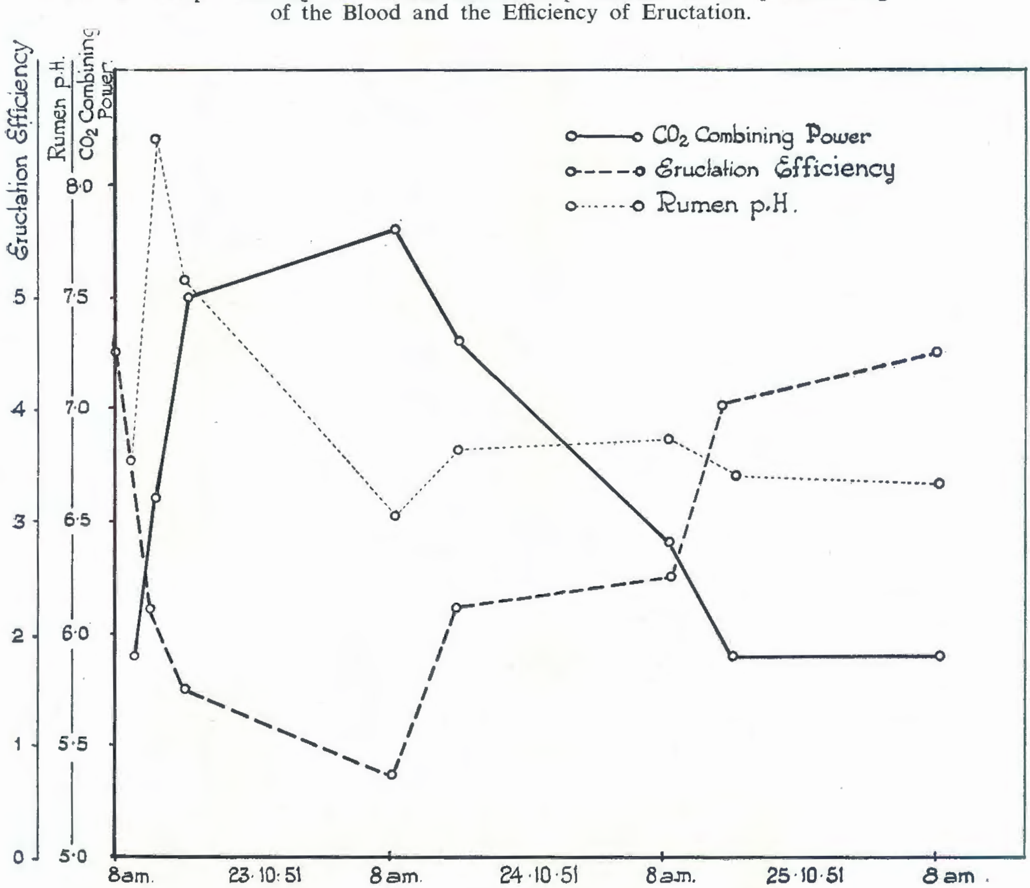


Failure of Eructation after introduction of further 8 litres of water.

FIG. 7b.

shown in the graph (Fig. 8) the average eructation efficiency of the six sheep (as rated on an arbitrary scale) showed a remarkable inverse correlation to the average CO_2-combining power of the blood. It will be noted that these two factors took 72 hours to return to normal, although the pH of the rumen had become acid within 24 hours. Probably owing to the numerous other factors affecting eructation, the inverse relationship between eructation efficiency and the alkali reserve of the blood of individual sheep was not always constant. The tracings in Figs. 9 and 10 illustrate the effects of alkalosis on sheep and cattle respectively.

FIG. 8.—Graph showing the Inverse Relationship between the CO_2 Combining Power of the Blood and the Efficiency of Eructation.



N.B. For CO_2 combining power figures read 50, 55 (volts %) etc. corresponding to 5·0, 5·5 etc. for pH values.

C. *The Effects of Abdominal Vagotomy.*

As far back as 1883 Ellenberger demonstrated that chronic tympany could be produced by section of both vagus nerves in the region of the neck. It is now well-known that the vagi are the motor nerves to the entire alimentary tract. Mangold and Klein (1927) studied the effects of left- and right-sided abdominal vagotomy on the behaviour of the ruminant forestomachs. They showed that cutting both these branches at the level of the cardia abolished eructation. Bloat, however, was never encountered when only one of the branches was cut, probably due to variable distribution of these nerves. According to these authors the left dorsal branch of the vagus innervates mainly the rumen but also sends a few fibres to the reticulum. The right ventral branch supplies mainly the reticulum, omasum and abomasum, with a few fibres to the rumen. Cross-over fibres connect these two nerves proximal to the cardia.

