Factors Affecting the Utilization of Food by Dairy Cows

4. The Action of the Reticulo-Omasal Orifice

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In any part of the digestive tract the time available for the breakdown and absorption of food is determined by the rate at which food residues pass through that piece of the gut. The reticulo-rumen is a major site of digestion in the cow and the digestion of food, particularly the crude fibre fraction, is affected by changes in the rate of passage of the food through the reticulo-rumen, provided there are no compensating changes in the rate of breakdown of the food (Balch, 1950; Balch & Johnson, 1950). Since undigested food can pass from the reticulo-rumen to other parts of the digestive tract only through the small reticulo-omasal orifice, the movements of this orifice are likely to influence the rate of passage of food.

The material passing through the reticulo-omasal orifice must come from the reticulum and possibly from the anterior part of the rumen. It will, therefore, tend to contain 90–95 % water (Balch, 1950), particles of solid food and micro-organisms in suspension and substances in solution.

Several observations suggest that there is a steady flow of digesta through the reticulo-omasal orifice throughout the day. Paloheimo (1939) slaughtered cows at intervals after giving them chromium sesquioxide, and found that the passage of this very heavy substance to the omasum had begun even in those cows killed immediately after administration. Phillipson (1946) suggested that there must be a constant flow of digesta through the reticulo-omasal orifice because the omasum, abomasum and intestines contain digesta at all times. In sheep the flow of digesta from the abomasum was found to be in gushes with usually less than 15 min. between each gush (Phillipson, 1948), which also suggests a continuous flow of digesta from the reticulo-rumen.

The forces that activate the passage of digesta from the reticulo-rumen to the omasum are not fully understood. Wester (1926) and Schalk & Amadon (1928) considered that the movements of the omasum play an important part in drawing semi-liquid digesta through the reticulo-omasal orifice into the omasum, but Phillipson (1946) did not support this contention. Both Wester and Schalk & Amadon described a sudden fall in pressure at the top of the pressure gradient in the omasum, illustrating the fall with kymograph records of varying clarity. Wester also gave a kymograph record of the contraction of the reticulo-omasal orifice.

The present experiments were undertaken in order to study, in greater detail than was given by Wester or Schalk & Amadon, the relationship between pressure changes

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in the reticulo-rumen, reticulo-omasal orifice, omasum and abomasum and to discover whether these relationships were affected by any of the normal activities of the cow. It seemed likely that such a study would aid understanding of the forces activating the passage of digesta from the reticulo-rumen.

METHODS

The experiments were conducted on the two Shorthorn cows with rumen fistulas that had been used in earlier experiments of this series (Balch, 1950; Balch & Johnson, 1950; Balch & Kelly, 1950). Of these, cow W (Winsome) was receiving a daily diet of 9 kg. hay and cow Y (Halora) one of 7·7 kg. hay and 8·2 kg. concentrates. Cow Y was producing about 16 kg. milk daily.

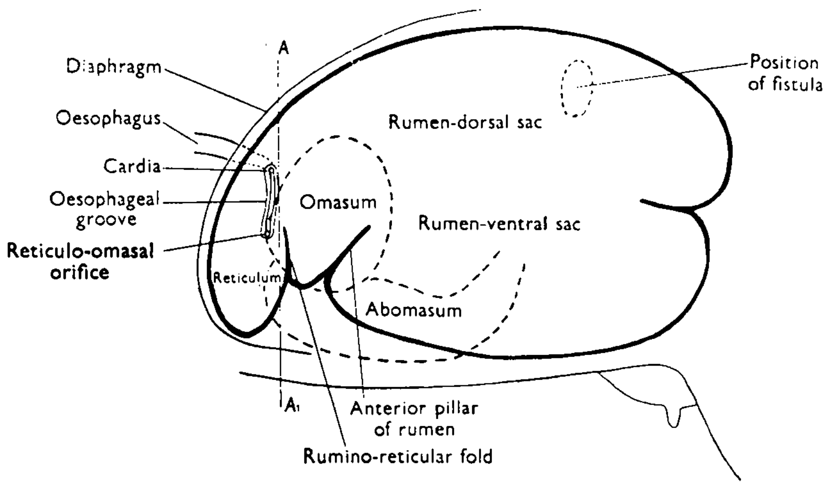


Fig. 1. Diagram showing the approximate position of the reticulo-rumen, against the left side, and the omasum and abomasum, against the right side, in the cow. A–A_1 is the approximate position at which the section shown in Fig. 2 cuts the median plane.

