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THE MECHANICAL ACTIVITY OF THE RETICULO-RUMEN OF CATTLE

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OF RECENT YEARS, much attention has been given to the microbial breakdown of the feed in the ruminant stomach, but comparatively little to the organ in which it takes place. Yet the mechanical activity of the vat—the reticulo-rumen—is complementary to the fermentation and essential to its maintenance as a vigorous and continuous process. If this mechanical activity is abolished by sectioning of the motor nerves, stagnation occurs with the accumulation of feed and gas, and within a few days the animal dies. That the paralysis is not of itself the immediate cause of death is indicated by the fact that animals survive for several weeks if fed through an abomasal fistula (Duncan, 1953).

The functions of the reticulo-rumen activity are complex. Powerful mixing and kneading movements ensure the thorough inoculation of incoming feed and aid in its disintegration; they assist in the absorption of fermentation products and in the maintenance of a suitable environment for the microbionta. An important function concerns the eructation of free gas, large volumes of which are produced during the fermentation process. Another is the transference of digesta to the omasum, while some part also appears to be taken in the regurgitation of boli for rumination. The ways in which these functions are performed, however, are by no means fully understood.

The writers became interested in the motility of the reticulo-rumen when looking for possible causes of the differences between animals with regard to their susceptibility to bloat. Before any role of the organ could be assessed, it was necessary to determine the normal patterns of activity. Some of the results of the investigation were considered to be of general interest and are therefore briefly outlined in this paper.

Experimental

The three commonly used methods for examining the activity of the reticulo-rumen are direct internal palpation through a fistula, the recording of the pressure changes that accompany movements, and fluoroscopic examination after radio-opaque meals.

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Palpation through a fistula was used by Fluorens (1833), who carried out the first experimental investigation of the ruminant stomach, some 125 years ago. Fluorens' subjects were sheep, but extensive observations in fistulated cows were made by Colin (1854). Since then, the most thorough examination of the motility of the reticulo-rumen of cattle has been that of Schalk and Amadon (1928).

Pressure recording was introduced by Toussaint (1875), who inserted lightly-inflated balloons through the fistula and connected them to tambours writing on a kymograph. This technique and its modifications have been employed widely with sheep, goats and cattle, for example by Schalk and Amadon (1928), Quin *et al.* (1938), Phillipson (1939), Balch *et al.* (1951). More recently, it has been refined by the substitution of electronic pressure-sensing devices, *e.g.* Dziuck and Sellers (1955), Bell (1958), Andersson *et al.* (1958).

Fluoroscopy, although valuable, has had only limited application. It has been successfully used with small ruminants—sheep, goats and calves (Czepa and Stigler, 1926; Phillipson, 1939; Dougherty and Meredith, 1955; Benzie and Phillipson, 1958). However, in its present form, it is not conveniently applicable to large ruminants, nor, in any case, is it suitable for continuous observation over a period of time.

The writers commenced their investigations by recording the pressure changes in the various compartments of the reticulo-rumen. For this purpose, an apparatus consisting of special pressure transducers, electronic amplifiers, and a Sanborn heated stylus writing unit, was designed and constructed by the Medical Instrumentation Section of the Auckland Industrial Development Laboratory. The apparatus enabled the pressures at four different points to be registered simultaneously, as well as a time signal and other information. A system of weights kept the transducers in their places within the animal during recording (Figs. 1 and 2).

Characteristic sequences of pressure changes were found to occur in each of the different compartments (Figs. 2 and 7). The patterns were essentially the same in all of the six available fistulated cows. They were generally similar to those described by other workers, *e.g.*, Schalk and Amadon (1928), Dziuck and Sellers (1955) but differed in detail.