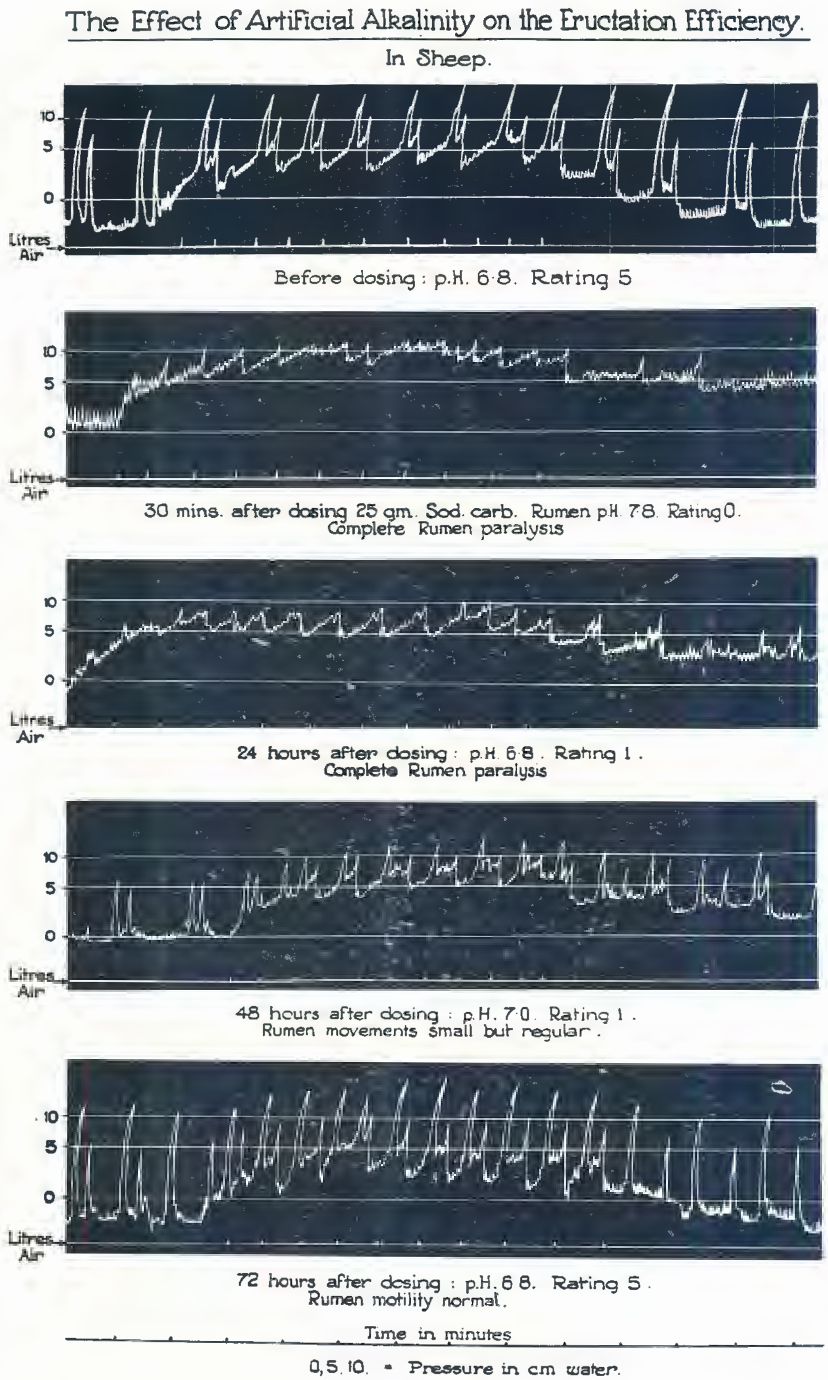

The Effect of Artificial Alkalinity on the Eructation Efficiency.
In Sheep.
10
5
0
Litres Air
Before dosing : p.H. 6·8. Rating 5
30 mins. after dosing 25 gm. Sod. carb. Rumen pH 7·8. Rating 0.
Complete Rumen paralysis
24 hours after dosing : p.H. 6·8. Rating 1.
Complete Rumen paralysis
48 hours after dosing : p.H. 7·0. Rating 1.
Rumen movements small but regular.
72 hours after dosing : p.H. 6·8. Rating 5.
Rumen motility normal.
Time in minutes
0,5.10. = Pressure in cm water.

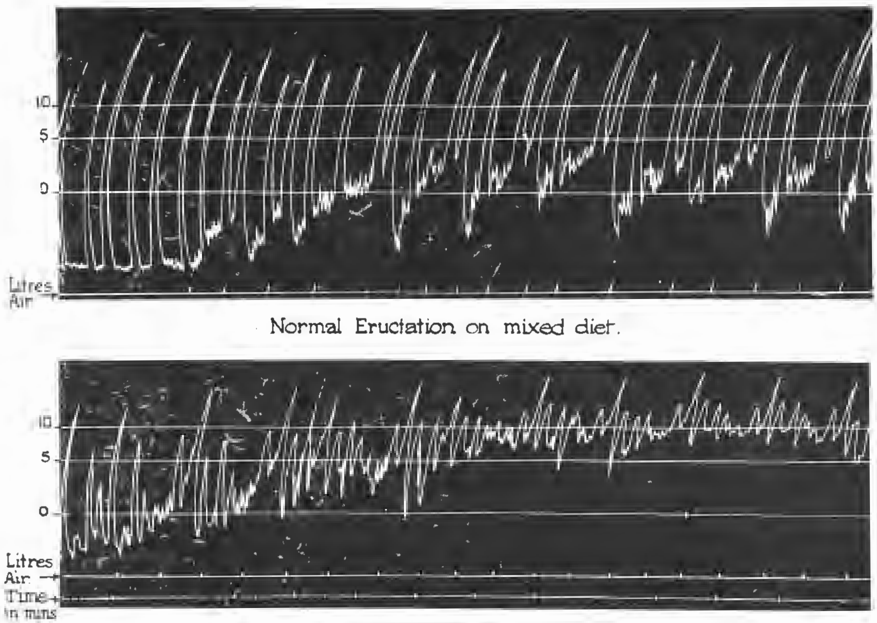
FIG. 9.

Hoflund (1940) confirmed the work of Mangold and Klein, and showed that pyloric stenosis with abomasal distension resulted from damage to the right ventral branch of the vagus and other collateral fibres supplying this area. He further showed that this condition can arise spontaneously as a result of traumatic reticulitis and peritonitis involving damage to these nerves.

In order to study the effect of section of the abdominal branches of the vagus nerve on the eructation reflex, two adult goats with permanent ruminal fistulae were used. In goat No. 1 the right ventral branch of the vagus was cut at the level of the cardia, approximately one inch of the nerve being removed. In the case of goat No. 2 a similar operation was performed on the left dorsal branch.

The Effect of Artificial Alkalinity on the Eructation Efficiency.

In the Bovine.



Interference with eructation caused by dosing 150gm. Sod.carb.. Rumen pH 6.9

0, 5, 10, • Pressure in cm. water.

FIG. 10.

Recordings of the eructation of artificially introduced air had been made prior to vagotomy and both animals had been found to be normal in all respects. Similar observations were made periodically starting two days after the operation. The animals were fed on lucerne hay *ad lib.* and their food and water consumption, together with the amount of faeces passed, were determined daily. The following are the main observations on the two animals over a period of one month:—

Goat No. 1 (right ventral branch severed).—For the first eight days after the operation both types of ruminal contractions were found to be almost doubled in strength. Normal rumination was observed on the eighth post-operative day. From this time onwards it was noticed that the backward moving contractions decreased progressively in strength and rate, while the eructation contractions remained exceptionally strong throughout. The diminution in the strength of the backward contractions can be ascribed to abomasal distension (*vide infra*).

