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# DIET AND THE MOTILITY OF THE FORESTOMACHS OF THE SHEEP

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## SUMMARY

The technique of partial exteriorization of the reticulum and rumen of the sheep is briefly described. Partial exteriorizations have been used to study the motility of the reticulum and rumen and to observe the effects of dietary factors on the motility. A characteristic pattern of motility is present in animals fasted until their stomach contents have become freely liquid. The pattern alters when the animals feed. The changes include, in addition to changes such as an increase in the frequency of co-ordinated contractions, a change in the form of the co-ordinated contractions. The extent of the changes in form, and their persistence after feeding stops appears primarily determined by the nature of the feed and the amount eaten. The origin of the changes and their possible effects on gastric functions are briefly discussed.

## INTRODUCTION

A MAJOR OBSTACLE to the study in conscious animals of the motility of internal organs is their inaccessibility. Sometimes the physiologist can find out what he wants to know simply by feeling the organ through the body wall. Usually, however, he has to resort to special techniques such as radiological examination, or the measurement and recording of physical changes associated with the activity in which he is interested. Whichever of these methods he employs, he can only deduce what is happening. It would be simpler, more certain, often more informative, if the organ could be seen by eye.

There are two methods by which direct visual observation of an internal organ is possible. A window or cannula can be inserted in the body wall over the organ: this method has been used, for example, to observe the ovaries of pigs (Betteridge and Raeside, 1962). Alternatively, the organ, or part of it, can be brought outside the body wall: the spleen has been studied in this manner (Barcroft and Florey, 1929). Both methods have limitations. An obvious limitation to the second is that not many organs can be exteriorized, as the process is termed, while at the same time preserving intact their nervous and vascular con-

nections. Much of the gut, however, is suitable for exteriorization, and the method has been used in various forms to study the motility of the small and large intestines, *e.g.*, Barcroft and Robinson (1929), Biebl (1930), Barcroft and Steggerda (1932), Raiford and Mulinos (1934), Bass *et al.* (1961).

Partial exteriorization of the rumen wall was first carried out by van der Heyde (1927) to record the electrical phenomena associated with rumen contractions. Toman (1928) appears to have been the first to use exteriorizations to observe the motility itself. The advantages offered by this method of observation were not generally recognized, however, and it was neglected for some 25 years. An improved type of rumen exteriorization was used by le Bars *et al.* (1953) to correlate changes in intra-ruminal pressure and contractions of the dorsal rumen. The method was taken a step further when Titchen (1958a) and Bost (1958), independently, developed techniques for partially exteriorizing the reticulum. Since then, partial exteriorizations of the reticulum and of various regions of the rumen have been used in systematic studies of the motility of these compartments of the sheep's stomach (Reid and Titchen, 1959; Reid, 1962; Reid and Titchen, 1962).

The object of this paper is to draw attention to the influence of dietary factors on the motility of the forestomachs of the sheep.

That there are relationships between the motility of the forestomachs and the state of the animal — whether fasting, feeding, or ruminating — is well established (see, for example, Schalk and Amadon, 1928; Quin and van der Wath, 1938; Phillipson, 1939; Balch, 1952; Reid and Cornwall, 1959; Nestic, 1960; Phillipson and Reid, 1960). Evidence of relationships between the motility and dietary factors has also been found, *e.g.*, Colvin *et al.* (1958), Popescu and Florescu (1958), Freer *et al.* (1962). However, the extent of the changes in motility with different circumstances has not been appreciated. Nor has an overall pattern been discerned in the changes. In part, this has been due to the inadequacy of the methods of observation used, in part to the way in which the observations have been made, particularly their common restriction to the reticulum and/or the dorsal rumen. Some of the deficiencies can be avoided by the use of partial exteriorizations. Thus the uncertainties of indirect methods of observation are avoided because direct observation of the motility is possible. Again, exteriorizations readily allow simultaneous

observation of both dorsal and ventral regions of the rumen. Largely because of the difficulty of observing them by the more usual methods, the ventral regions have received little attention in the past. In the present studies, the changes in motility found to occur in these regions have provided important clues as to the overall pattern of the changes in motility of the forestomachs and to their origin.

The use of partial exteriorizations has thus enabled a better definition of the relationships between the motility of the forestomachs and the state of the animal and the diet. Major deficiencies remain. Exteriorizations have provided little useful information regarding the motility of the pillars: it seems that other methods, *e.g.*, level recording (Reid and Cornwall, 1959), must be used for this purpose. Again, knowledge of the changes in motility of the omasum is still slight.

In this paper, a brief description is given of the motility of the reticulum and rumen of fasting and feeding sheep, as observed by means of partial exteriorizations of the stomach, together with the results of some preliminary experiments on the effects of different diets on the motility.

#### METHODS

The greater part of this work was carried out in England, at the Physiological Laboratory, Cambridge University, using Welsh mountain sheep. Additional observations have been made in New Zealand at Plant Chemistry Division, using Romney sheep.

