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GASTRIC EMPTYING AND SECRETION IN THE MILK-FED CALF

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SUMMARY

1. For a few weeks, immediately post-natally, the abomasum of the ruminant stomach can be regarded as the analogue of the simple stomach for at this time food passes directly to the abomasum because of closure of the oesophageal groove.

2. Using standard fractional and serial test meal techniques discussed by Hunt (1956) and adapted for use in the calf, abomasal emptying, acid and pepsin secretion have been examined. Phenol red was used as a marker to measure volume changes of the test meal.

3. Abomasal emptying is exponential in character whether large or small volumes of fluid are instilled into the abomasum. The initial and end phase of emptying shows variable rates between animals.

4. Glucose and lactose solutions inhibit abomasal emptying as well as acid production.

5. Sodium chloride and sodium bicarbonate of low concentration, near isotonic with blood plasma, stimulate abomasal emptying but the bicarbonate is most effective. Hypertonic solutions of these salts inhibit abomasal emptying.

6. Pepsin secretion in the abomasum of the calf is not affected by test meals of glucose, lactose, sodium chloride or sodium bicarbonate.

7. These results shows a great similarity between the physiology of the abomasum of the milk-fed calf and the simple stomach. This suggests that the same duodenal receptors, discussed by Hunt & Knox (1968), which control gastric movement in man are also effective in controlling gastric emptying in the milk-fed calf.

INTRODUCTION

The effector systems of gastric muscle and secretion are under multifactorial control by facilitatory and inhibitory mechanisms activated

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reflexly and neurohumorally from receptors situated mainly in the gut itself (Thomas, 1957). Hunt & Spurrell (1951) described the pattern of emptying of the human stomach and showed clearly that the simultaneous activity of gastric muscle and glandular secretion is associated with the movement of gastric chyme to the duodenum.

The earlier investigations of gastric emptying, apart from Alexis St Martin, were made on dogs with duodenal or gastric fistulae and it was shown that the inhibitory effects on gastric muscle arose in the duodenum (Marbaix, 1898) but that salt solutions close to isotonicity with plasma caused less inhibition than hypotonic or hypertonic solutions (Carnot & Chassevant, 1905*a*). The osmotic control of the human stomach was confirmed by McSwiney & Spurrell (1933) and studied further by Hunt (1959) who postulated that gastric emptying is regulated by receptors in the duodenum which react to various molecules and ions fed to them from the stomach.

Only for a brief period of a few weeks can the ruminant stomach be regarded as the strict analogue of the simple stomach of other mammals. This period occurs immediately post-natally when, because of the reflex closure of the oesophageal groove brought about by suckling milk, food (milk) passes directly to the abomasum. As the calf matures the reticulorumen commences to function and the analogy between abomasum and simple stomach is lost.

For the most part investigators of abomasal physiology have studied the relationship between the formation of milk clot and the digestion of milk protein. Benzie & Phillipson (1957) in a radiographic study of the alimentary tract of the ruminant showed that rapid emptying of the abomasum occurred in the milk-fed calf. In a study of ionic exchange in the alimentary tract of the calf, Smith (1964) gives information mainly on the long term transference of liquid from the abomasum to the intestine. Ash (1964) investigated some aspects of abomasal secretion and emptying in suckled calves and suggested the possibility of 'an inter-relation in the abomasum and the duodenum which influenced the rate of emptying'.

The experiments reported in this paper were undertaken because of paucity of information on abomasal emptying in the milk-fed calf and to investigate whether the known mechanisms controlling the simple stomach also affected the abomasum.

METHODS

Animals

Friesian bull calves were allowed 4–6 days with their dams but had no appreciable access to roughage. They were housed separately at 60–70° F and maintained exclusively on a whole milk or milk substitute diet. The calves were trained to

mount a Pavlov type stand and after a few days learned to stand quietly for up to 2–3 hr. When the calves were 10–14 days old, an abomasal cannula was fitted under fluothane anaesthesia and experiments commenced about 1 week later.

Determination of the volume of abomasal contents

To determine the responses of the abomasum in terms of emptying and secretion, a single recovery technique introduced by Gorham (1921) and used extensively in human gastric analysis was adapted for our purposes (Hunt, 1959). Simple solutions, including phenol red as a marker, were instilled into the abomasum through the abomasal cannula and, after a fixed digestive period, recovered for analysis. In some experiments a 'serial meal' technique similar to that used for studying gastric function in man was adopted (Hunt & Spurrell, 1951; Hunt, 1959) but, because of the extensive abomasal folds which prevent complete withdrawal of the abomasal contents by aspiration, a modification suggested by Hildes & Dunlop (1951) was used to enable accurate determination of the volume of the abomasum.