On the ninth day the animal showed clinical bloat; free gas escaped on opening the fistula. On the 12th to 22nd day the animal showed continuous bloat, the rumen being filled with a frothy slimy mass of light straw-coloured ingesta notwithstanding the food consisted of good quality green lucerne hay. The disappearance of chlorophyll was an indication of the length of time the ingesta had remained in the rumen. Food and water consumption was very low and dropped progressively during the month to almost nil. The amount of faeces passed was likewise minimal, being frequently less than ten grams per day towards the end of the period.

Eructation efficiency, as determined by air insufflation, was markedly reduced up to the 12th day after which a progressive improvement was noticed. From the 22nd day eructation was normal but could be reduced markedly by the addition of two litres of water to the rumen. The improvement in eructation efficiency was probably due to a gradual reduction in the volume of ruminal contents.

The animal was finally destroyed one month after the operation. The rumen was found to be relatively empty containing a total of three litres of watery, straw-coloured ingesta. The abomasum was enormously distended and occupied the major portion of the abdominal cavity as shown in the photograph reproduced in Fig. 11. The abomasal contents weighed six kilograms and contained coarse particles resembling normal ruminal ingesta. The intestines were practically empty and distended with gas.

Section of the right ventral branch of the vagus, therefore, did not affect the forward contraction of the rumen, nor eructation, provided the rumen was relatively empty. The paralysis of the reticulum, however, rendered the animal particularly sensitive to overfilling. This is further evidence of the rôle of the reticulum in clearing the cardia for the free passage of gas.

Goat No. 2 (left dorsal branch severed).—Both types of ruminal contractions were markedly reduced in strength for the first 20 days. From then on progressive recovery took place. Food and water consumption were practically normal and spontaneous bloat never occurred. Rumination was observed on the twelfth post-operative day.

The eructation efficiency was markedly reduced for the first 20 days, but later improvement ran parallel with the recovery in the strength of the ruminal contractions.

After destruction, the abdominal organs appeared normal, the rumen containing $5\frac{1}{2}$ litres of ingesta.

Section of the left dorsal branch of the vagus, therefore, did not cause complete ruminal paralysis due to the presence of crossover fibres from the right ventral branch mentioned before. The eructation efficiency was found to parallel the strength of the ruminal contractions. The gradual improvement can only be ascribed to the adaptation of the ruminal musculature to a diminished nerve supply.

11175—4

D. Reflex Inhibition from the Posterior Digestive Tract.

(1) *The Abomasum.*

Wester (1935) considered the motility of the fore-stomachs to be largely dependent on the state of the abomasum. Conditions such as abomasitis, distension, sand impaction, etc. were said to cause reflex ruminal paresis and tympany.

Phillipson (1939) showed conclusively that distension of the abomasum, either by the introduction of warm saline or by the insertion and inflation of a balloon, inhibited reticular contractions and markedly influenced the character and rhythm of the ruminal motility.

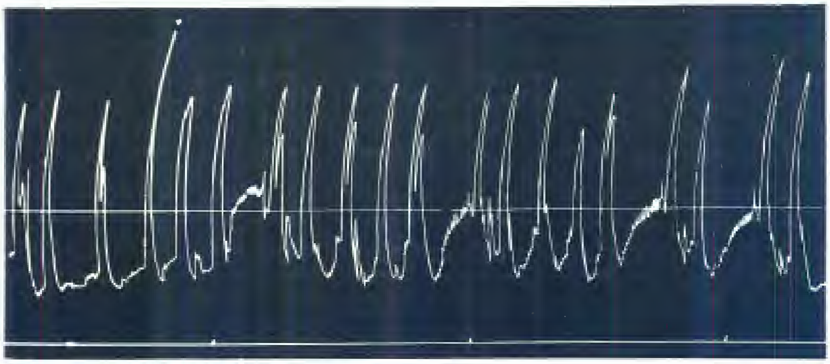
FIG. 11.—Distension of the Abomasum of a Goat one month after section of the Right Ventral Branch of the Vagus Nerve.

Note. Distended abomasum occupying the majority of the abdominal cavity. The emptied rumen and gas-filled intestines can be seen dorsal to the abomasum.

The effect of abomasal distension on the eructation reflex was studied in an experimental sheep with both ruminal and abomasal fistulae. Ruminal pressure during air insufflation was recorded in the usual manner. Abomasal distension was induced by the introduction of either air or warm saline by means of the apparatus depicted in Fig. 1.

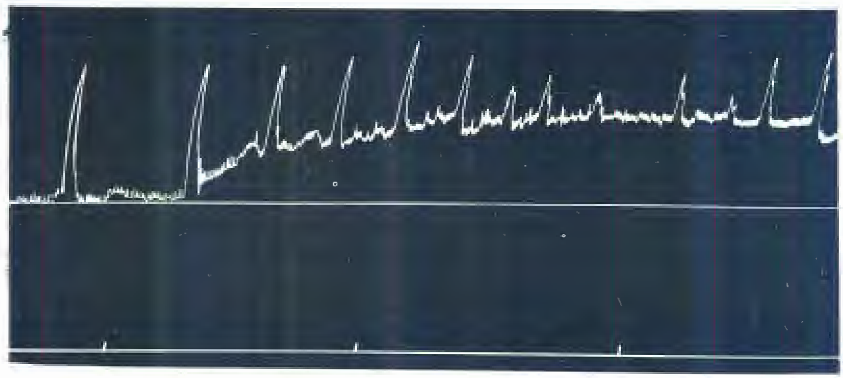
An aspirator bottle (E) was connected directly to the abomasal fistula (G). By means of a T-piece (F) the fistula was also connected to one arm of a water manometer (H). The other arm of the manometer was connected to a tambour which recorded abomasal pressure simultaneously with ruminal pressure.. Saline was run by gravity from the aspirator bottle into the abomasum. When air was used, this was forced in by water pressure in exactly the same way as for insufflation of the rumen.

The Relation between Abomasal Distention and Degree of Rumen Filling on the Eructation Efficiency in sheep.



Normal Eructation - Abomasum not distended. Rumen relatively empty.

Eructation after Abomasal Distention - Rumen relatively empty.



Interference with Eructation after addition of 2 litres water to rumen. Abomasum distended.

FIG. 12.