The next stage was to compare the pressure changes recorded with what could simultaneously be felt by hand. It was soon dis-

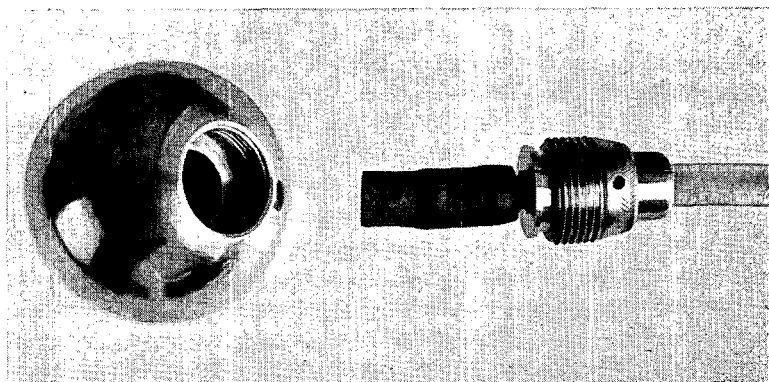


Fig. 1: Transducer with lead ready to be screwed into brass anchor weight.

covered that whereas the pressure changes to a large degree reflected contractions and relaxations of the compartment within which a transducer lay, much important activity—particularly of the pillars and of the posterior rumen—was poorly registered or not registered at all. It was found further that in the records from the reticulum and anterior sac of the rumen, falls of pressure which might otherwise be attributed to relaxations, were in fact associated with hydrostatic changes due to the raising of the floors of these compartments during contraction.

A more direct method of recording movements was therefore sought.

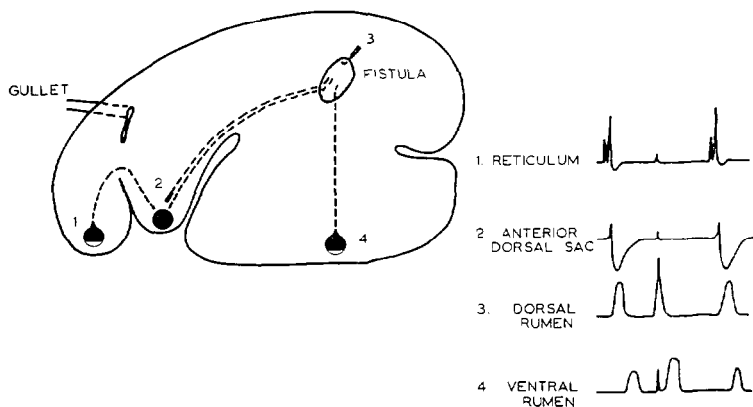


Fig. 2: Diagram of rumen and reticulum showing four recording points and typical pressure patterns obtained from a non-bloated cow.

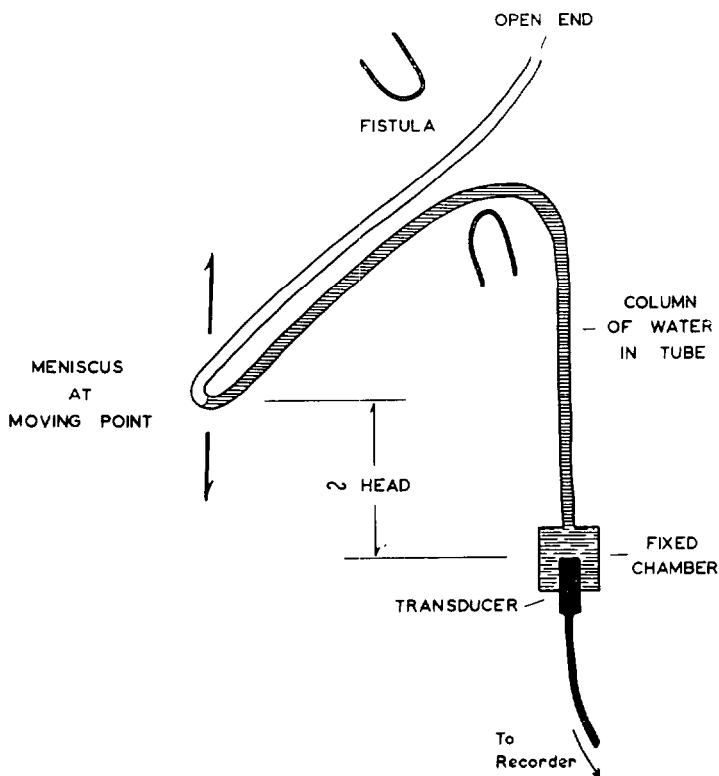


Fig. 3: Level recording device for indicating movement of pillars and stomach floor.