Records of gastric movements and of the movements of the reticulo-omasal orifice were made by means of lightly inflated toy balloons operating tambours. The tambours were placed vertically in an Evershed and Vignoles operation recorder (Evershed and Vignoles Ltd., Acton Lane, Chiswick) (Pl. 1) giving ink records on ruled white paper 60 ft. long. With tambours in this position it was necessary to add small weights on short projections at right angles to the levers supporting the writing points. The weights ensured that the levers remained in contact with the triangles of cork on the membranes of the tambours. The entire apparatus, enclosed in a dust-proof cover measuring 50 × 20 × 20 cm., was permanently attached to the cowshed wall.

The position of the reticulo-omasal orifice is shown diagrammatically in Fig. 1. The activity of the orifice was studied in relation to the activity of the reticulum, the anterior pillar of the rumen, the neck of the omasum and the abomasum. The positions of the various balloons are shown diagrammatically in Fig. 2. Balloons were maintained in the reticulum by means of a 1 kg. brass weight. They were held by hand near the anterior pillar of the rumen and were fixed in the omasum and in the reticulo-omasal orifice by means of an 'anchor'. The 'anchor' consisted of a circle (diameter 5·5 cm.) of 0·3 cm. brass welding rod, which was inserted in the omasum. A 6·5 cm. shank was attached to a cross-piece, forming a diameter of the circle and passed through the orifice. The balloon detecting orifice movements lay along the shank of the anchor. Balloons were placed in the abomasum by means of wire guides but once in position, at a point 60 cm. from the reticulo-omasal orifice, they needed no further support.

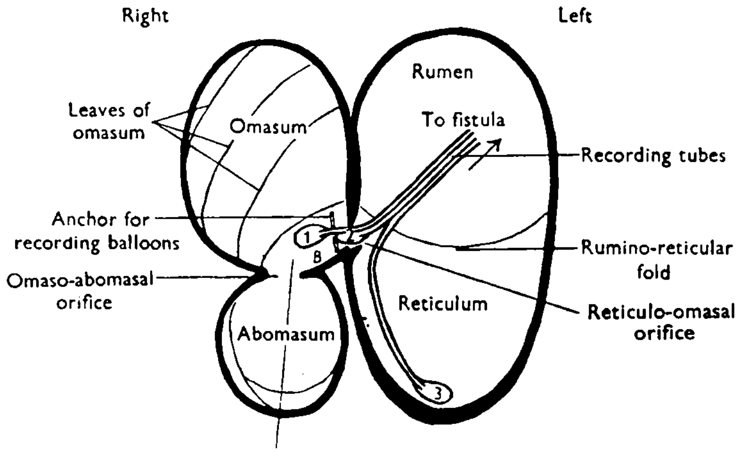


Fig. 2. Diagrammatic vertical cross-section in a slightly oblique plane passing through the reticulo-omasal and omaso-abomasal orifices and cutting the median plane approximately at A–A_1 in Fig. 1. The positions of the recording balloons are shown in: 1, the omasum; 2, the reticulo-omasal orifice, and 3, the reticulum. The bridge of the omasum is marked B.

Preliminary estimates of absolute pressures in the reticulum and abomasum were made. For this purpose a single tambour was used, and the recording balloon was replaced by a metal membrane-holder. This holder was shaped like a thistle funnel, a rubber membrane being stretched across the cup (diameter 2·5 cm.), and the recording tube attached to the tube. Before and after recording, the tambour was calibrated by placing the recording surface and tube inside a large vessel, maintained at rumen temperature, in which pressures could be varied. Pressures in this vessel were measured by means of a mercury manometer.