It was found that distension of the abomasum, with either fluid or air, caused inhibition of the backward ruminal contractions. This inhibition was proportional to the degree of distension. Even severe distension, however, did not inhibit the forward moving contractions of the rumen, although eructation was rendered less efficient depending on the degree of filling of the rumen. Referring to Fig. 12, tracing 2, it will be seen that the backward contractions were inhibited entirely, the only movements being those related to eructation. As the rumen was relatively empty, the expulsion of gas was entirely efficient. The addition of two litres of water to the rumen (tracing 3), however, completely prevented eructation.

These findings confirm the statement of Phillipson quoted above, that abomasal distension causes reticular paralysis. As already shown reticular motility is of paramount importance in eructation when the rumen is relatively full. The hyper-sensitivity of the animal to overfilling of the rumen, when the abomasum was distended, therefore, can be ascribed to reticular paralysis.

The recordings of the abomasal pressure revealed that the introduction of even two litres of air caused only a transitory rise in intra-abomasal pressure, the organ apparently losing tone to accommodate the new volume. The effects of abomasal distension, however, persisted for up to 1½ hours.

When the abomasum had been distended with saline, drainage was followed by almost immediate recovery of ruminal motility. On the other hand, removal of the abomasal fistula stopper after air had been introduced, did not at once restore eructation efficiency. As the fistula was inserted near the pyloris the air was probably trapped in the fundus.

The presence of a gas bubble in the fundus of the abomasum was a constant feature of the X-ray observations of Czepa and Stigler (1926), Magee (1932) and Phillipson (1939). An increase in the size of the bubble was noted when fluid passed in bulk directly to the abomasum.

Stålfors (1926) showed that young succulent grass can pass to the abomasum within 20 minutes after ingestion. Any distension of the abomasum, whether caused by gas formation or overloading with ingesta therefore will result in inhibition of the reticulum with consequent impairment of eructation.

(2) *The Caecum.*

The animal with both the caecal and ruminal fistulae was used to determine the effect of caecal distension on eructation. The method was similar to that described for the abomasal experiments. As shown in Fig. 13 the effects of caecal distension were identical with those found in abomasal distension.

After air had been introduced into the caecum there was no escape of gas on subsequent removal of the fistula stopper, although the inhibition of the reticulum was still present. The air had presumably been moved into other regions of the intestinal tract from whence it exerted its effect.

Stålfors (1926) recorded cases of bloat in which rectal examination revealed gas formation and distension of the intestinal tract in conjunction with ruminal tympany.

E. The Effect of Drugs Influencing Ruminal Motility.

(1) *Those Causing Hypomotility.*

(*a*) *Prussic Acid.*—The association between prussic acid and bloat has been the subject of considerable controversy for many years. Quin and Van der Wath

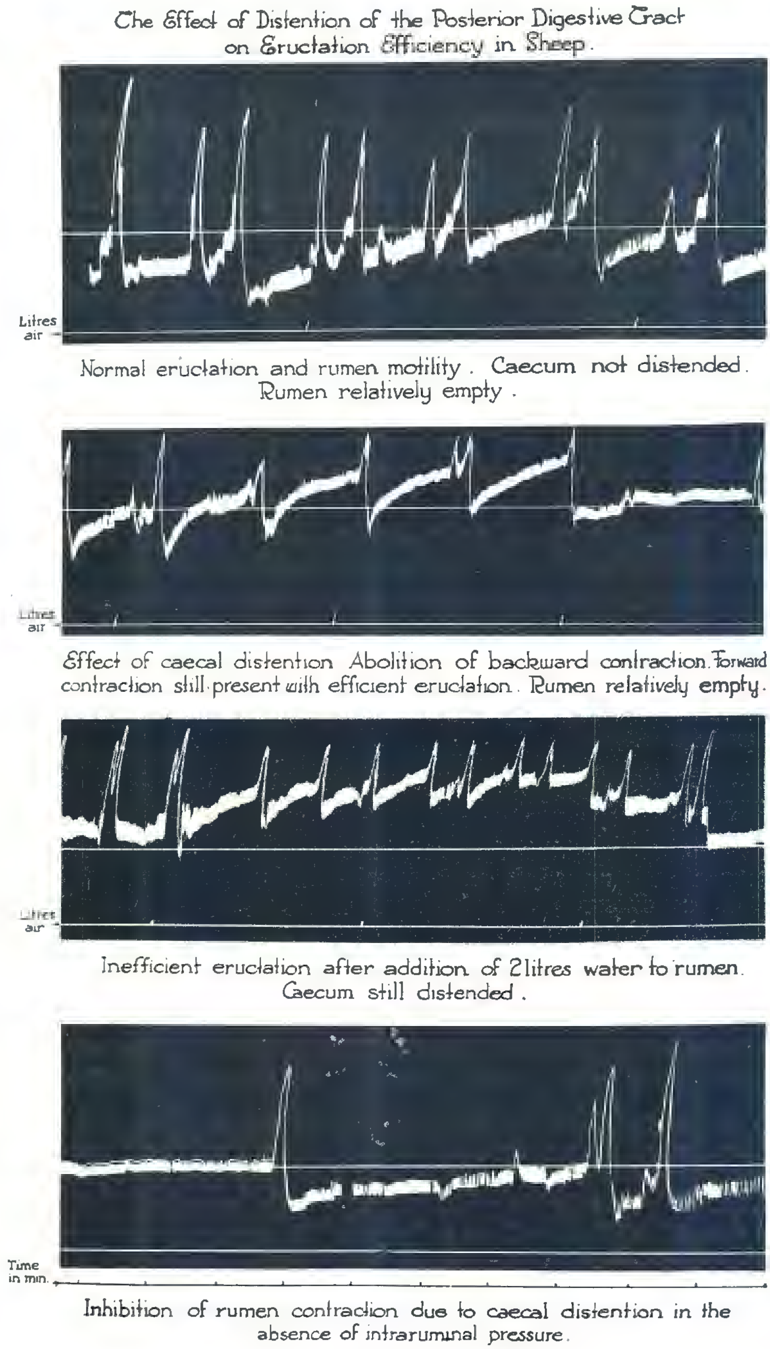

The Effect of Distention of the Posterior Digestive Tract
on Eructation Efficiency in Sheep.
Litres air
Normal eructation and rumen motility. Caecum not distended.
Rumen relatively empty.
Litres air
Effect of caecal distention Abolition of backward contraction. Forward
contraction still present with efficient eructation. Rumen relatively empty.
Litres air
Inefficient eructation after addition of 2 litres water to rumen.
Caecum still distended.
Time in min.
Inhibition of rumen contraction due to caecal distention in the
absence of intraruminal pressure.

