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ABOMASAL SECRETION AND EMPTYING IN SUCKLED CALVES

By R. W. ASH*
From the Rowett Research Institute, Bucksburn, Aberdeen

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The rumen, reticulum and omasum, the first three compartments of the compound stomach of ruminants, do not develop fully and assume their characteristic digestive functions until the young animal begins to ingest substantial quantities of solid food. When the young calf swallows milk nearly all of it bypasses the reticulo-rumen and flows rapidly through the omasum and into the abomasum as a result of reflex closure of the oesophageal groove.

From the point of view of digestive functions the suckled calf is regarded as a monogastric animal but there does not appear to have been a systematic investigation of the events occurring in the abomasum following a milk feed. A few studies have been made on the secretory responses of abomasal pouches in suckled calves but there is no general agreement concerning the chief factors influencing secretion (Espe & Cannon, 1937; Shoptaw, Espe & Cannon, 1937; Grosskopf, 1959). A possible explanation for this is that the age of the calves used by the different workers ranged from a few weeks to several months and the type of preparation, the stimuli, and the experimental conditions also differed.

The experiments reported in this paper were an attempt to define some of the major stimuli influencing abomasal secretion in calves and to provide an account of the sequence of events occurring in the abomasum following the ingestion of milk.

METHODS

Animal preparations and maintenance. Ayrshire bull calves 3–7 days old were obtained from the Rowett Institute dairy herd and from other farms where there was a high standard of calf husbandry. Strong and vigorous calves were selected and they all underwent a period of acclimatization to experimental conditions before any operations were carried out. They were housed in individual pens in a heated (approximately 15° C) experimental room and the bedding material was wood shavings. The feeding times were 9.0 a.m., 12.30 p.m. and 4.30 p.m. when cows' whole milk warmed to 39° C was sucked from a bottle which was fitted with a teat. The volume of milk given at each feed was restricted to 560–1100 ml. and, with one exception, diarrhoea and digestive disturbances were not a problem.

Pentobarbitone injected intravenously was used to anaesthetize the calves and glucose-saline was infused continuously throughout the operations. Three calves were fitted with

* Present address: A.R.C.Institute of Animal Physiology, Babraham, Cambridge.

innervated abomasal pouches (Hill & Gregory, 1951) and a small ebonite cannula was inserted into the main body of the abomasum. The operations were performed when the calves were 11, 17 and 34 days old. An attempt to carry out the operation on a calf with diarrhoea failed. Three other calves, 10–11 days of age, were fitted with plastic re-entrant cannulae (Ash, 1962) in the duodenum, immediately posterior to the pyloric sphincter.

Immediately the operations were completed the barbiturate antagonist β-ethyl-β-methyl-glutarimide sodium was injected to aid recovery from the anaesthetic. One calf was able to suck from a bottle 4 hr after the operation but the others were insufficiently recovered until the following morning. On the first day after the operation 200 ml. of 3 % (wt./vol.) glucose solution was sucked four times daily. The next 2 days whole milk was diluted with equal volumes of water and 5 g glucose was added to each 200 ml. feed. Thereafter whole milk was given without the addition of glucose, so that within 7 days a three times daily feeding régime was resumed. During the recovery period, which was remarkably rapid and uneventful, 1 g terramycin/day was injected intramuscularly.

In order to prevent the calves from eating bedding material while maintained entirely on milk they were transferred to metabolism cages made of metal and fitted with wire mesh floors (Duthie, 1959). Experiments began not sooner than seven days after the operations and were continued for 17–28 days. Subsequently the animals were allowed access to dried grass and an appropriate ration of a cereal mixture was given once or twice daily.

All the calves were maintained in a healthy condition but the useful experimental life of those fitted with re-entrant cannulae ended when substantial quantities of solid food were ingested. Apparently the cannulae were too small to conduct the large volumes of food material and leakage from the proximal fistula became excessive.

Collection and sampling. Secretions from the pouches, samples of abomasal contents and measurements of the flow of material from the abomasum were obtained by methods described previously (Ash, 1961*a*). A permanent record of the physical nature of the material leaving the abomasum was obtained by storing representative samples in a centrifuge tube and photographing them.