RESULTS

Pressure changes in the reticulo-omasal orifice and in the compartments of the stomach

During rest. Changes of pressure in the reticulum, the reticulo-omasal orifice and the omasum of the two cows while they were standing at rest are shown in Fig. 3. The reticulum showed the usual double contraction at a rate of about sixty/hr. The omasum showed a typical rather slow rise and fall in pressure beginning before the reticulum contractions. Near the peak of high pressure in the omasum there was a sudden and very marked fall which invariably coincided with the second reticular contraction. This fall was of short duration and the high pressure was regained, usually reaching a somewhat higher peak than had been recorded before the drop. The balloon in the reticulo-omasal orifice recorded a varying amount of movement at the time of the first reticular contraction. At the time of the second reticular contraction there was a drop in pressure in the orifice, immediately followed by a powerful contraction. Palpation showed that the reticulo-omasal orifice was normally loosely open, the first

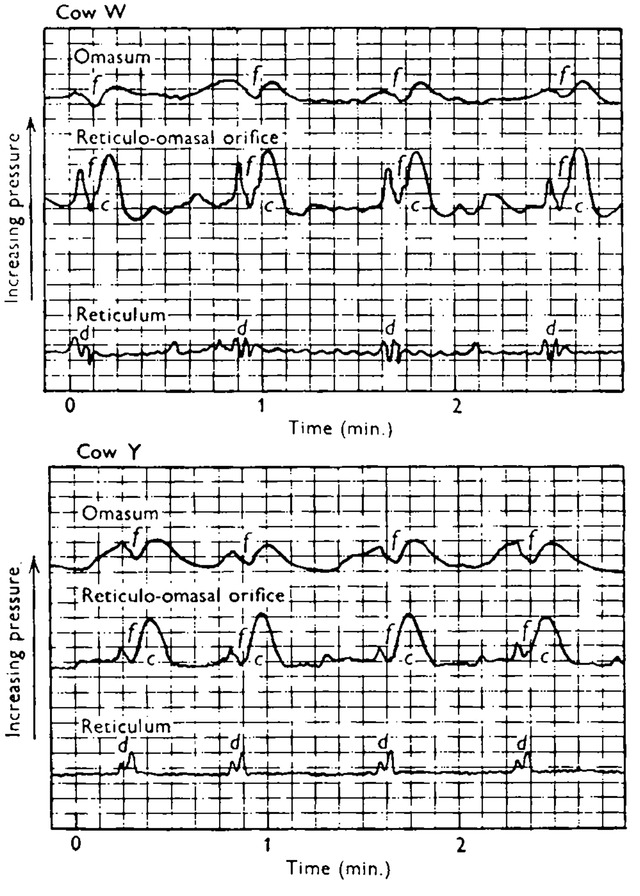


Fig. 3. Pressure changes in the reticulum, the reticulo-omasal orifice and the omasum of two cows at rest. The double contraction of the reticulum (*d*), the sudden fall in pressure in the omasum and in the reticulo-omasal orifice (*f*) and the powerful contraction of the orifice (*c*) are shown.

small peak of pressure recorded by the balloon being due to movement of the surrounding muscular wall. During the first reticular contraction the larger movement was a powerful closing of the orifice. Similar observations were made by Wester (1926).

During eating. During eating the rate of contraction of the reticulum was considerably increased, often reaching a rate of 105 double contractions/hr. However, the movements of the reticulo-omasal orifice and of the reticulum continued to bear the same relationship to the contractions of the reticulum as they did when the cow was at rest.

During rumination. During rumination the reticulum has an extra contraction which precedes the two normal contractions and forms an essential part of the regurgitation reflex. This contraction was recorded by the balloon in the reticulo-omasal orifice as an additional small movement preceding the main contraction of the orifice (Fig. 4). In other respects the relationships of the pressure changes in the reticulum, the omasum

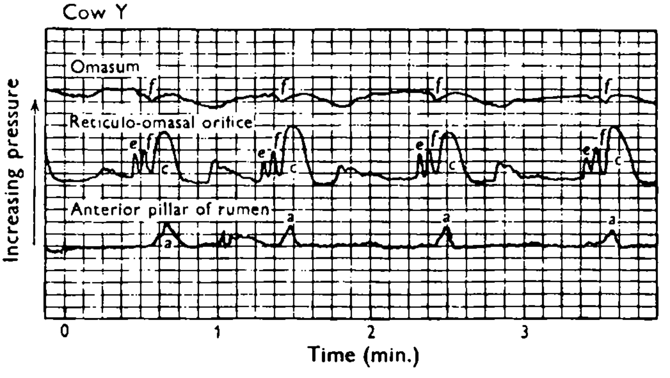


Fig. 4. Pressure changes near the anterior pillar of the rumen, in the reticulo-omasal orifice and in the omasum of cow Y during rumination. The extra contraction of the reticulum during regurgitation (*e*), the sudden fall in pressure in the omasum and in the reticulo-omasal orifice (*f*), the powerful contraction of the orifice (*c*) and the contraction of the anterior pillar of the rumen (*a*) are shown.