FIG. 13.

(1938) showed that small doses of prussic acid caused complete though transitory paralysis of all ruminal movements. In 1949 Evans and Evans reported ruminal paralysis caused by clover juice and claimed that prussic acid was the active principle.

In the present series of experiments it was found that small doses of potassium cyanide inhibited the reticular and backward moving contractions of the rumen. Introduced air could thus be eructated provided the rumen was not overfilled. Larger doses caused complete inhibition of all motility and eructation, but at this stage the animals exhibited hyperpnoea and other symptoms of acute prussic acid poisoning. Fig. 14 illustrates these reactions.

It would appear therefore that subclinical poisoning with prussic acid could cause bloat only in conjunction with overfilling or other complications.

(*b*) *Atropine*.—The action of atropine as a cause of ruminal paralysis by blocking the parasympathetic nerve endings of the vagus is well known.

It was found that even small doses of atropine, insufficient to cause complete ruminal paralysis, resulted in complete inhibition of the eructation reflex. This is illustrated in Fig. 15.

As many poisonous plants are known to contain atropine, their presence in the pasture or hay might well result in the incidence of acute bloat.

(*c*) *Histamine*.—In 1942 Dougherty showed that the intravenous injection of histamine caused ruminal paralysis and suggested this as a possible factor in the aetiology of acute bloat. Furthermore, large amounts of histamine (·9 to 2·4 mgm. per 100 c.c.) were found in the ruminal ingesta of steers that had died of bloat. The histamine content of the ruminal ingesta was found to be increased on a high protein diet.

As shown in Fig. 16, the intravenous injec ion of 2 mgm. of histamine into a sheep completely inhibited all ruminal movements and eructation.

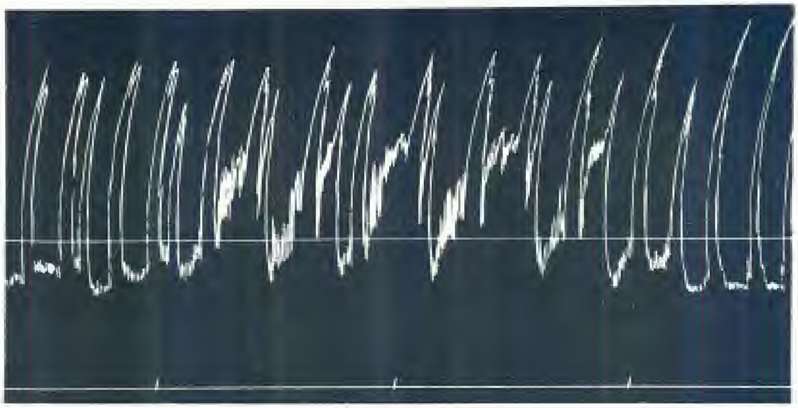
Clark however (unpublished report) introduced up to 250 mgm. of histamine into the rumen with no effect on ruminal motility. This would indicate that under certain conditions the histaminase activity of the ruminal contents is exceedingly high. On the other hand the presence of free histamine in ruminal ingesta found by Dougherty would indicate that this is not always the case. The rôle of histamine in the etiology of bloat is another aspect requiring further investigation.

(*d*) *Adrenalin*.—It has been shown by Dougherty (1942) that adrenalin causes marked depression both in strength and speed of ruminal contractions in cattle.

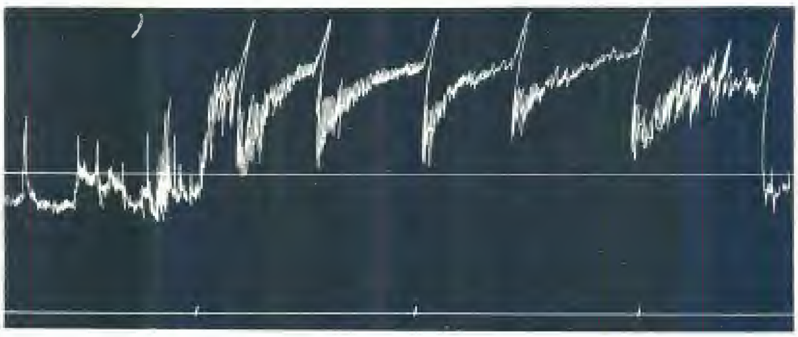
In the present series of experiments, the intravenous injection of 1 c.c. adrenalin hydrochloride (1 : 1,000) into sheep was found to cause varying degrees of depression and even total paralysis of rumino-reticular activity, lasting for at least 30 minutes. Susceptibility to adrenalin appeared to be very variable even in the same animal. Eructation was inefficient during the period of depression of ruminal motility. This is illustrated in Fig. 17.

From this finding it would be logical to assume that the liberation of adrenalin during excitement would tend to inhibit the eructation reflex and so contribute to the occurrence of bloat in conjunction with other factors. This would be a parallel to the well-established inhibition of the " milk let-down reflex " under similar conditions and also induced by adrenalin.

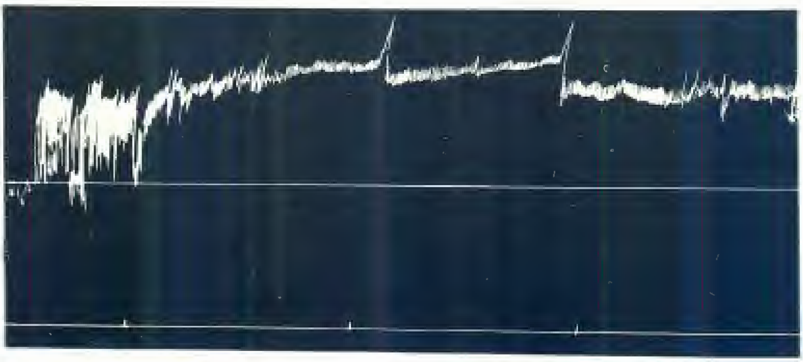
The Effect of K.C.N. on Eructation Efficiency in sheep.



Normal Eructation.



Eructation 5 mins. after dosing 150 mgm. KCN.