Analytical. The methods used for estimating pH, total titratable acidity and steam-volatile fatty acid have been described (Ash, 1961*a*). Proteolytic activity in the pouch secretion was estimated by the method of Hunt (1948). Single estimations only were made since in most instances the volume of secretion was small. The clotting activity of the secretion was measured by a method similar to that described by Berridge (1952*a*, *b*). Ten millilitres of cows' whole milk was incubated in a water bath at 39° C for 15 min and 0·25 ml. of secretion was added from a syringe. The tube containing the milk and added secretion was rotated continuously by a mechanical device and the time taken for the milk to clot was noted. This value is equivalent to the measurement of a concentration of an enzyme system and therefore due account must be given to volume changes before interpreting changes in secretory activity. The ratio of milk to secretion adopted seemed reasonable in view of the volume of juice secreted by the pouch and the volume of milk ingested. The milk used for estimating clotting activity was a sample of that fed to the calves and was usually obtained from the bulked milk supply of the Institute dairy herd; occasionally it was obtained from an individual cow. The osmotic pressure of samples of abomasal contents was measured with a Fiske Osmometer.

RESULTS

Secretory responses of abomasal pouches to sucking

Acid secretion. Serial collections of secretion from the pouches and samples of abomasal contents were obtained at 15 min intervals for 30–60 min before allowing the calves to suck. Although the collections began approximately 18 hr after the last feed, appreciable amounts of

acid were being secreted by the pouches and the ranges of pH values of the abomasal contents for the three calves were 1·07–2·07, 1·15–1·67 and 1·36–1·83. The concentration of acid in the pouch secretion before sucking was 44–104 m-equiv/l. The abomasal contents consisted of a clear, slightly viscous fluid containing small milk clots and were occasionally bile stained.

The secretion of acid and water by the pouches in calves 2 and 3 in response

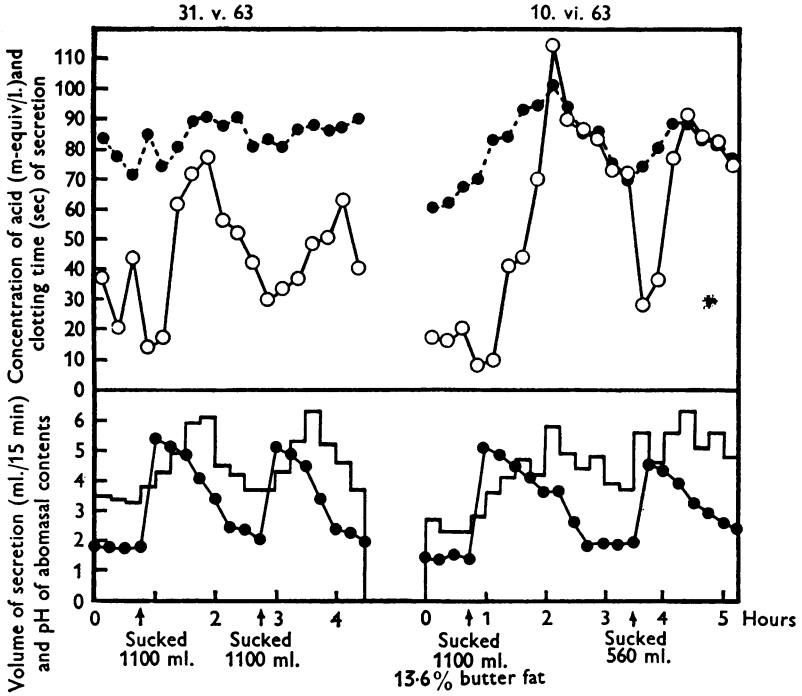

Fig. 1. Secretory responses of an innervated abomasal pouch when the calf sucked milk from a bottle. The experiments began at 9.30 a.m. each day and sucking is indicated by the arrows. Concentration of acid, ●---●; clotting time, ○——○; pH of abomasal contents, ●——●; volume of secretion, ——. Calf 3, born 26. iv 63.; operation 13. v. 63.

to sucking 560–1100 ml. of milk was qualitatively similar. Within 15 min both the volume of secretion and the concentration of acid increased and reached a peak in 30–90 min; thereafter the output of acid gradually declined. Similar responses were obtained when milk was sucked at 1½–2¼ hr intervals. The time taken by the calves to suck the milk was 1–3½ min. The pH value of the abomasal contents increased to 3·05–5·83 within 15 min and then decreased slowly until immediately after the next feed. Examples of these responses are shown in Fig. 1.