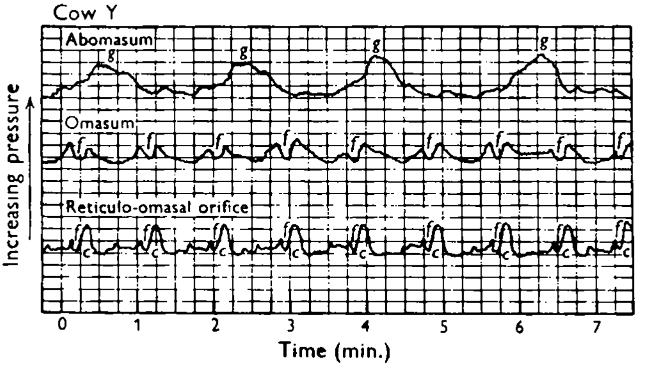


Fig. 5. Pressure changes in the reticulo-omasal orifice, the omasum and the abomasum of cow Y lying at rest. The sudden fall in pressure in the omasum and in the reticulo-omasal orifice (*f*), the powerful contraction of the orifice (*c*) and the peak of pressure in the abomasum (*g*) are shown.

and the reticulo-omasal orifice were the same during rumination and during rest although the cycle of activity occurred typically at about fifty contractions/hr. Fig. 4 shows that the powerful contraction of the reticulo-omasal orifice coincided with the contraction of the anterior pillar of the rumen.

During lying. When the cows lay down there was a slight increase in the basal pressure, and respiratory movements were more prominent in the recordings from all the stomach compartments. The changes of pressure in the various parts continued unchanged in the manner described above (Fig. 5).

During drinking. When the cows drank water, from cowshed drinking bowls, the general pattern of pressure changes in the reticulum, the reticulo-omasal orifice and the omasum remained unchanged (Fig. 6). During drinking the contraction of the orifice appeared to be slightly less powerful than during resting. Frequent palpation established that in these two cows the act of drinking was accompanied by a considerable stiffening and raising of the lips of the oesophageal groove; water flowed down the groove to some extent but could be felt escaping at the lower end into the reticulum and anterior rumen; water did not appear to pass into the omasum to any considerable degree.

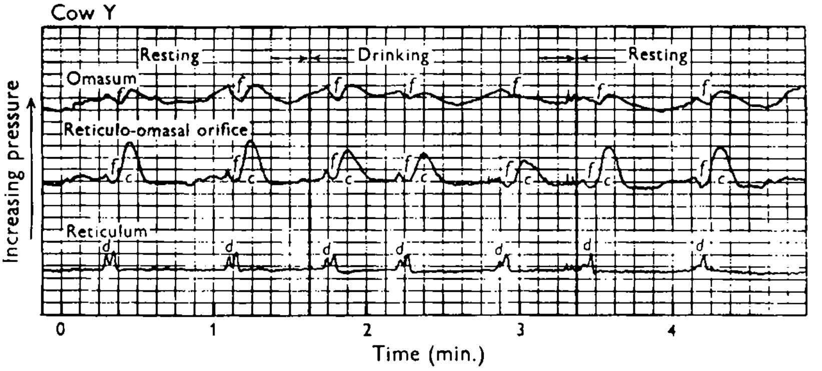


Fig. 6. Pressure changes in the reticulum, the reticulo-omasal orifice and the omasum of cow Y at rest and during drinking. The double contraction of the reticulum (*d*), the sudden fall in pressure in the omasum and in the reticulo-omasal orifice (*f*) and the powerful contraction of the orifice (*c*) are shown.

During milking. During milking there was no characteristic change in the pattern of pressure changes in the reticulum, the reticulo-omasal orifice or the omasum. It was sometimes noticed that when a cow was milked there was a fall in basal pressure in the reticulum and an increase in the amplitude of the double contraction, but similar changes were also observed at other times.