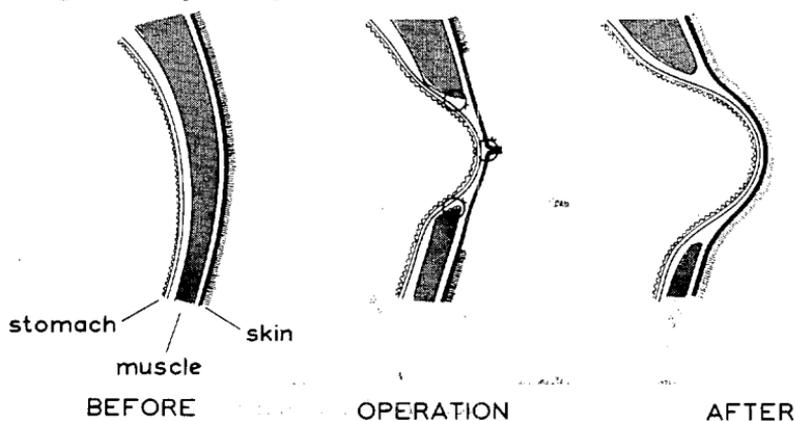
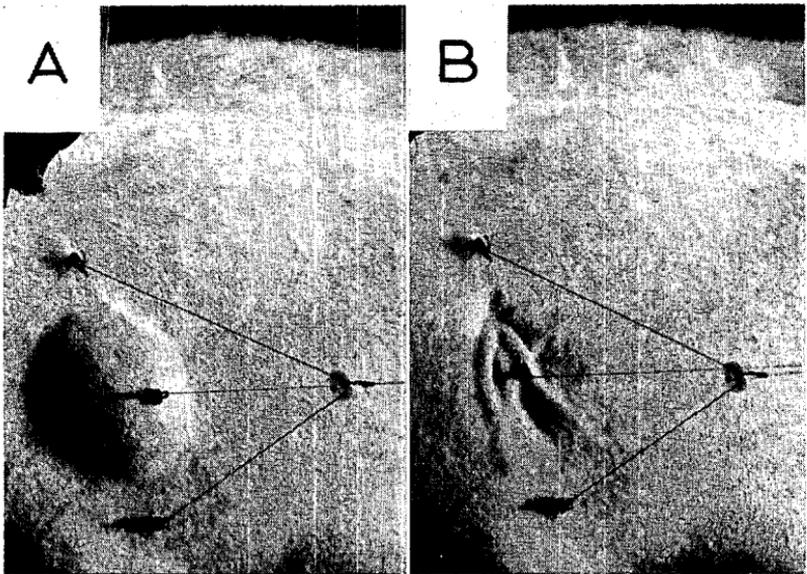


Fig. 1: Method of partially exteriorizing the rumen, shown in simplified cross-sections. The circles represent stitches: those between the stomach and the muscle layers are of catgut and will be absorbed during healing; those in the skin are of nylon and are removed a week after the operation.

The method of making a partial exteriorization of the rumen is shown diagrammatically in Fig. 1. The operation is carried out with the animal under anaesthesia. The main steps are as follows:

- (1) A simple cut is made in the skin over the region of the stomach to be exteriorized. An opening is made in the body wall by cutting or splitting the several muscle and tissue layers.
- (2) The desired portion of the stomach is brought up through the opening in the body wall and stitched to its edges.
- (3) The skin is separated from the subcutaneous fascia for a short distance on either side of the wound. The skin edges are then stitched together over the exteriorized portion of the stomach, which is deliberately caught up in some of these stitches.

During healing, adhesions form between the stomach and the body wall thus permanently anchoring it in position. Adhesions also form between the exteriorized stomach and the skin, so that when the stomach contracts it pulls the skin with it. Exteriorizations in the lateral and ventral



*Fig. 2: Effect of a contraction of the reticulum on a partial exteriorization of the reticulum. A, the reticulum relaxed; B, the reticulum contracted. Note the herniation of the exteriorization when the reticulum is relaxed. The threads are part of the apparatus used for recording the motility.*

regions of the stomach tend to herniate when relaxed: in such exteriorizations, gastric contractions are especially well defined (see Fig. 2).

Partial exteriorization of the reticulum is carried out in essentially the same way as described above. However, because this organ lies within the rib cage, the operation is more complicated (see Titchen, 1958a).

Once healed, the exteriorizations are ignored by the animals. They do not appear to have any adverse effects on the health of the animals, which eat well and put on weight.

In each of the sheep a reticulum exteriorization and up to five exteriorizations of different parts of the lateral face of the rumen were prepared.

The animals were usually housed indoors, in stands. Some observations were made on animals feeding *ad lib.*; but more commonly feeding was restricted, the standard regime being 24 hr fasting, up to 3 hr feeding, followed by a further 24 hr fasting. Water was freely available at all times. The feeds included several hays, concentrate pellets (commercial "sheep nuts") and cut green herbage. Some observations were also made on animals grazing a mixed ryegrass/white clover pasture.