The secretory responses to sucking in calf 1 differed from the preceding

results in that the initial increase in the volume of secretion and concentration of acid was followed by a 15–75 min period of inhibition. This response to sucking was consistent throughout the milk feeding period and did not depend on the volume of milk taken. By contrast, when milk

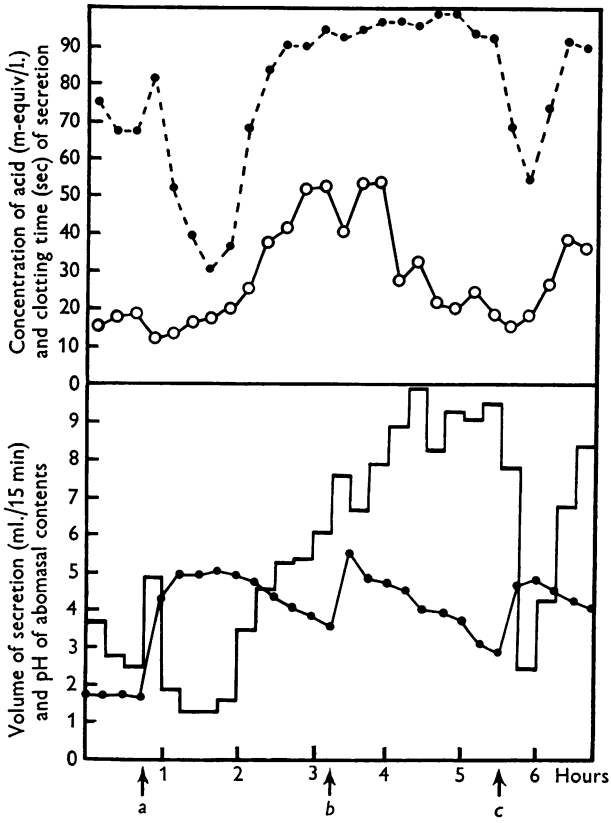

Fig. 2. Secretory responses of an innervated abomasal pouch to sucking milk from a bottle and to introducing milk directly into the abomasum through a cannula. *a*, 1660 ml. sucked; *b*, 1100 ml. direct into abomasum; *c*, 1100 ml. sucked. Concentration of acid, ●---● clotting time, ○——○; pH of abomasal contents, ●——●; volume of secretion, ——. Calf 1, born 9. x. 62.; operation 18. x. 62. Experiment began at 9.30 a.m. on 1. xi. 62.

was introduced directly into the abomasum of this calf through the abomasal cannula and when the calf was allowed to drink from a pail there was a response similar to that obtained in calves 2 and 3. The inhibitory response to sucking was still obtained after the calf was eating dried grass and meals and the nature of the abomasal contents was typical of the adult ruminant. Figures 2 and 3 show examples of the secretory responses to

sucking, to the introduction of milk directly into the abomasum and to drinking milk from a pail.

Proteolytic activity of the secretion. The concentrations and total outputs of proteolytic activity in the pouch secretion collected before feeding