The relationship between the contractions of the reticulo-omasal orifice, of the abomasum and of the anterior pillar of the rumen

The main contraction of the reticulo-omasal orifice coincided with the contraction of the anterior pillar of the rumen (Fig. 4). The data collected in this investigation are insufficient to indicate whether the two movements were linked directly or only indirectly by virtue of their both being initiated by the same pace-maker, which could have been either the reticulum or the omasum.

Only limited recordings of abomasal pressure changes have been made. The abomasum sometimes appeared to have a slow peristaltic type of movement with peaks every 2–4 min. A good example obtained when cow Y was lying down at rest after her evening meal is shown in Fig. 5. These were presumably the peristaltic waves that occur at the pyloric end of the abomasum (McAnally & Phillipson, 1944). There was no apparent relationship between the cycle of movements in the reticulo-omasal orifice and the movements of the abomasum.

Absolute pressures in the reticulum, omasum and abomasum

The recording of absolute pressures in these organs was considerably hampered by shifting of the base-line after calibration, due apparently to expansion of the air in the recording tube caused by the heat of the animal's body. This difficulty was partly overcome by calibrating in a vessel at rumen temperature. The results, which must be regarded as preliminary estimates, suggest that the mean pressure in both the reticulum and abomasum at the time of recording, which was always between the hours of 9·0 a.m. and 6·0 p.m., was within the range 2·5–3·5 cm. mercury above air pressure. During the double contraction of the reticulum, increases in pressure of 1–2 cm. mercury were recorded. The pressure in the abomasum varied from its mean by about $\pm$0·7–1·0 cm. mercury. This suggests that for periods of perhaps 2 min. at a time the pressure in the abomasum was lower than the basal pressure in the reticulum. At the time of the reticular contraction, pressure in the abomasum was also usually lower than that in the reticulum.

Movement of small supported balloons and of the recording capsule used for estimating absolute pressures in the omasum, where they had remained for a considerable period, to the reticulum showed that the characteristic drop in pressure at the height of the wave of pressure in the omasum was frequently to a pressure lower than that recorded in the reticulum at the time of the last reticular contraction.

DISCUSSION

The movements of the reticulo-omasal orifice were shown to bear a very constant and characteristic relationship to the pressure changes in the reticulum and omasum. The pattern was found to continue without interruption when the animal was resting, eating, ruminating, drinking, lying down, or being milked.

The reticulum had the usual short, powerful, double contraction, preceded in rumination by an additional contraction at the time of the regurgitation. The omasum exhibited a slow rise and fall in pressure with a highly characteristic drop in pressure at about the highest point. This drop never exceeded the main fall between cycles of activity and coincided with the contraction of the reticulum. It reached its lowest point about 3 sec. after the last contraction of the reticulum. The frequency of the cycles of pressure changes in the reticulum and omasum varied considerably, being fastest during eating (up to 105/hr.) and slowest during rumination (typically, about fifty/hr.).

The reticulo-omasal orifice remained loosely open for 60–70 % of the time occupied by the co-ordinated cycles of pressure changes in the reticulo-rumen and omasum. In each cycle there was, during resting, an increase in pressure in the orifice at the time of the first reticular contraction. During rumination this increase was preceded by a similar increase in pressure at the time of the extra reticular contraction. At the time of the last reticular contraction pressure in the orifice fell to a point on, but never below, the base-line recorded between cycles of activity.

The greatest differential pressure between the reticulum and the abomasum occurred at the time of the reticular contraction and was probably about 1 cm. mercury. At this time a flow of digesta might be expected. The rate of such a flow has been expressed on theoretical considerations as a function of the differential pressure, and the resistance between the two regions (Werle, Brody, Ligon, Read & Quigley, 1940–1)