One possibility appeared to be to record the changes in vertical height of the different structures relative to a fixed external point. A simple apparatus was evolved to do this (Fig. 3). A water-filled chamber containing a pressure transducer was attached to a rigid support alongside the cow. The chamber was connected to the point under observation by a column of water in a small plastic tube which passed through the fistula. So that the meniscus of the column would be at atmospheric pressure, the tube was extended, empty, back out through the fistula again, where it was open to the air. As the point under observation moved up and down, so the head of pressure created in the chamber by the column of water increased or decreased. These changes were sensed by the transducer and recorded.

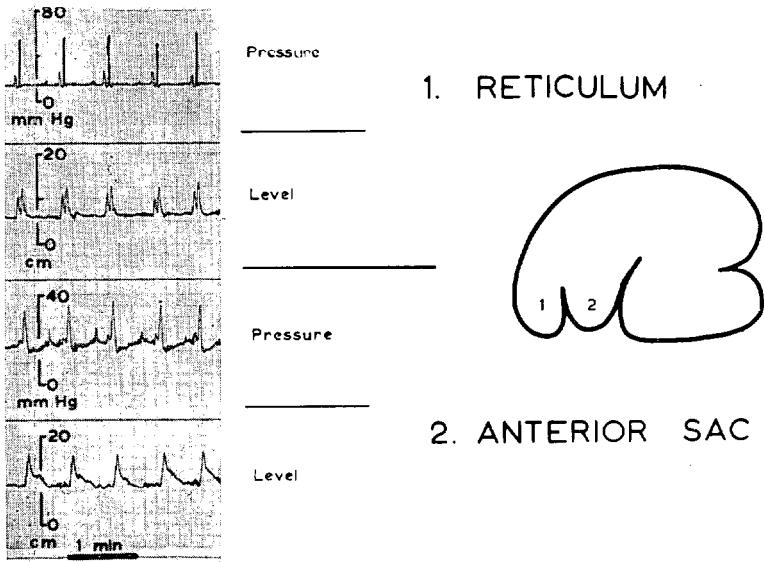


Fig. 4: A comparison of pressure and level records obtained from the reticulum and anterior sac.

A typical record obtained from pressure and level recording from the reticulum and from the anterior sac of the rumen is shown in Fig. 4.

Although limited by the fact that it measured only one component of what are complex actions, this technique immediately proved to be of considerable value. It was superior to pressure recording as an index of the contractions of the reticulum and the anterior sac of the rumen. But even more important, it also allowed some quantitative measurement of the activities of the reticulo-ruminal fold and the anterior, posterior and coronary pillars.

The Basic Movement Cycles

Two basic sequences of movement have been recognized in the reticulo-rumen, termed here the "mixing" and the "belching" cycles. The mixing cycle starts in the reticulum and is primarily concerned with the circulation of the contents within the organ as a whole. The belching cycle—the "secondary peristaltic wave" of Schalk and Amadon (1928) or the "extra" ruminal contraction of Weiss (1953)—appears to start posteriorly, and is associated

with the transference of the gas bubble downwards and forwards to the cardia whence it is usually eructated.

Using the techniques described above, an analysis of the salient features of the cycles was attempted.

THE MIXING CYCLE

The mixing cycle (Fig. 5) was accomplished by three successive groups of contractions involving different structures; it took 25 to 30 sec to complete.

The cycle was initiated by a sharp contraction of the reticulum and the reticulo-ruminal fold.

The second phase commenced about 3 sec after the first and lasted about 15 sec. Before the reticulum had fully relaxed after its first contraction, it contracted again, this time together with the fold, the anterior rumen sac, the anterior pillar, the dorsal rumen sac, and the posterior and the dorsal coronary pillars.