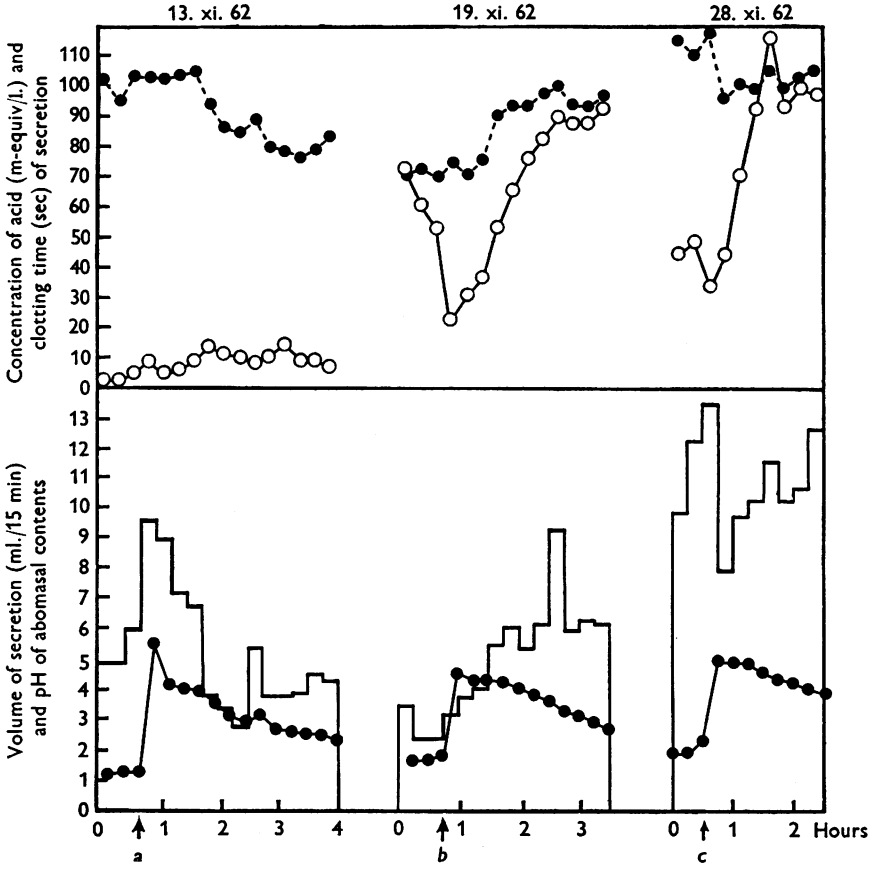

Fig. 3. Comparison of the effects of *a*, introducing milk directly into the abomasum, *b*, drinking milk from a pail and *c*, sucking milk from a bottle. All the experiments began at 9.30 a.m. and the volume of milk given in each instance was 1660 ml. The calf ingested substantial quantities of solid food between experiments *b* and *c* but the inhibitory response to sucking persisted. Note the over-all increase in secretory rate in experiment *c*. Calf 1. Concentration of acid, ●---●; clotting time, ○——○; pH of abomasal contents, ●——●; volume of secretion, ——.

were higher than in the post-feeding period (Fig. 4). There was an increase in concentration and output of proteolytic activity within 15 min of sucking but this was followed by a rapid decrease so that 30–45 min later both concentration and output were less than in the pre-sucking period. The maximum depression occurred 90–120 min after sucking and was followed

by a very gradual increase, but the over-all reduction in output was maintained for at least 4 hr. A second period of sucking 2½–3¼ hr after the first again increased the output of proteolytic activity; the response was less than in the first period and the output rapidly returned to about the level observed immediately before sucking.

Clotting activity of the secretion. The time taken for whole milk to clot with the samples of pouch secretion obtained before sucking was in the range 3–73 sec and in most instances the time was 10–40 sec. The clotting activity of the secretion increased within 15 min of sucking and then rapidly decreased until it was much less than in the pre-sucking period (Figs. 1, 2 and 3). The most prolonged clotting times occurred with samples obtained about 90 min after feeding but the maximum was never more than 120 sec; subsequently the clotting time tended to decrease. When the first milk feed of the day was introduced directly into the abomasum instead of being sucked, the clotting activity of the secretion tended to remain at a high level (Fig. 3*a*).

The time taken for milk to be clotted by the pouch secretion tended to be inversely related to the concentration of proteolytic activity (Fig. 4) but the over-all relation was markedly curvilinear. The milk clot produced *in vitro* was always well defined, firm and separated rapidly from the whey.

Responses in relation to milk intake. In an attempt to standardize the experimental conditions, the secretory responses to the first sucking period of the day were compared in order to assess the influence of milk intake on secretion. When the over-all daily intake of milk was increased the patterns of secretion were qualitatively similar but the outputs of acid and of proteolytic activity increased. These increases were due partly to an increased rate of secretion and also to an over-all increase in concentrations; the increase in the concentration of proteolytic activity was most marked in the pre-sucking and actual sucking periods. The changes in output of acid and especially that of proteolytic activity lagged behind the change in milk intake (Fig. 4).

Responses in relation to the butter fat content of the milk. A comparison was made of the secretory responses to sucking equal volumes of skimmed milk, whole milk and whole milk enriched with cream to increase the butter fat content to 13–15 %. Again, the first feed of the day was used for comparative purposes and whole milk was used otherwise. The patterns and the volumes of secretion obtained were similar for all the milks. In calf 2 the outputs of proteolytic activity over the experimental periods were 2246 and 2419 Hunt units for whole milk and skimmed milk, respectively, but only 841 units for milk containing 15 % butter fat. The significance of the latter value is difficult to assess since on the day of the experiment the output of proteolytic activity was depressed before feeding. The

outputs of proteolytic activity in calf 3 were 1689 and 1717 Hunt units for whole milk and milk containing 13% butter fat respectively (see Fig. 4).