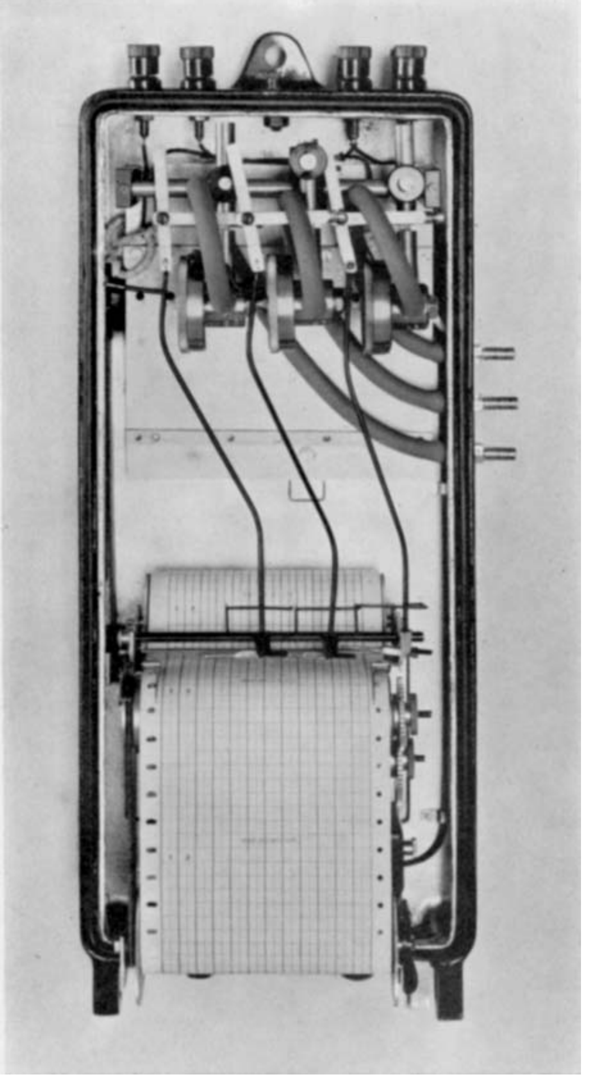
$$\text{Rate of flow} = K \times \frac{\text{pressure } A - \text{pressure } B}{\text{resistance to flow}},$$

where A = pressure in compartment being evacuated and B = pressure in compartment into which food is flowing.

In the cow the distance between the reticulo-omasal and omaso-abomasal orifice is about 10 cm. (Ellenberger & Baum, 1926). It is not clear whether the passage from the reticulum to the omasum should be considered a one-stage process with the digesta in the neck of the omasum providing merely a resistance to the flow, or whether it should be considered a two-stage process, with the digesta in the omasum, and possibly a contraction in the region of the bridge of the omasum (Wester, 1926) preventing an uninterrupted flow. In either instance it is likely that the transfer of digesta would occur at the time of the last reticular contraction and would be a continuous process occurring most rapidly during eating.

In view of the solid nature of digesta in the neck of the omasum, as found by palpation through the reticulo-omasal orifice, it seems likely that the transfer of digesta from the reticulum to the abomasum was in two stages, controlled by a valve-like action of the omasum. We feel that in further investigations on this point the following hypothesis should be borne in mind. During each cycle of movement the first rise in pressure in the omasum may have represented a constriction of digesta in the neck, and possibly a movement of digesta onward to the abomasum. At the time of the fall in pressure in the neck of the omasum, semi-liquid digesta may have entered from the reticulum and with the resumption of high pressure in the omasum there may have been a transfer of digesta to the abomasum, backflow to the reticulum being prevented by the closed orifice. It also seems likely that, during the periods of high pressure in the neck of the omasum, liquid, and not solid as suggested by Wester (1926), would tend to be squeezed between the leaves of the omasum as if the digesta were pressed against a sponge. The particles of solid which are undoubtedly to be found on post-mortem examination between the leaves may represent only the particles that would inevitably be carried by accident with the liquid. The contents of the omasum represent only 7–8 % of the contents of the whole stomach (Schalk & Amadon, 1928); if, therefore, all digesta were to pass between the leaves, such passage would need to be very rapid, but the fact that no mechanism by which digesta may be expelled from between the leaves has yet been described suggests that there is no such rapid expulsion and that much of the solid digesta does not pass between the leaves.

The reticulum is the pace-maker for the cycle of movements which involves the reticulo-rumen. Recordings taken during this study showed that some part of the omasum invariably began to contract before the reticulum, suggesting that the omasum may have been the pace-maker for the reticulum. Further support for this theory is provided by an observation by Wester (1926), that the contractions of the reticulo-rumen could be stopped by applying pressure to the bridge of the omasum.