Interference with Eructation 5 mins. after dosing another 50 mgm. KCN. (Total dosage 200 mgm. KCN.)

FIG. 14.

A striking example of the rôle that psychic disturbances can play in the pathogenesis of bloat occurred in a dairy herd coincidental with the change-over from hand- to machine-milking. Careful investigation could disclose no possible reason for the bloat other than the inevitable psychic disturbance of the animals reflected in a sharp drop in milk yield.

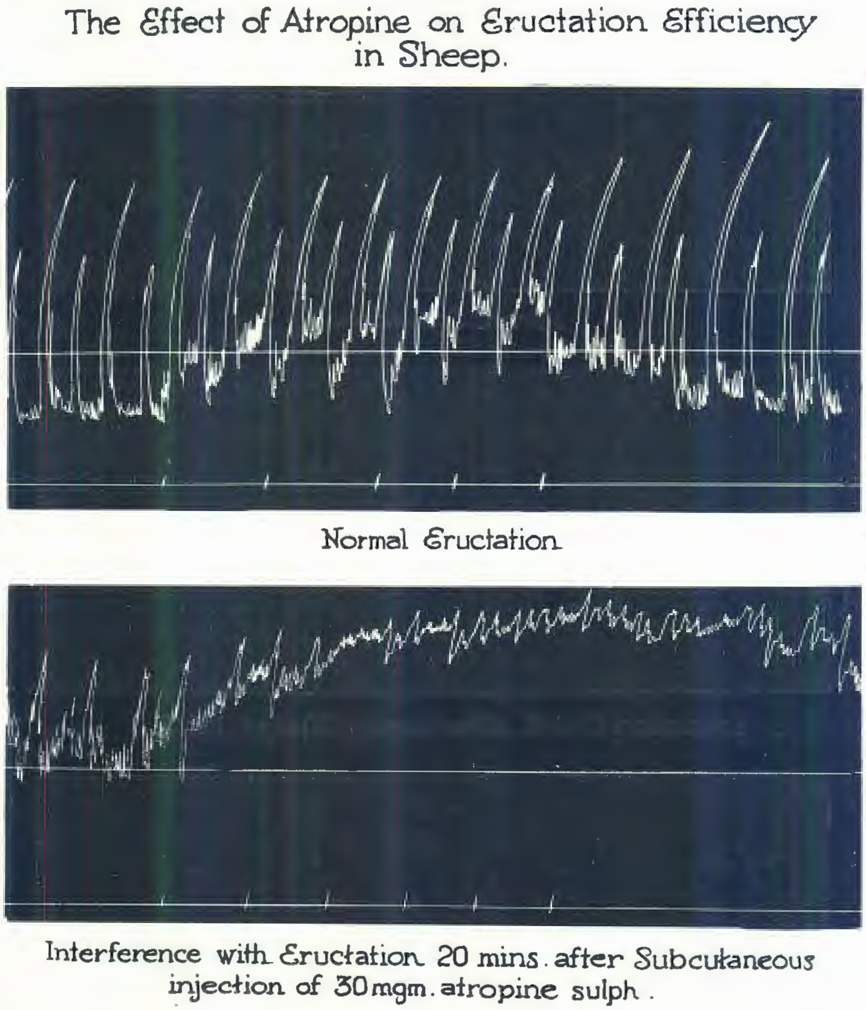


FIG. 15.

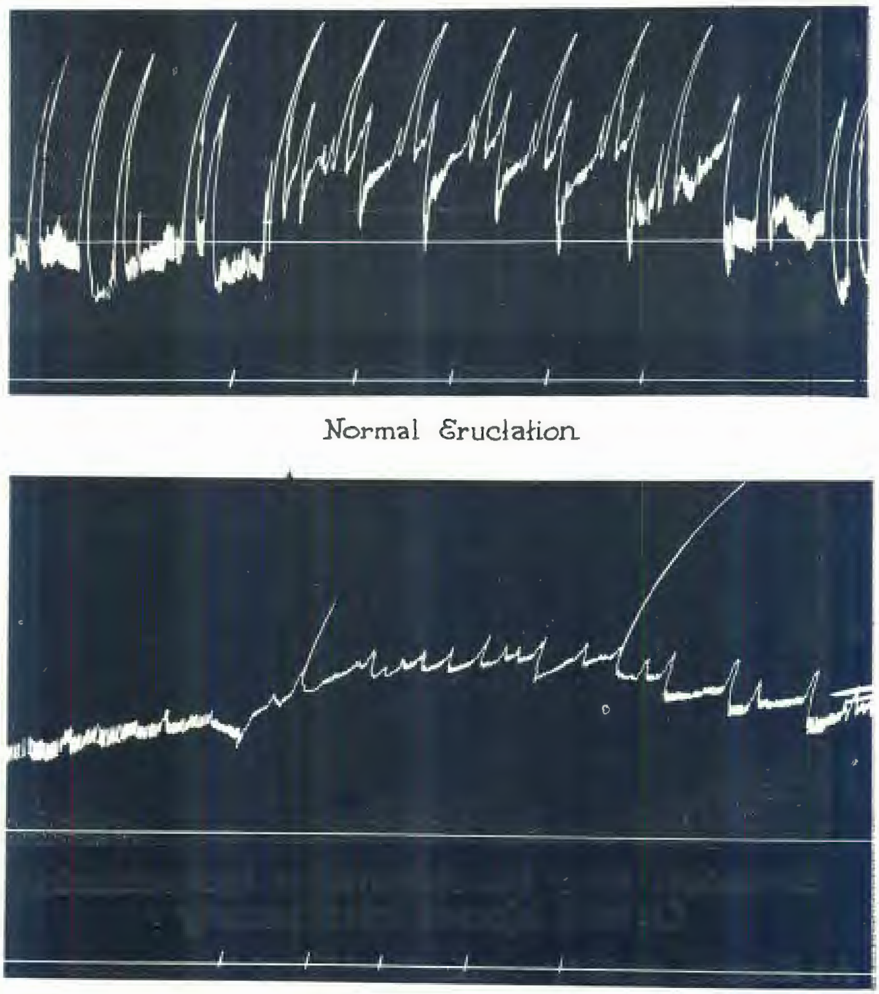
(2) *Those causing Hyper-motility.*

(*a*) *Carbamylcholine chloride* (Carbachol).—The use of carbachol for the treatment of bloat has been advocated frequently. In the author's opinion this is an exceedingly dangerous practice if only because of the inhibition of a heart already embarrassed.