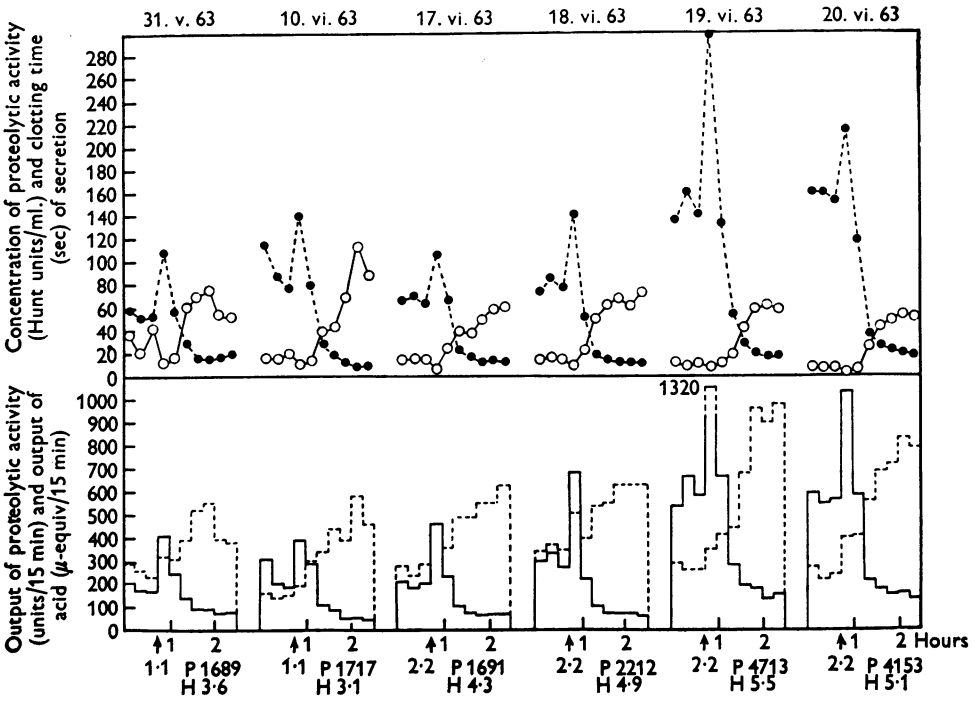

Fig. 4. The effect of increasing the daily milk intake on the secretion of proteolytic activity and of acid. Concentration of proteolytic activity, ●---●; clotting time, ○——○; output of acid, ----; output of proteolytic activity, ——. The total outputs of proteolytic activity (P) and of acid (H, m-equiv) in the experimental period are shown below the graph. The numbers immediately below the arrows indicate the volume of milk sucked in the experiment but the daily consumption was increased from 3·3 l. to 6·6 l. on 17. vi. 63. Note that in the experiment on 10. vi. 63 the milk contained 13·6% butter fat. Calf 3.

The flow of material from the abomasum

Patterns of flow. All the experiments began about 18 hr after the previous feed and there was a 30 min collection before the calves were allowed to suck the first meal of the day. The mean rates of flow during the pre-sucking period were: calf 4, 113 ml. (range 24–182 ml.) calf 5, 218 ml. (range 170–289 ml.) and calf 6, 75 ml. (range 45–152 ml.). It is not known whether these apparently high rates of flow would have been maintained over a longer period or whether they were due partly to rapid emptying of the abomasum when the re-entrant cannulae were opened. It is possible

that there is a small but continuous flow of saliva into the abomasum from the rumen (Smith, 1959) and the serial 5–15 min collections did not suggest that the volume and rate of flow was decreasing progressively or consistently. The material consisted of a clear fluid with small milk clots and the mean pH values were: calf 4, 2·98 (range 2·17–4·2) calf 5, 2·42 (range 1·92–4·8) and calf 6, 1·94 (range 1·55–2·84).

The rate of flow increased almost immediately the calves began to suck and within 5 min volumes of 80–300 ml. were recorded. Very high initial rates of flow were not maintained for more than 5–10 min and they were followed by a short period of reduced flow. This rhythmic pattern was most pronounced in calves 5 and 6. The fluid leaving the abomasum immediately after sucking was opalescent and contained many small clots. These disappeared rapidly from the flow and were absent for about 1½–2 hr: gradually the flow became less opalescent and the amount of clotted material increased.