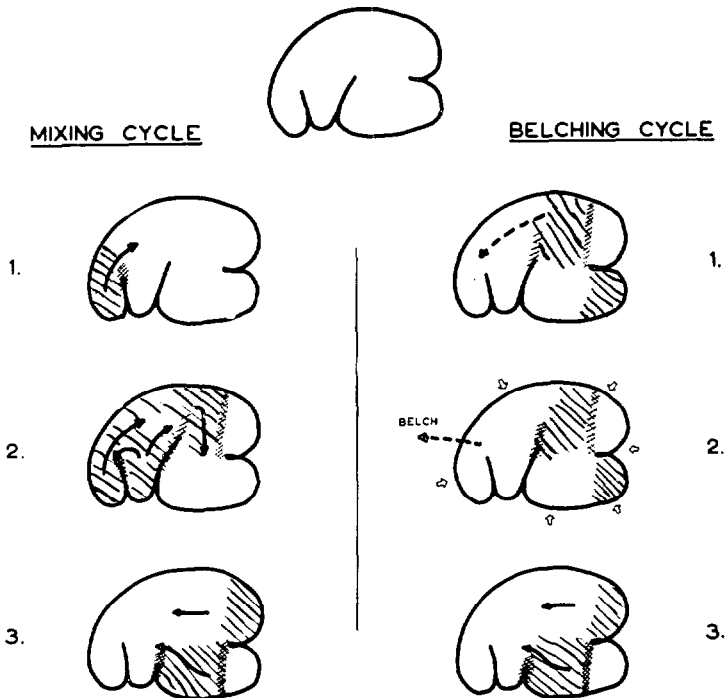


Fig. 5: Diagrammatic representation of sequence of events in the mixing and belching cycles.

The contractions did not, however, develop at the same rate, the reticulum and fold reaching their peak first, followed by the anterior rumen sac and then the remaining structures more or less simultaneously. Relaxation occupied about as much time as did the individual contractions, with the exception of the anterior sac, which usually relaxed more slowly. In the case of the reticulum and fold, relaxation was complete before any of the other structures reached its contraction peak.

The third or ventral phase commenced 7 to 10 sec after the start of the second and also lasted about 15 sec. A simultaneous contraction occurred of the anterior, the posterior and the ventral coronary pillars, the ventral rumen sac and the posterior dorsal blind sac. In this phase, the anterior pillar contracted downwards until it formed a low ridge between the anterior and ventral sacs of the rumen, and, whereas the other structures subsequently relaxed to their previous state, it remained in this low position until the following cycle.

The mixing cycle resulted in a series of ingesta fluxes—from the reticulum to the anterior sac and the dorsal sac, from the anterior sac back into the reticulum (as the sac floor rose and the reticulum relaxed), from the dorsal sac to the ventral sac, and from the posterior, particularly the ventral, region forwards over the anterior pillar. The fluxes did, in fact, constitute a cycle, the direction of which was determined by the timing of the contraction peaks and the sequence of phases.

THE BELCHING CYCLE

The belching cycle (Fig. 5) was composed of two main groups of contractions, the first of which was associated with eructation. The cycle took 25 to 30 sec to complete.

The first detectable change was an increase in pressure in the posterior dorsal blind sac, associated with a powerful contraction of the dorsal coronary pillars. This had not long commenced, however, before the anterior pillar, and the dorsal and the posterior ventral blind sacs also started to contract. When these last three structures reached the peak of their contraction, when, in fact, the pressure in the posterior dorsal blind sac was beginning to fall, eructation occurred.

Eructation was accompanied by a sharp, transitory rise in pressure throughout the organ. This was apparently due to a general rise in intra-abdominal pressure, caused, in part at least, by a contraction of the abdominal walls.

During eructation, the pressure in the posterior dorsal blind sac fell very rapidly.

The last phase of the belching cycle appeared to be identical with the last phase of the mixing cycle, *i.e.*, the anterior pillar sank to its lowest level as the ventral coronary pillar, the ventral sac and the posterior dorsal blind sac contracted. This ventral phase commenced 10 to 15 sec after the start of the cycle and lasted about 15 sec.

The most important effect of the belching cycle was, of course, to move the gas pocket from the dorsal rumen down to the cardia, during the first 7 to 9 sec. As well, the contraction of the dorsal coronary pillars had a powerful kneading action, while the strong ventral phase assisted mixing.

Although belching was normally associated with the cycle described, eructation could also occur during the mixing cycle or even in the absence of any movement at all.