On the day of experiment the morning feed was withheld and residual abomasal contents were removed by gentle suction and the organ washed out several times with water at 37° C until the washings were clear. The test meal, warmed to 37° C and including phenol red, was then instilled into the abomasum, a sample being retained for subsequent analysis. After instillation of the test meal the abomasal contents were mixed using a 250 ml. syringe and a 50 ml. aliquot of the mixed abomasal contents retained for analysis. The absolute volume of the abomasal contents was calculated from the ratio of the phenol red marker in the two samples. The test meal was usually left in the abomasum for 45 min.

At the completion of the test period, the abomasal contents were mixed several times and as much of the contents as possible removed by aspiration, measured and a sample retained for analysis. A known solution of phenol red was instilled into the abomasum and mixed several times and another aliquot was withdrawn for estimation of the volume not aspirated. Finally, after washing out test meal and phenol red, the calf was given its morning feed 1 hr later than normally.

Phenol red has been examined in detail as a suitable marker for human gastric contents (Penner, Hollander & Salzman, 1938; Hunt, 1949). It is also suitable as a marker for abomasal contents since 100% recovery can be achieved 1 hr or more later when the dye is instilled together with substances like calcium chloride, magnesium chloride and hydrochloric acid which completely inhibit abomasal emptying.

The method used to estimate the phenol red marker in abomasal liquor was essentially that described by Hunt (1947). To ensure accurate spectrometer determination of the dye in abomasal liquor two modifications were introduced to remove particulate matter; the aliquot of abomasal contents was first centrifuged and then filtered through Hemming bacteriological filters to remove the final slight turbidity which occasionally persisted.

The aliquots for phenol red analysis were alkalinized by the addition of trisodium orphophosphate and the filtrate examined for optical density using a D.P. spectrophotometer. Samples were read against a distilled water blank and a wave-length of 520 mu. This wave-length is equivalent to the ortho green filter (no. 404) which minimizes the effect of bile (Hunt & Knox, 1962). With the standard phosphate buffer there is no detectable loss of colour in phenol red samples at pH 11–12 over a period of 6 weeks.

Determination of acidity of abomasal contents

Total acidity. 1 ml samples of abomasal contents were titrated against 0·01 N sodium hydroxide using 1% phenolphthalein as indicator. By determining the concentration of acid at both the beginning and end of the test meal, the increase in concentration of acid was obtained. Because the volume of abomasal contents was measured, the total amount of acid secreted during a test period could be determined to give an index of acid secretion during the test period (Hunt, 1959). The results were expressed in m-equiv/l.

pH determination. The pH of the test meal before and of the abomasal contents after the digestive period was measured electrometrically.

Determination of proteolytic activity

The method used to assess the concentration of pepsin in the recovered abomasal contents was that described by Hunt (1948) for the estimation of peptic activity in human gastric contents using dried citrated plasma or dried serum as substrate for peptic digestion. The concentration of pepsin in Hunt units/ml. was calculated for the abomasal contents recovered at the end of the test period and for the amount passed to the duodenum (see Hunt, 1959).

RESULTS

The relative merits and nomenclature of different forms of test meal in man are discussed by Hunt & Spurrell (1951) and more fully by Hunt (1959). Although the term 'test meal' is used here, in fact the meal was a simple water based solution which was introduced directly into the abomasum via the cannula. The abomasum was carefully washed out and emptied before instillation of the solution to be tested, so that the solution being examined as a facilitatory or inhibitory stimulus was readily isolated from other interfering substances. The use of an abomasal cannula for instillation and removal of samples of test meal overcomes many of the criticisms of fractional test meal techniques in human clinical medicine.

Fractional test meal

Pattern of emptying. The results of abomasal emptying were obtained in six calves. Abomasal emptying was measured by introducing a known volume of glucose solution and phenol red marker into the abomasum and assessing the amount of test meal evacuated by estimating the amount of phenol red marker remaining in the abomasum from samples removed at timed intervals. One litre volumes of glucose solution were used as the test meal and usually most of it was transferred to the duodenum in about 2 hr.

Abomasal evacuation is seen to be an orderly process with the volume of test meal steadily decreasing with time (Fig. 1). Three phases of abomasal emptying can be observed.

(*a*) For most of the transfer time of abomasal contents to the duodenum

the emptying process is exponential in character indicating that abomasal emptying is a function related to the volume of the abomasal contents.

(*b*) Preceding the exponential phase is a temporary initial phase when the rate of abomasal emptying is variable.

(*c*) A terminal phase of abomasal emptying occurs when the exponential rate of emptying again becomes variable; the rate of emptying may then be increased or slowed.