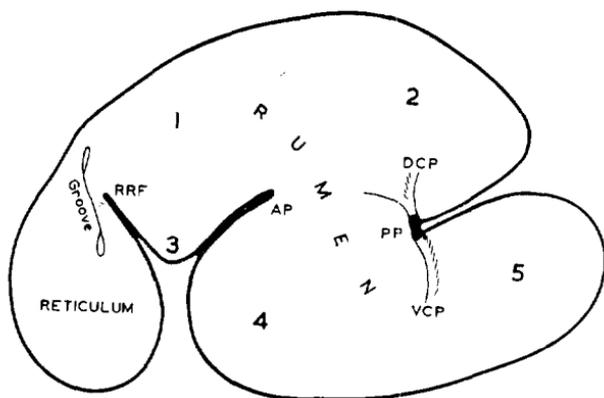


Fig. 3: The reticulum and rumen of the sheep. Diagrammatic longitudinal vertical section, based on paramedian sections of frozen cadavers of Welsh mountain sheep. The entrance (the cardia) lies at the upper end of the oesophageal groove (Groove), the exit (the reticulo-omasal orifice) at the lower end of the groove. RRF—reticulo-ruminal fold; AP, PP— anterior and posterior pillars; DCP, VCP—dorsal and ventral coronary pillars; 1, 2— anterior and posterior regions of the dorsal sac of the rumen; 3— anterior ventral rumen sac; 4— main ventral rumen sac; 5— posterior ventral blind sac of the rumen.

The motility of the stomach was observed by eye, using a stop-watch to time the occurrence and duration of contractions. Permanent records were made by attaching to the exteriorizations threads which ran to levers writing on smoked paper on a kymograph. A system of jockey pulleys was used to reduce artefacts caused by body movements (Reid and Titchen, 1959).

The various regions of the rumen are identified in Fig. 3.

### OBSERVATIONS

Exteriorizations of the reticulum and rumen exhibit both active and passive changes. Active changes are caused by contractions of the stomach wall. Passive changes, on the other hand, are mechanical; they result from events such as coughing, bleating, or changes in posture. Active changes can usually be distinguished from passive changes without difficulty.

The term "motility" is used here to denote the active changes. These are of two kinds, local or "tonic" activity, and co-ordinated activity. Tonic activity is restricted to an individual exteriorization (or part of an exteriorization) whereas co-ordinated activity involves several or all exteriorizations in organized sequences of contraction. Of the two kinds, the co-ordinated activity is the more prominent: it comprises the so-called "movements" of the reticulum and rumen.

There are two distinct types of co-ordinated activity. The first involves both the reticulum and the rumen. This is called here the "A" sequence: it corresponds to the "primary peristaltic wave" of Schalk and Amadon (1928), and to the "mixing cycle" of Reid and Cornwall (1959). The second involves the rumen only. This type is called here the "B" sequence: it corresponds to the "secondary peristaltic wave" of Schalk and Amadon, and to the "belching cycle" of Reid and Cornwall.

The motility of the reticulum and rumen may be described in general terms as a continuous series of A sequences interspersed with B sequences, with a background of tonic activity. Within this framework, the motility exhibits variation in almost every dimension. Thus variation is seen in:

- (1) The absolute frequency of sequences,
- (2) The relative frequency of A and B sequences,
- (3) The degree of tonic activity,

- (4) The magnitude, duration and complexity of the contractions of individual regions of the stomach during either sequence, and
- (5) The time of onset of the contractions of the different regions of the rumen relative to the start of a sequence.

The greater part of this variation appears to be related to two factors: the state of the animal — whether fasting, feeding or fed — and the diet.

Basically, two extreme states of the motility may be recognized: that present in the animal fasted until the contents of the stomach are freely liquid, and that present in the animal feeding hungrily.

#### THE MOTILITY OF THE RETICULUM AND RUMEN IN THE FASTED SHEEP

The motility of the reticulum and rumen in sheep fasted for 18 to 24 hr is characterized by:

- (1) A low frequency of co-ordinated sequences (the interval between successive sequences is commonly of the order of 1 to 3 min);
- (2) A low proportion of B sequences — there may be as few as one B sequence to every five A sequences;
- (3) A low level of tonic activity;
- (4) Short, simple, relatively weak rumen contractions — the ventral regions may not contract at all during A sequences; and
- (5) The emergence of a characteristic form of both A and B sequences.

*The Fasting A Sequence* consists of a double contraction of the reticulum and a contraction of the rumen which begins in the anterior dorsal region of the rumen and spreads rapidly to its posterior and ventral regions. The onset of the rumen contraction occurs 1.5 to 2.5 sec after the start of the reticulum contraction: 2 to 3 sec later, the entire rumen is involved. Since the duration of the contraction in the individual regions of the rumen is of the order of 7 to 9 sec, there is an appreciable period during which all regions will be contracting simultaneously. The form of this rumen contraction as a whole may be loosely described as "concurrent" to distinguish it from the form seen in the feeding sheep, described later.