Belching during mixing cycles was observed not infrequently in certain animals before the morning feed, *i.e.*, after 18 h starvation. The eructation was found to occur at the peak of the anterior sac contraction and was accompanied by a synchronous contraction. Belching during mixing cycles could be induced fairly readily at other times by insufflating gas into the rumen at 8 to 10 l./min. As would be expected, the frequency of the belching cycles also was increased by this procedure.

In experiments with sheep, it was found that paralysis of the reticulo-rumen musculature by atropine (which does not affect the oesophagus at the dose rate used—D. A. Titchen, pers. comm.) did not prevent eructation of insufflated gas. Belching in this case appeared to be accomplished by an abdominal wall contraction during exhalation. This suggested that the synchronous pressure rise that accompanied normal belching might be concerned with the passage of gas from the cardia into the oesophagus.

Digestion and Motility

Apart from changes in muscle tonus, the mechanical activity of the reticulo-rumen appeared to consist entirely of a sequence of mixing and belching cycles. However, in any one animal, marked variation occurred in the frequency of cycles, the ratio of the two kinds, the strength of the individual contractions and the detail of the cycles. These changes could largely be correlated with the state of the digestion.

FEEDING

Feeding was characterized by vigorous movements and the highest absolute frequency of cycles. The ratio of belching to mixing cycles increased, presumably in response to the increased gas formation.

For each animal, the average frequency of mixing cycles during feeding was found to be an individual characteristic. There appeared to be some genetical basis for this because, whereas consistent, statistically significant differences occurred between unrelated cows, the rates for identical twins were similar (Johns *et al.*, 1958).

The increase in motility was not associated simply with feeding, but paralleled the rate of food intake. During any one feed, therefore, the frequency was highest at the start and decreased as eating slackened off. This is shown in Fig. 6.

RESTING

Only under unusual circumstances is the reticulo-rumen fully quiescent for any length of time. The term "resting" used here for periods when an animal was neither feeding nor ruminating,

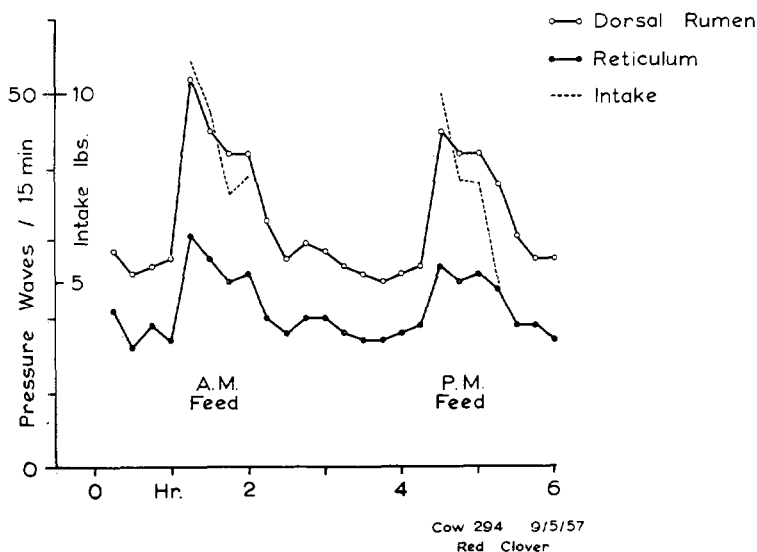


Fig. 6: The relationship between ruminal and reticular activity and rate of feed intake.

is therefore misleading, particularly as it included both the replete and the fasting states. It is not surprising, therefore, that motility of the organ during "resting" showed more variation than at other times.

The frequency of cycles was affected by events in the immediate future and past.

Before feeding, particularly in the mornings, temporary increases in rate often occurred while the clover was being weighed out in front of the cows. Drooling of saliva occurred at the same time and it appeared as if this was a psychic effect. Similar salivary responses to the sight of food have been described by Denton (1957) for sheep.