The over-all pattern of flow in calves 5 and 6 usually consisted of a peak occurring 30–60 min after sucking followed by a fall. The flow from the abomasum of calf 4 tended to occur in two phases; maximum flows of approximately equal magnitude occurred between 30 and 60 min and again between 120 and 180 min. The flow was depressed in the intervening period and decreased rapidly after the second peak.

The total volume of material which flowed from the abomasum of calves 4 and 5 in the 2½ hr period following the ingestion of 1100 ml. of milk was 1432—1520 ml. whereas the cumulative value for calf 6 was only 614–730 ml.

In three experiments a second feed of 560 ml. of milk was sucked 2½–4½ hr after the first and a volume of material equal to or greater than the amount ingested flowed from the abomasum within 30–60 min.

Examples of the flow patterns are shown in Fig. 5.

Flow in relation to the butter-fat content of the milk. There was no consistent or appreciable differences in either the pattern of flow or in the cumulative rates of flow when calves 4 and 5 sucked skimmed milk, whole milk or milk with a high butter-fat content (Fig. 6). The initial increase in the rate of flow in calf 6 was reduced following the ingestion of milk containing 7·6 and 17·6 % butter fat (Fig 7).

The material flowing from the abomasum of all the calves after the high butter-fat content meals was very viscous and when samples were allowed to stand in a tube a thick layer of creamy material settled on the top.

Acidity of the material leaving the abomasum. The pH value increased immediately after sucking began and reached peak values of 4·75–6·08 within 15–30 min. Thereafter the pH decreased, usually in a progressive

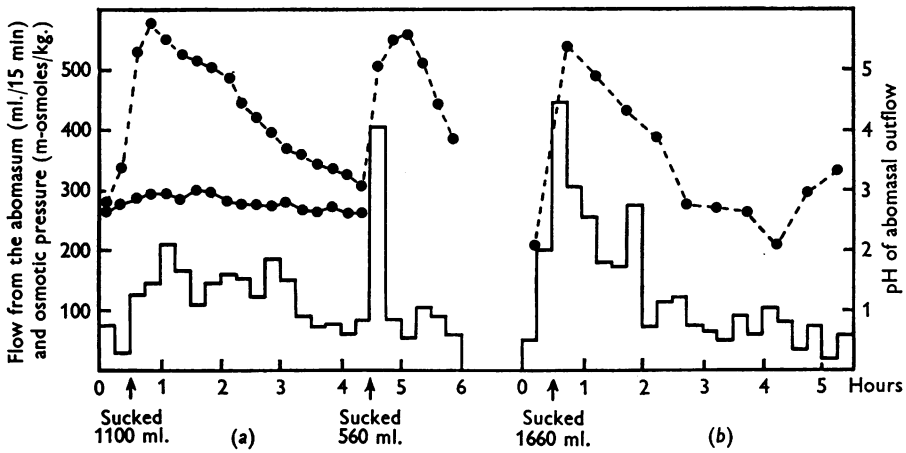

Fig. 5. Patterns of flow from the abomasum. (*a*) Calf 4, born 29. x. 62.; operation, 8. xi. 62. Experiment performed 15. xi. 62. (*b*) Calf 5, born 11. xi. 62.; operation 22. xi. 62. Experiment performed 13. xii. 62. pH of outflow, ●---●; volume of outflow, ——; osmotic pressure of outflow, ●——●.

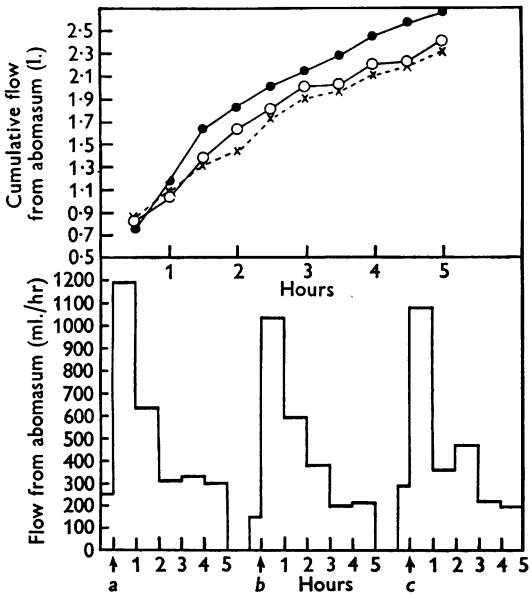

Fig. 6. Comparison of the patterns and rates of flow from the abomasum when a calf sucked milk containing different amounts of butter fat. The volume of milk given was 1660 ml. in each experiment; (*a*) whole milk, (*b*) milk containing 9·5 % butter fat and (*c*) skimmed milk. The top panel shows the cumulative rates of flow; whole milk, ●——●; 9·5 % butter fat, ○——○; skimmed milk, ×---×. Calf 5.