*The Fasting B Sequence* starts with a contraction of the posterior ventral blind sac, usually a continuation of the posterior ventral blind sac contraction of the previous A sequence. The contraction spreads to involve the dorsal

rumen; but unlike the dorsal rumen contraction in the A sequence, the contraction in the B sequence spreads from the posterior region to the anterior. A contraction of the anterior and main ventral sacs of the rumen occurs during the contraction of the dorsal rumen, and a second, weaker

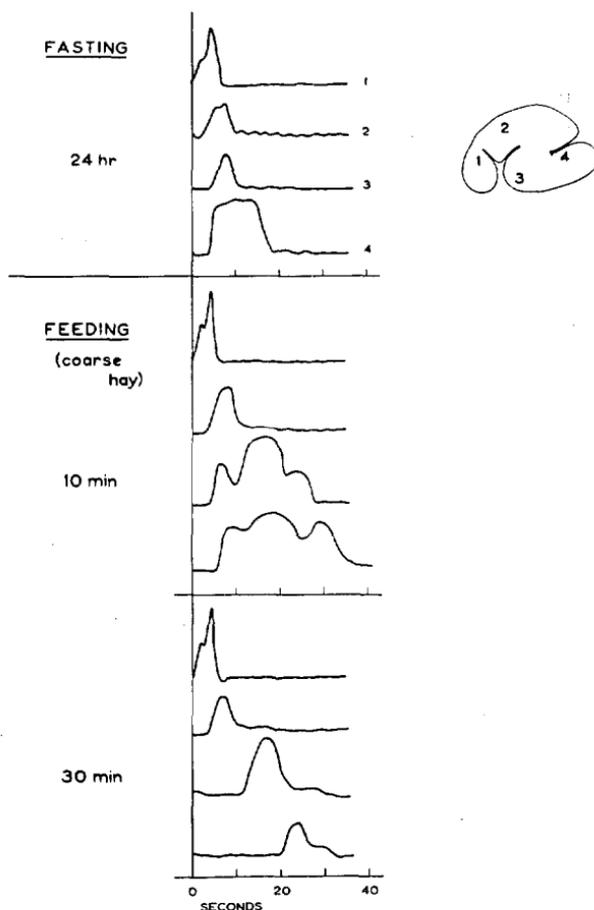


Fig. 4: The changes in form of the co-ordinated contractions of the reticulum and rumen during feeding: A sequences. Tracings of kymographic records made from partial exteriorizations of the reticulum and rumen of a Welsh mountain sheep fasted for 24 hr and then fed on coarse meadow hay. The positions of the exteriorizations are indicated in the diagram of the stomach: 1—reticulum; 2— anterior region of dorsal rumen sac; 3—main ventral sac of rumen; 4— posterior ventral blind sac. Top tracing— an A sequence in the fasting animal, showing the "concurrent" form of the rumen contraction; middle— intermediate stage in transition; bottom— an A sequence after the animal had been eating coarse hay for 30 min, showing the "serial" form of the rumen contraction.

contraction may follow. As stated earlier, the reticulum does not contract during the B sequence.

Eructation is commonly associated with B sequences. In fasting sheep, eructation may be seen (by watching the oesophagus in the neck) and/or heard to take place during

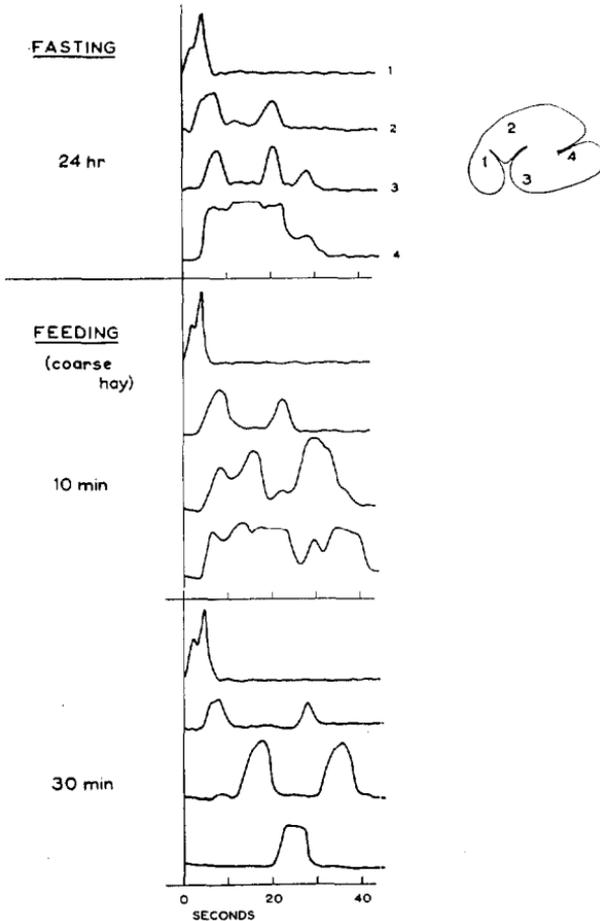


Fig. 5: The changes in form of the co-ordinated contractions of the reticulum and rumen during feeding: A sequences followed by B sequences. Tracings of kymographic records made from same sheep as in Fig. 4, during the same experiment. Top tracing—an A sequence followed by a B sequence in the fasting animal; middle—intermediate stage during transition; bottom—an A sequence followed by a B sequence after the animal had been eating coarse meadow hay for 30 min. Note the complexity of the contractions in the ventral regions during the transitional stage and the relative simplicity later when the feeding types of sequence had been established.

one out of every 2 to 5 B sequences. It occurs at the peak of the dorsal rumen contraction, and is accompanied by a brief contraction of the abdominal wall.