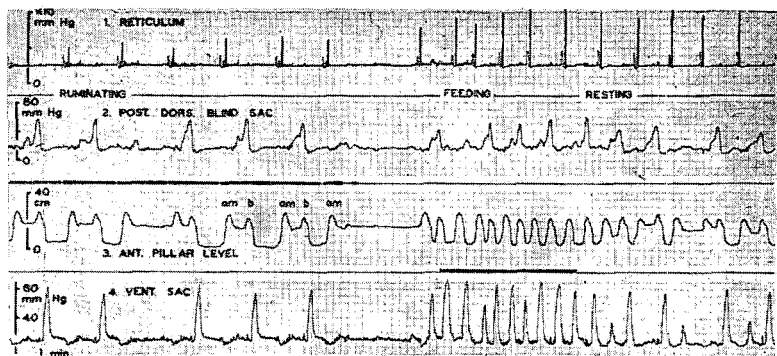
After feeding, the frequency of movements fell off rapidly in the first 15 min, and then tended to decrease slowly over a long time.

Individual movements were weaker and smaller during resting. Thus at the peak of the contraction of the anterior rumen sac, the level reached by the floor was only some three quarters of the height reached during feeding.

The most striking change during resting, however, was the complete disappearance, for long periods, of the ventral phase of the mixing cycles. The first two stages of an abbreviated cycle appeared to be normal, except that, at the conclusion of the second phase, the anterior pillar came to rest a little above the mid-point of its displacement range. The only apparent remnant of the third phase was a variable contraction of the posterior dorsal blind sac, and this terminated the cycle. In contrast, the ventral phase of belching cycles during these periods remained unaltered, the anterior pillar descending to its full extent, accompanied by a strong contraction of the ventral coronary pillars.

Since the anterior pillar remained where it came to rest after relaxation, its position between cycles depended on the kind of cycle that had occurred last. Thus, if a series of abbreviated mixing cycles occurred, the pillar did not descend below its mid-point level until a belch cycle was interposed. This effect is shown in Fig. 7.

The change-over from normal to abbreviated mixing cycles and vice versa did not usually occur abruptly, but took place over several minutes during which the ventral movements progressively decreased or increased in strength.



am ABBREVIATED MIXING CYCLE

b BELCHING CYCLE



Fig. 7: A recording illustrating the activities of the reticulo-rumen associated with ruminating, feeding and resting.

RUMINATING

During rumination, the activity of the reticulo-rumen resembled that during resting. Abbreviated mixing cycles usually occurred, while, as before, belching cycles remained normal. The major change was the appearance of an extra reticulum contraction about 4 to 5 sec before the reticulum contraction that ushers in the mixing cycle. Regurgitation appeared to take place at the peak of this contraction. However, the extra contraction was not necessary for the act of regurgitation, since extra regurgitations commonly occurred at other times, unaccompanied by either pressure increase or level rise in the reticulum.

When rumination stopped, a period of quiescence, often lasting several minutes, always followed. This occurred whether cessation was voluntary or had been induced.

Discussion

The cycles and the patterns of activity described here occurred consistently in all six animals (five Jerseys and one Shorthorn) during the 3 years that the investigation has been in progress. In general, the observations are consistent with those of other workers, notably Schalk and Amadon (1928). The same patterns

have been found in fistulated cattle (Friesians and Ayrshires) at the Rowett Research Institute (A. T. Phillipson, pers. comm.).

The descriptions of the cycles are by no means complete. Although level recording allowed a more quantitative examination of certain features than had previously been possible, the observations were limited in other directions. Thus no method for recording dilatations of compartments was found. Nor could the activity of the lateral pillars be recorded satisfactorily. Because of these deficiencies, the writers have been unable to obtain a full picture of what was happening during the clearing of the cardia in the belching cycle. Again, because recording was of necessity limited to the middle 6 to 7 h of the day, which time included the two 2 h feeds, it was not possible to observe the long periods of settled rumination that occur at other times. That there may be some change in activity during such periods is suggested by the finding of Balch (1952) that there was a substantial drop in the frequency of mixing cycles when rumination occurred while an animal was lying down as against standing.

However, while the development of new techniques may help to fill these gaps, it is clear that the results have already raised most interesting questions. What causes the change from normal to abbreviated mixing cycles? Why should the ventral phase of the mixing cycle be affected but not that of the belching cycle? How is the anterior pillar, whose activities are obviously more complex than previously suspected, controlled. What is the significance of these changes in terms of energy expenditure? Answers to these questions must await more fundamental, analytical examination of the kind recently carried out by Titchen (1958) on the activity of the reticulum.

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