manner until 3–5 hr after feeding when the values were 2–3 (Fig. 5). The pH curve in calf 6 tended to be diphasic in that the initial rise and fall was followed by a secondary increase occurring after about 1½–2 hr and this was followed by a more rapid and progressive decrease.

Osmotic pressure of the material leaving the abomasum. Before sucking the osmotic pressure was in the range 241–265 m-osmole/kg of fluid and after the ingestion of milk it increased immediately to 267–309 m-osmole/kg.

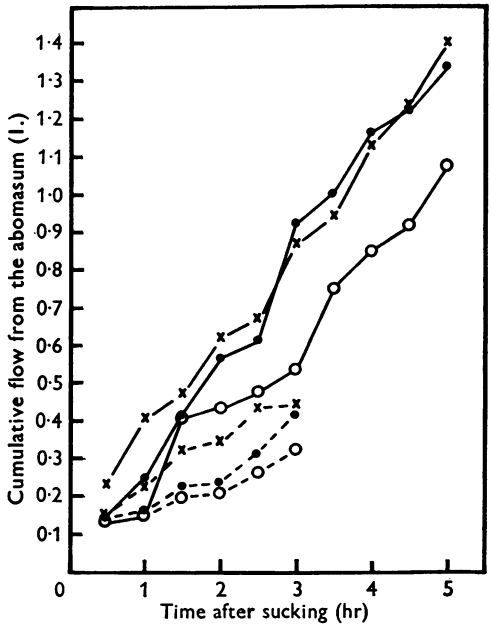

Fig. 7. The influence of the volume and butter-fat content of the milk sucked on the flow from the abomasum of calf 6. 1100 ml. feeds: normal milk, ●——●; skimmed milk, ×——×; 17·6% butter fat, ○---○; 560 ml. feeds: normal milk, ●---●. skimmed milk, ×---×; 7·6% butter fat, ○---○.

The increase was usually maintained for 1–2 hr and then slowly decreased. The osmotic pressure of the jugular plasma of one calf was measured on two occasions and was 288 and 292 m-osmole/kg.

Steam volatile fatty acid in the material leaving the abomasum. Usually the concentration was less than 1 m-mole/l. in the period before sucking. After sucking skimmed and normal milk the concentration increased to 3·8–10 m-mole/l. and to 11–16 m-mole/l. with milk containing a high concentration of butter fat. The greatest concentration occurred in 30–90 min and declined quicker after meals of skimmed milk than after whole and high butter-fat milk.

DISCUSSION

A striking feature of the present experiments is the variability between calves in their responses to sucking. This may be a true example of individuality or the result of surgical interference. Irrespective of the cause, the characteristic responses to sucking were consistent throughout the milk feeding period of each calf and in one investigation persisted into the weaning stage.

The ability of abomasal secretion to promote the clotting of forty times its own volume of milk within 3–73 sec accounts partly for the patterns and nature of the flow from the abomasum. The rapid disappearance of the small visible clots from previous meals was probably due to their being incorporated into the newly formed clot as freshly sucked milk flowed through the abomasum. In the period of rapid emptying it was presumably the whey fraction of the newly ingested milk that was being transferred to the duodenum. The clotted material was transferred to the duodenum at a much slower rate and at a lower pH.

The short-term rhythmic patterns of flow suggest that there was an inter-relation between the abomasum and duodenum which influenced the rate of emptying but the over-all rates of flow were related mainly to the volume of milk ingested. It is not known whether the initially slow rates of flow in calf 6, with high fat milks, were caused by a chemical effect of the fat or its digestion products or to the thick consistency of the material entering the duodenum. Flow from the abomasum of this calf was particularly sensitive to the introduction of material into the duodenum.