Examples of records of an A sequence and an A followed by a B sequence in a fasted sheep, are shown in Figs. 4 and 5.

#### THE MOTILITY OF THE RETICULUM AND RUMEN IN THE FEEDING SHEEP

The motility of the reticulum and rumen in hungrily feeding sheep is characterized by:

- (1) A high frequency of co-ordinated sequences — as many as 3 a minute;
- (2) A high ratio of B to A sequences — of the order of 1 : 1;
- (3) A high level of tonic activity;
- (4) Strong rumen contractions — during the first 20 min of feeding especially, the contractions of the ventral regions are vigorous, prolonged and polyphasic; and
- (5) The emergence, after the animal has been feeding for 30 min or more, of a new form of both A and B sequences.

*The Feeding A Sequence*, like the fasting A sequence, consists of a double contraction of the reticulum and a contraction of the rumen. Unlike that in the fasting A sequence, however, the rumen contraction in the feeding A sequence is not "concurrent" but plainly "serial" in form. It first involves the dorsal regions which contract and have almost completely relaxed again before the anterior and main ventral sacs contract, and these in turn are almost completely relaxed before the posterior ventral blind sac starts to contract. The whole sequence takes some 30 sec from start to finish: it may be cut short by the commencement of a new sequence. The differences between fasting and feeding A sequences are shown diagrammatically in Fig. 6.

*The Feeding B Sequence*, like the fasting B sequence, starts with a contraction of the posterior ventral blind sac of the rumen, and again most commonly this is a prolongation of the posterior ventral blind sac contraction of the preceding A sequence. The dorsal rumen contraction is similar to that occurring in the fasting B sequence. The behaviour of the anterior and main ventral sacs, however, is different: they contract weakly, if at all, during the contraction of the dorsal regions, but undergo a powerful contraction following the relaxation of the dorsal regions. The contraction of the ventral sacs finishes the sequence.

Eructation occurs in association with the majority of B sequences during feeding.

Examples of records of an A sequence and of an A followed by a B sequence in a feeding sheep are shown in Figs. 4 and 5.

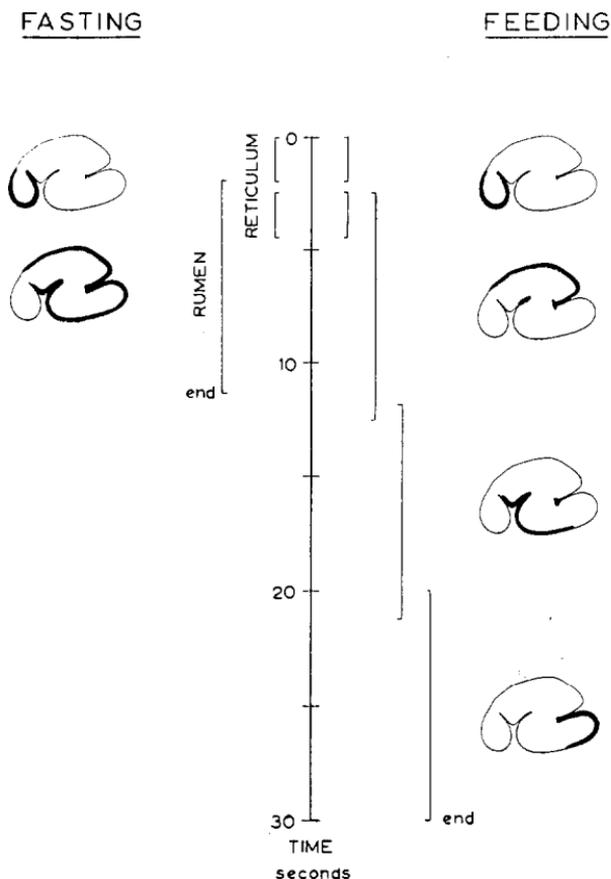


Fig. 6: The time course of the major contractions of the reticulum and rumen during A sequences in the fasted and the feeding sheep. The time scale (down centre) starts from the onset of the reticulum contraction. Contraction of the various regions is indicated by thickening of their outline, the duration by the brackets. On the left, the A sequence in the well-fasted animal. The rumen contraction is "concurrent" in form (see text). The total duration of the sequence is usually about 12 sec, but, depending on the duration of the contraction of the posterior ventral blind sac, may be longer, as in the example in Fig. 4. On the right, an A sequence in the feeding animal after it has been eating coarse hay for 30 min or more. The rumen contraction is "serial" in form, involving in stages the dorsal regions, then the anterior and main ventral sacs, and, lastly, the posterior ventral blind sac. The total duration of the sequence is of the order of 30 sec.