As shown in Fig. 18 even small doses of carbachol cause spasm of the ruminal musculature and interference with eructation. This effect frequently leads to idiopathic bloating. Acute bloat has been seen to occur in cattle following the administration of carbachol in the dosage recommended by the makers. (Clark, personal observations). It would appear that spasm of the rumen and reticulum abolishes the co-ordinated movements required for eructation.

On these grounds the use of carbamylcholine in acute bloat would appear to be completely contra-indicated.

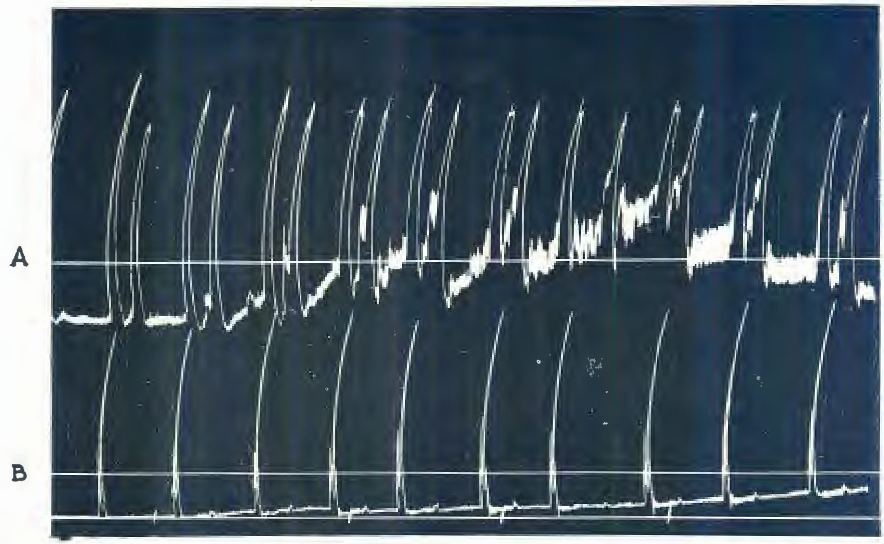
The Effect of Histamine on Eructation Efficiency in sheep.



Interference with Eructation after intravenous injection of 2mgm. Histamine.

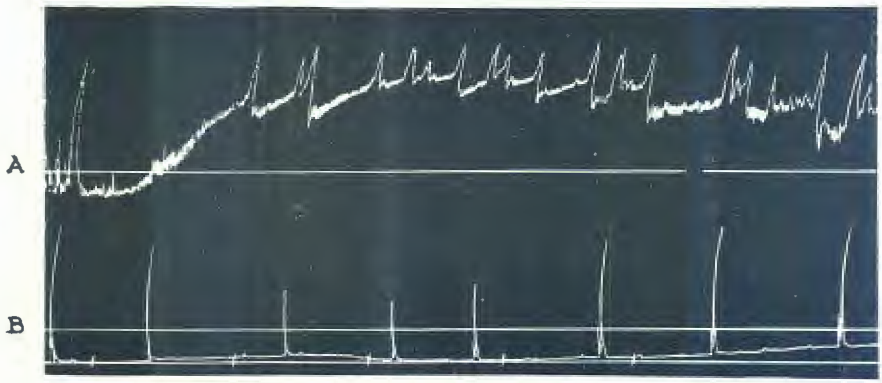
FIG. 16.

The Effect of Adrenaline on Eructation Efficiency in Sheep.



Normal Eructation

A : Ruminal Motility . B : Reticular Motility .



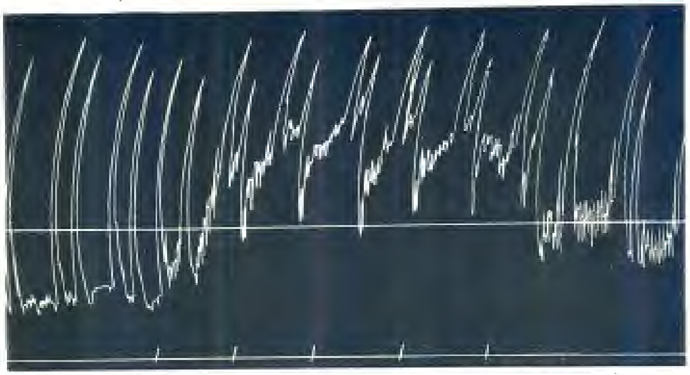
Eructation after 1c.c. Adrenaline hydrochloride (1:1000) injected intravenously .

A : Rumen motility : note inefficient eructation .

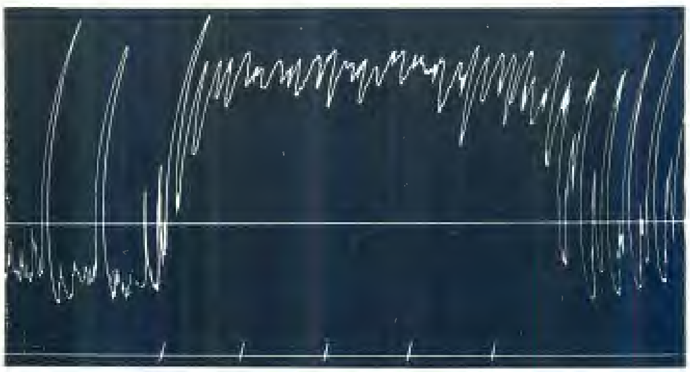
B : Reticular Motility : note temporary inhibition and recovery coinciding with return of eructation efficiency

FIG. 17.

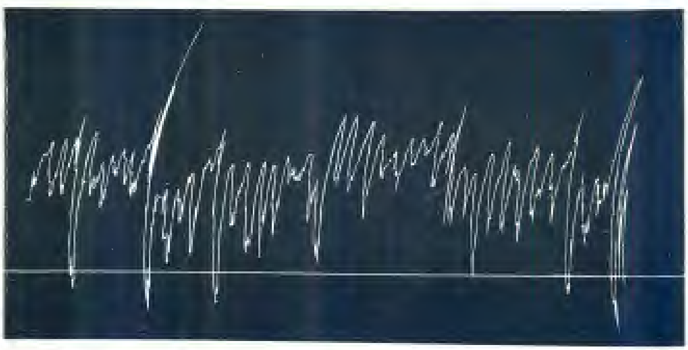
The Effect of Carbachol on Eructation Efficiency in Sheep.