The secretion of acid by the innervated pouches in the pre-sucking period was relatively high and the pH values of the abomasal contents was below 2. A high acidity in the pyloric antrum and duodenum of monogastric animals and of adult sheep inhibits the further secretion of acid from gastric pouches, although it is likely that the stronger the excitatory stimulus, the less easily will acid cause inhibition (Gregory, 1962). During the pre-sucking period the calves were very obviously expecting to be fed and it is possible that the high rate of acid secretion was due to strong vagal excitation to the gastric mucosa. The patterns of secretion of proteolytic activity, which will be discussed later, also suggest that a strong form of cholinergic excitation occurred in the pre-sucking period.

The over-all increase in acid secretion following sucking and drinking appeared to be due chiefly to the flow of milk into the abomasum. The acts of sucking and drinking *per se* were not directly responsible for the acid secretory response since the introduction of milk into the abomasum through a cannula also increased the output of acid. Acid secretion by the

abomasum of adult sheep is stimulated by distension and potentiated by the presence in the abomasum of short chain steam-volatile fatty acids, provided the acidity of the abomasal contents is not greater than pH 2 (Ash, 1961*b*). If a similar combination of factors is an effective stimulus in the calf, the conditions in the abomasum immediately following the ingestion of milk are ideal for evoking and maintaining the acid secretory response. However, the concentration of short chain fatty acid present, which is probably nearly all butyric (Ramsey & Young, 1961) is less than that found to be necessary to cause potentiation in the adult sheep. The reasons for the profound inhibition of acid secretion in calf 1 are not known but it appeared to be related to the sucking process.

Recent experiments by Henschel, Hill & Porter (1961) indicate that the young calf may secrete either or both rennin and pepsin and that the type of enzyme secreted is not predictable from the age of the animal or the nature of its diet. In the present work the total proteolytic activity of the pouch secretion was estimated at pH 2·1 in terms of Hunt units and no attempt was made to discriminate between rennin and pepsin. It is important to note that both enzymes will clot milk. Gregory (1962) has tentatively suggested that pepsin *output* may be an index of cholinergic excitation of the gastric glands either directly by extrinsic vagal action or indirectly through the stimulation of motor activity in the stomach. If this be accepted, the patterns of proteolytic output again suggest that there was a strong form of cholinergic excitation in the pre-feeding period and this was increased still further during sucking and drinking. It is possible that the rapid and profound decrease in the output of proteolytic activity after feeding was due partly to a decrease in vagal activity as a result of satiation of appetite (Pavlov, 1902). Stimuli which might be considered to have an inhibitory effect were either ineffective or apparently absent. For example, the decrease in proteolytic output occurred both with skimmed and high butter fat milks and the osmotic pressure of the material flowing to the duodenum was never markedly hypertonic. Furthermore, the depression of proteolytic secretion coincided with the period of increased acid secretion in calves 2 and 3 and the period of rapid emptying.

The mechanism whereby the output of proteolytic activity is apparently reduced and its relation to other events in the abomasum and duodenum of the suckled calf requires further investigation.

SUMMARY

1. The secretory responses of the abomasal mucosa to sucking were studied in three calves prepared with innervated abomasal pouches and cannulated abomasal fistulae. Measurements of the flow of milk from the

abomasum were made on three other calves fitted with duodenal re-entrant cannulae.

2. Variability between calves was observed in their secretory responses and in the patterns and cumulative rates of flow from the abomasum.

3. Acid secretion by the pouches was relatively high about 18 hr after the previous meal although the pH of the abomasal contents was below 2.

4. The secretion of proteolytic activity was high before the first feed of the day, increased further on sucking and drinking and then rapidly fell to below the pre-feeding level. Further periods of sucking temporarily increased proteolytic secretion.

5. Pouch secretion promoted the clotting of forty times its own volume of whole milk within 3–120 sec under *in vitro* conditions. The clotting activity was greatest in the pre-sucking and sucking periods.

6. The over-all rate of secretion and the outputs of acid and proteolytic activity increased when the daily volume of milk ingested was increased. The changes in output lagged behind the changes in diet.

7. The secretory responses of the pouches and the patterns and rates of flow from the abomasum were not influenced consistently or appreciably by the butter-fat content of the milk. The over-all rate of flow from the abomasum was related chiefly to the volume of milk ingested.

I wish to thank Messrs J. Dunnet and C. Robb for their skilled technical assistance and management of the calves. I am indebted to Mr J. Aitken for estimating the butter-fat content of the milk samples. Mr J. Gunn of the Duthie Experimental Stock Farm was responsible for selecting the calves.

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