### THE TRANSITION FROM FASTING TO FEEDING SEQUENCES

The gross differences between the fasting and feeding forms of the two basic sequences, as observed by means of partial exteriorizations of the walls of the reticulum and rumen, lie in the activity of the ventral regions of the rumen — the anterior and main ventral sacs, and the posterior ventral blind sacs.

In the A sequence, the simplest way in which these differences might come about would be for the contractions of the ventral regions merely to be delayed during feeding. Such a delay does in fact occur, but it is not the only change involved. When the sheep starts to feed, strong contractions of the ventral regions appear following on the "concurrent" contractions of these regions. That is, there is an intermediate stage during which the ventral regions exhibit two major contraction phases in each A sequence, one apparently corresponding to the "concurrent" contraction, the other to the "serial" contraction (see Fig. 4). As feeding continues, three trends become evident. First, the "concurrent" phase progressively weakens: as a consequence, the major contractions of the ventral regions now follow those of the dorsal regions. Secondly, the onset of the "serial" phase is increasingly delayed: this is more pronounced in the case of the posterior ventral blind sac than it is in the case of the other ventral regions, with the result that the contractions of the blind sac come to follow the major contractions of the other ventral sacs. Thirdly, the "serial" phases tend to become simplified and their duration shortened. These several changes, if maintained, lead to the A sequence's assuming the characteristic feeding form.

The changes in form of the B sequence during feeding are similar to the changes in the form of the A sequence, especially as regards the behaviour of the anterior and main ventral rumen sacs. There is an important difference, however: the B sequence continues to start with a major contraction of the posterior ventral blind sac and the general relationship between this contraction and that of the dorsal rumen is preserved.

When feeding stops, a progressive reversal of the changes in form takes place. Complete reversion may take many hours.

### DIETARY FACTORS AND THE CHANGES IN GASTRIC MOTILITY DURING FEEDING

The extent and persistence of the changes in the motility of the reticulum and rumen during feeding appear to be

primarily determined by dietary factors. These include the amount and nature of the feed eaten during the present meal, the interval of time elapsed since the last meal, and the amount and nature of the feed eaten during that and earlier meals. The influence of the previous meals can be reduced by withholding food until the gastric motility has reverted to the fasting form. A regime of 24 hr fasting, up to 3 hr feeding, followed by a further 24 hr fasting, has been found satisfactory for experimental purposes: under these conditions, the effects of different feeds on the motility can be readily demonstrated. At least two days' feeding *ad lib.* must be allowed between consecutive experiments. Preliminary trials have been carried out in this fashion with several feeds, including hays (3), concentrate pellets (2), and cut green herbage (red clover, Italian ryegrass, and a mixture of perennial ryegrass and white clover). The main findings are summarized below.

- (1) For a given feed and an individual animal, there was a direct relationship between the amount eaten and both the extent and persistence of the changes in form of the sequences during feeding. The relationship between intake and persistence was particularly marked.
- (2) The changes in form were most complete and most persistent when the feed was coarse hay. Reversion to the fasting form could take as long as 24 hr following an intake of approximately 1 kg of coarse meadow hay.
- (3) In contrast, the changes in form were least complete and least persistent when the feed was pelleted meal. If the pellets disintegrated readily in the stomach, reversion to the fasting form of the sequences could occur in less than 4 hr following an intake of approximately 1 kg.
- (4) A range of intermediate effects occurred when the feed was cut green herbage. In general, the higher the dry matter ratio of the herbage, the more persistent the changes in form of the sequences. If fasted sheep were put out to graze, the changes in motility appeared to be similar to those seen when cut herbage was fed in the stalls.
- (5) The frequency of contraction sequences during the first 20 min of feeding was related to the palatability of the feed. The more palatable a feed, the more rapidly was it eaten and the greater the frequency of contractions.

## DISCUSSION

Relationships between the diet — the nature of the food and the quantity eaten — and the motility of the forestomachs of the sheep have been described in this paper. Such relationships will not be restricted to the forestomachs, nor are they peculiar to the sheep. Rather, they are of a fundamental character, playing an important part in the normal regulation of gut function. Relationships between diet and gut motility have long been known in non-ruminants. We have paid scant attention to them so far in our considerations of the functioning of the ruminant digestive tract.

Any definition of the relationships between diet and gut motility must start with a definition of the motility itself. It is for this reason that much of the present paper is devoted to description of the two contrasting states of the motility of the reticulum and rumen. Briefly, it would appear that there is something akin to a basal state of the motility of the reticulum and rumen of the sheep, seen only in well-fasted animals. Specific changes occur in the "basal" motility when the animal is fed. It is the extent or degree of these changes and their persistence after feeding stops that are influenced by dietary factors.