If a cow were receiving a diet containing 10 kg. dry matter daily, of which 60 % was digested, and if 50 % of the total digestion of dry matter occurred in the reticulo-rumen, then 7 kg. dry matter would have to pass through the reticulo-omasal orifice each day. If the mean rate of reticulum contraction were sixty/hr. the mean flow of dry matter through the orifice would be 4·6 g. per cycle of contraction. The mean dry-matter content of reticulum contents is about 6 % (Balch, 1950). It is likely, therefore, that about 80 ml. water would also pass through the orifice at each contraction, or more than 100 l./24 hr.

SUMMARY

1. A description is given of a simple type of kymograph suitable for taking tambour readings over periods of up to 24 hr.

2. The movements of the reticulo-omasal orifice in relation to the contractions of the reticulum, the anterior pillar of the rumen, the omasum and the abomasum were studied by means of small, lightly inflated balloons.

3. During resting, eating, ruminating, lying, drinking and while the cow was being milked, the reticulo-omasal orifice functioned to a constant pattern. For the greater part of the reticulo-ruminal cycle of contraction the reticulo-omasal orifice was loosely open, but following the last reticular contraction the orifice closed strongly.

4. The last reticular contraction was accompanied by a marked fall in pressure in the neck of the omasum, followed by a marked rise of pressure in the omasum which coincided with the closure of the reticulo-omasal orifice.

5. The transfer of digesta from the reticulum and anterior rumen was most likely to occur at the time of the last reticular contraction, coinciding with the fall in pressure in the omasum. It is therefore probable that the passage of digesta from the reticulo-rumen is relatively continuous throughout the 24 hr. and is largely controlled by the valve-like action of the omasum.

We wish to thank Dr S. Bartlett for his support of this work and for arranging that two of us (A.K. and G.H.) should do it while visiting this Institute. We are also much indebted to Dr A. T. Phillipson of the Rowett Research Institute who read the manuscript and offered most valuable suggestions. We also wish to thank Messrs Evershed and Vignoles Ltd., Acton Lane, Chiswick, for their advice on the choice of the recorder and Mr H. S. Hall and his staff in the Engineering Department of this Institute for carrying out the modifications. We are grateful to Mr N. Gruber for his care in photographing the apparatus.

EXPLANATION OF PLATE

Pl. 1. Front view of the instrument for recording pressure changes in the stomach of a cow. Three tambours are clamped to a crossbar at the top. The compensating weight on a projection from the writing arm can be seen clearly in the left-hand tambour. The paper moves forwards and downwards. In this view the lid of the instrument has been removed.

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Excretion of Vitamin C in Urine Following Repeated Administration of Big Test Doses

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The vitamin C saturation test as introduced by Harris & Ray (1935) is based on counting the number of days necessary for administration of standard test doses of vitamin C before a large overflow of the vitamin appears in the urine, this number increasing in proportion to the lowness of the past intake. For convenience in examining large groups of subjects, a simplified procedure, involving the collection of a single specimen of urine each day during the peak of excretion rather than of the whole day's output, was recommended by Harris & Abbasy (1937) as sufficiently accurate for routine surveys. Thus modified, the saturation test is easily applicable to group surveys and has been found capable of distinguishing between groups of children or adults at slightly different levels of intake (e.g. Harris, 1940, 1943; Atkins, 1943). The procedure adopted by various workers has, however, differed somewhat, not only as to the size of the test dose but also in choice of excretion period.

In carrying out a small-scale survey using the simplified saturation test as outlined by Harris & Abbasy (1937), it was thought that some supplementary tests, involving the estimation at graded intervals of the total 24 hr. output, might be of interest. This would give some idea of the relation in time between the peak of excretion on approaching saturation and the test period selected (e.g. a 3 hr. period, from the 4th to the 7th hour after the test dose); at the same time information might be obtained about the reliability of this short-period excretion as a criterion of the total overflow.

EXPERIMENTAL

Subjects and their treatment. Five male students at a residential college, 20–21 years of age were given big test doses of ascorbic acid by mouth on each of 4 consecutive days (6–9 June 1950).