Normal Eructation.



Interference with eructation 30 mins. after subcutaneous injection of 1mgm. Carbachol.



Spontaneous rise in intra-ruminal pressure, and interference with eructation 40 mins. after subcutaneous injection of 1mgm. Carbachol.

FIG. 18.

(*b*) *Veratrine.*—Wester (1935) recommended the use of veratrine as a ruminatoric.

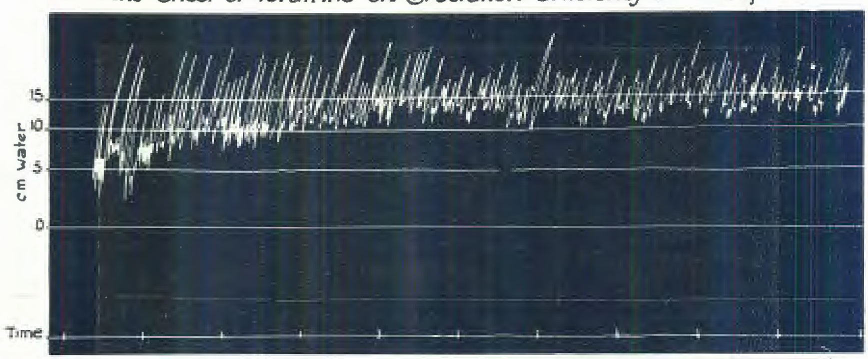
In the present series of experiments it was found that the intravenous injection of 10 mgm. veratrine hydrochloride into a sheep caused acute ruminal spasms and bloat (see Fig. 19). Doses of 5 mgm. resulted in ruminal spasm and interference with eructation. Smaller doses had no visible effect.

The use of veratrine in bloat, especially with an overloaded rumen therefore must be condemned for the same reasons as the use of carbachol.

CONCLUSION.

It has been shown that eructation is a complex co-ordinated reflex involving the rumen, reticulum, cardiac orifice and oesophagus. The rôle of the fore-stomachs is to bring the free gas forward and downward to the cardia.

The Effect of Veratrine on Eructation Efficiency in Sheep.



Spontaneous bloat after intravenous injection of 10mgm. Veratrine hydrochloride
Rumen full

FIG. 19.

Frothing of the ingesta reduces the amount of free gas present and so interferes mechanically with eructation. In the absence of frothing the efficiency of eructation at any given moment will be determined by the balance between the efficiency of the rumino-reticular mechanism, on the one hand, and the relative positions of the gas and the cardia, on the other. The rumino-reticular mechanism has been shown to be influenced by various factors. The relative positions of the gas and the cardia depend on the degree of filling of the rumen and the posture of the animal with frothing as an additional complication.

Bloat therefore is an expression of an adverse balance between the efficiency of the eructation mechanism and the factors militating against it. In other words, if the efficiency of the reflex is kept constant, bloat may occur through excessive overfilling or frothiness or a combination of the two. With an impaired reflex a correspondingly lesser degree of overfilling or frothiness may result in bloat.

It is apparent that bloat may occur under widely varying conditions and its incidence will depend more often on a combination of contributary or supplementary circumstances than on any single factor alone. These factors dealt with in the text are enumerated and summarized below.

SUMMARY.

(1) The eructation reflex in sheep and cattle, and factors affecting it, have been studied mainly by the method of forced air insufflation and direct recording of intraruminal pressure.

(2) Eructation is a complex, co-ordinated reflex involving the rumen, reticulum, cardiac orifice and the oesophagus. It consists essentially in the movement of free gas from the dorsal rumen, forwards and downwards to the cardia. This is accomplished by—

(*a*) A forward wave of contraction of the ruminal musculature (as distinct from the usual backward cycle of contractions).

(*b*) Opening of the cardiac orifice which is brought about by contraction of the lateral and medial pillars of the rumino-reticular fold.

(*c*) The clearing of the cardia of fluid ingesta is affected by relaxation of the reticulum. The relative importance of this phase depends on the degree of filling of the rumen.

(3) The main stimulus for eructation is gas pressure in the posterior dorsal sac of the rumen.

(4) From variations amongst the individual experimental animals it is believed that the efficiency of the reflex may depend on hereditary factors.

(5) The factors affecting the reflex are:—

A. Mechanical.

(i) Obstruction of the oesophagus.

(ii) Frothing of the ingesta.

(iii) The degree of filling of the rumen and posture. Overfilling of the rumen was found to hinder eructation by increasing the distance between the free gas and cardiac orifice. Elevation of the hindquarters had a similar effect, while elevation of the forequarters mitigated the effects of overfilling. Animals with a non-functioning reticulum were found to be particularly susceptible to overfilling.

B. Alkalosis.

In the absence of other factors, the efficiency of eructation was found to vary inversely with the degree of alkalosis as determined by the CO_2-combining power of the blood. This was due mainly to reticular paralysis.

C. Abdominal Vagotomy.

Section of the right ventral branch of the vagus caused abomasal distension and chronic tympany, again due mainly to inhibition of reticular activity. Section of the left dorsal branch diminished the strength of ruminal contractions and eructation efficiency for the first three weeks with subsequent partial recovery.

D. Reflex inhibition from the Posterior Digestive Tract.

Distension of both the abomasum and caecum reduced the eructation efficiency again by inhibition of the reticulum.

E. The effect of Drugs influencing Ruminal Motility.

(i) Hypomotility.

(*a*) Small doses of prussic acid inhibited the reticulum and backward movement of the rumen with consequent inefficiency of eructation and abolition of the reflex.

(*b*) Atropine, histamine and adrenaline were found to inhibit the reflex completely even before a total paralysis of the rumen was induced.

(ii) Hypermotility.

Carbamylcholine and veratrine both cause spasm of the rumen and reticulum with consequent interference with eructation. Their therapeutic use is contraindicated.

Acknowledgment.

The author wishes to express his sincere thanks to Prof. Clark head of the section of physiology and pharmacology for his valuable advice, encouragement and constructive criticism during these investigations. The generous facilities provided by the Director of Veterinary Services and his editing of the text are acknowledged.

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