The observations themselves must be regarded as preliminary and qualitative in nature. They are incomplete for several reasons. First, the present studies were limited to the lateral walls of the reticulum and rumen: the motility of other structures and regions of the forestomachs must also be studied. Secondly, the trials with different feeds were only cursory: a systematic investigation is required, comparing a wider range of feedstuffs more fully defined, chemically and physically. Thirdly, only two dietary factors were considered; the type of feed and the amount eaten in one meal: other factors should also be considered, such as the frequency of meals, and the quantity and nature of feed residues in the lower gut. Fourthly, no account was taken of animal factors such as size, age, condition, or metabolic state. Lastly, no attention was paid to microbiological factors influencing the rate of breakdown of the feed in the forestomachs.

Only two aspects will be discussed further here, the cause of the changes in motility during feeding, and their likely effects on gastric functions.

## THE ORIGIN OF THE CHANGES IN MOTILITY DURING FEEDING

The changes in motility of the reticulum and rumen during feeding are most probably of reflex origin.

The co-ordinated contractions of the forestomachs are initiated by the activity of gastric motor centres situated in the hind-brain, from which nerve impulses pass down the vagus nerves to the stomach. In addition to its motor or efferent innervation, the stomach has a sensory or afferent innervation. Sensory nerve endings are present in the walls of all the compartments of the stomach, as they are, too, in all other regions of the digestive tract. The nerve impulses arising from the sensory endings are conducted by afferent nerve fibres to the brain where their effects come to bear on the gastric motor centres. This afferent input can modify the activity of the motor centres: that is, stimulation of the sensory endings in the gut can evoke reflex changes in the motility of the stomach. The effects of a given stimulus may be excitatory, inhibitory, or a mixture of both. It appears that the summed effects, excitatory and inhibitory, of the afferent input to the motor centres play a major part in determining the pattern of motility exhibited by the reticulum and rumen at any given time (see Titchen, 1958b, 1960; Stevens and Sellers, 1959; Comline and Titchen, 1961).

During feeding, the afferent input to the motor centres will be altered as a result of the sensory stimulation afforded by the acts of eating and swallowing feed and by the presence of the ingested feed within the gut. Two of the kinds of stimuli likely to be involved — tactile stimulation and stretch of the walls of the reticulum and rumen — were shown in other experiments (Reid, 1962) to be capable of inducing changes in the motility of the reticulum and rumen. The sheep used in these latter experiments had, in addition to the exteriorizations, a rumen fistula. Tactile stimulation was provided by gently rubbing the lining of the reticulum or rumen with a blunt rod, stretch by inflating rubber balloons inside the stomach, or by passing gas into the stomach.

The responses to tactile stimulation were complex and variable. They depended on the state of the animal at the time of stimulation, the region of the stomach to which the stimulus was delivered, and the intensity, duration, and frequency of repetition of the stimulus. The most marked responses were obtained in fasting sheep. In these animals, the effects included regurgitation (usually but not invariably, accompanied by rumination), an increase in the frequency of both A and B sequences, and a change in the form of the sequences towards the form seen in feeding animals. This last effect would seem of particular

significance in connection with the observations made on the influence of diet on the motility: feeds, such as coarse hays, which might be expected to afford a high degree of tactile stimulation to the stomach lining were associated with the most complete and most persistent changes in the form of the contraction sequences.

The responses to stretch were also complex and also dependent on the experimental conditions. There was a prominent differential effect on the contraction sequences. Distension of the reticulum was excitatory to A sequences but inhibitory to B sequences, which might disappear completely. On the other hand, distension of the rumen was excitatory to B sequences and possibly inhibitory to A sequences. The more generalized stimulus of distending the stomach with gas resulted in a mixture of these effects. Similar responses to stretch have been obtained in experiments with decerebrate sheep (Reid and Titchen, pers comm.).

Clearly, tactile stimulation and stretch of the walls of the reticulum and rumen are efficacious forms of stimulation in this context. They can bring about changes in the frequency and form of co-ordinated contractions, and in the relative proportion of A and B sequences, all of which are features of the changes in motility during feeding. It must be emphasized, however, that these are not the only kinds of stimuli that arise when the animal feeds, nor are sensory endings restricted to the reticulum and rumen. Further, important as it may be, the afferent input from the gut is not the only factor influencing gastric motility. Thus the gastric motor centres are also affected by the activity of higher centres in the brain. In addition, nerve and muscle cells are sensitive to changes in the composition and reaction of the fluids which bathe them. Such changes in the tissue fluids will occur as a result of the digestion of food in the gut. At present, we have little knowledge as to their extent, still less as to their effects on gastric motility.

#### THE EFFECTS OF THE CHANGES IN GASTRIC MOTILITY ON GASTRIC FUNCTIONS

The outstanding feature of digestion in the ruminant forestomachs is that it is a continuous flow fermentation process. Fresh feed is added before the breakdown of the feed already ingested is complete. The stomach normally contains the residues from a number of meals in various stages of digestion; it is never empty.

The motility of the reticulum and rumen appears to play an important part in helping to maintain the continuous nature of the fermentation. Probable ways in which it performs this function are:

- (1) By helping to disperse the mass of chewed, ensalivated feed swallowed during eating;
- (2) By mixing and circulating the stomach contents, thus ensuring continual inoculation of the feed fragments, as well as promoting efficient buffering;
- (3) By assisting in the disintegration of the feed fragments,
  - (a) by rubbing them together and against the stomach walls, and
  - (b) by taking part in rumination; and
- (4) By aiding the removal of the products of digestion,
  - (a) by continually changing the portion of the contents in contact with the stomach wall, thus facilitating direct absorption,
  - (b) by taking part in the eructation of gas, and
  - (c) by assisting the transfer of digesta to the omasum, and so on to the rest of the gut.

Any marked change in the motility might be expected to affect the efficiency of digestion in the forestomachs. However, while the actions of the motility listed above may seem self-evident, they are presumed and their importance is largely unproven. It is well established that section of the vagus nerves, which abolishes the motility, results in the accumulation of gas and semi-digested feed in the forestomachs (Duncan, 1953; Habel, 1956). Similarly, bloat is a well-known consequence of paralysis of the stomach in hypocalcaemia. On the other hand, hypermotility of the forestomachs in cows with adhesions between the reticulum and the diaphragm is associated with an excessive comminution of feed residues, the stomach contents having the consistency of thick pea soup (D. C. Blood, pers. comm.). These are grossly abnormal states: any evidence they may offer regarding the actions of the motility of the reticulum and rumen is confounded by the diversity of their effects. Of the functions of the motility in the normal animal, and the efficiency with which they are carried out, we know little.

The effects of the changes in motility seen during feeding must at present, therefore, be a matter of speculation. It is obvious that the degree of agitation of the stomach contents must be considerably increased. It is probable,

too, that the changes in form of the contraction sequences will lead to changes in the manner of circulation of the contents within the stomach. What the effects are on the processes of digestion, whether significant differences in the degree of such effects result from the differences in motility associated with the ingestion of different feeds, and the extent to which such differences in degree are involved in the differences in the efficiency of conversion of the different feedstuffs to meat, milk and wool, have yet to be determined.

A practical difficulty in the investigation of relationships between gastric motility and gastric function has been that of measuring the motility in quantitative terms. It is insufficient to measure the frequency of contractions without regard to their magnitude, or to measure the motility of one part of the stomach without regard to the motility of the organ as a whole. None of the present methods of recording gastric motility can be regarded as fully satisfactory. However, partial exteriorizations offer distinct advantages over the more common methods. Direct mechanical recording of the motility can be carried out simultaneously from several well-defined and easily-accessible points on the stomach wall. A further, important advantage is that no apparatus is inserted in the stomach: the risk of experimental artefacts is thereby greatly reduced.

#### ACKNOWLEDGEMENTS

I acknowledge with pleasure the assistance and encouragement given to me by Dr D. A. Titchen of the Physiological Laboratory, Cambridge University.

Miss M. Soulsby of the Grasslands Division, D.S.I.R., assisted in the preparation of the figures. The photographs in Fig. 2 were taken by P. Starling of the Physiological Laboratory.

Part of this work was carried out with financial assistance from the Agricultural Research Council (U.K.).

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## DISCUSSION

Q: *If, in the fasting animal, the A sequence does not always involve the posterior ventral blind sac, will the B sequence always start at the posterior ventral blind sac?*

DR C. S. W. REID: Yes. The contraction of the posterior ventral blind sac is a fundamental part of the B sequence, as the contraction of the reticulum is of the A sequence. If the blind sac is not involved in the preceding A sequence, the B sequence then starts with an independent contraction of the blind sac. Even when the blind sac is involved in the preceding A sequence, the B sequence may start independently in this fashion.

Q: *Would Dr Reid define the location of the gastric motor centres in the hind-brain?*

DR REID: The site and organization of the medullary centres controlling the motility of the ruminant stomach have not yet been satisfactorily defined. References to the main papers on the subject may be found in Dussardier, M., Flinois, J., and Rousseau, J. P. (1960): *J. Physiol.* (Paris), 52: 90.

Q: *Has any work been done using these methods to show the effects of saponins or other specific plant extracts on rumen motility?*

DR REID: No. Animals with partial exteriorizations of the reticulum and rumen would be valuable subjects for such investigations. They have been used to observe the effects on the motility of some common pharmacological agents, including adrenalin, histamine and atropine.

Q: *Dr Reid's paper dealt with the sheep. Has he any comparative data for the cow?*

DR REID: Not yet. A separate study of the relationships between diet and gastric motility in the cow is needed because of the differences in the anatomy and motility of the forestomachs of the sheep and cow, and because of the differences in husbandry of the two species.

Q: *The A sequence records show a small peak before the main peak of contraction in the reticulum. Is this an indication that a double contraction does take place in the reticulum?*

DR REID: Yes.