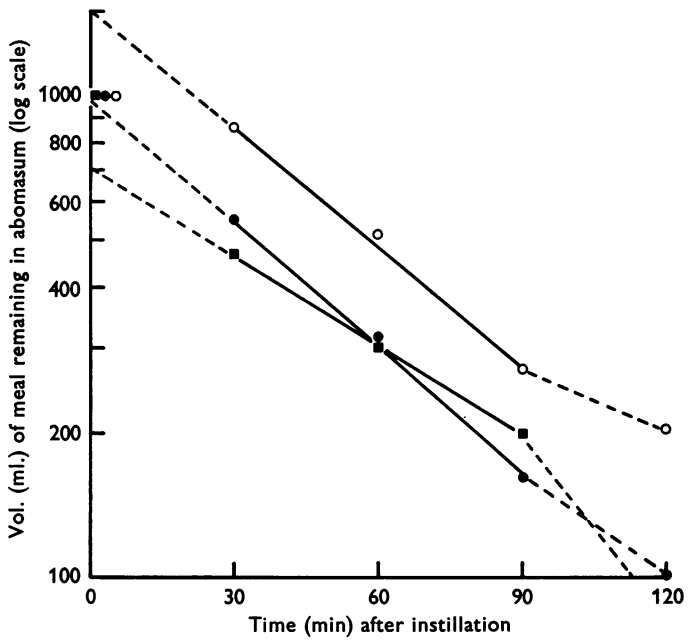

Fig. 1. The pattern of emptying of the abomasum. In each experiment 1000 ml. glucose solution was instilled into the abomasum and the volume remaining estimated at intervals using phenol red as a marker. The glucose solutions were 10% (○), 5% (●) and 3% (■). The main exponential phase of emptying is shown and the dashed lines indicate the initial and final phase of emptying (see text).

Hunt & Spurrell (1951), investigating gastric emptying in man, extrapolated the exponential phase of emptying to zero time to give a 'starting index' which, depending on whether the extrapolated exponential phase and the logarithm of the initial volume of the test meal intersect at a positive or negative time axis, is described as a positive or negative index. A positive starting index represents a slow onset, and a negative starting index a rapid onset, of gastric emptying.

In Fig. 1 where the same volume (1000 ml.) of different concentrations of glucose were examined, the middle exponential phase is very similar. The

'starting index' varies and for the 10% glucose solution is positive, indicating a slow beginning to emptying, and for the 3% solution is negative, showing rapid emptying at first. Because of the slow onset, the higher concentration of glucose is evacuated more slowly requiring 60 min for half the volume to be removed, whereas the 5 and 3% glucose solutions have a 'half-life' of 35 and 25 min respectively.

The effect of instilling different volumes of 10% glucose solution is illustrated in Fig. 2. The same three phases of abomasal evacuation are seen as in Fig. 1 with the main phase being exponential in character and the larger meals taking longer to empty.

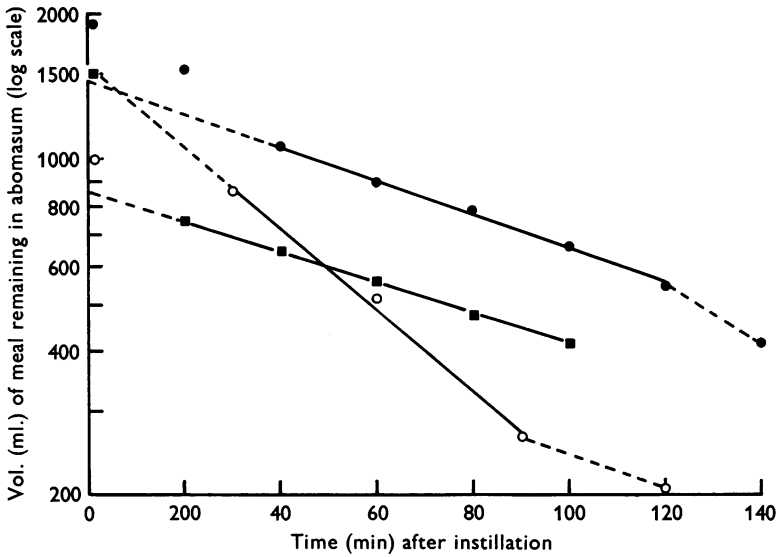

Fig. 2. The pattern of emptying of the abomasum. In each experiment 10% glucose solution was used but the volume instilled was varied. The volumes used were 1930 ml. (●), 1520 ml. (■), 1000 ml. (○). The main exponential phase of emptying is shown and the dashed lines indicate the initial and final phase of emptying.

Acid secretion. Aliquots of abomasal contents collected at timed intervals after instillation of the test meal were titrated for acid content and the pH was measured.

The results for acidity are in Fig. 3 and show a progressive increase in total acidity as the digestive period proceeds. There is, however, a reduced acid output when more concentrated glucose meals are introduced into the abomasum.

Pepsin secretion. The output of pepsin was continuous throughout the meal and appeared to be independent of the concentration of glucose in the test meal.

Serial test meal

A standard volume (950 ml.) of test solution was instilled and allowed to remain in the abomasum for 45 min. A similar volume of water was used to establish a control zero level. The volume evacuated by the stimulus of the test solution against the control can then be compared for effects on abomasal emptying and on acid and pepsin secretion.

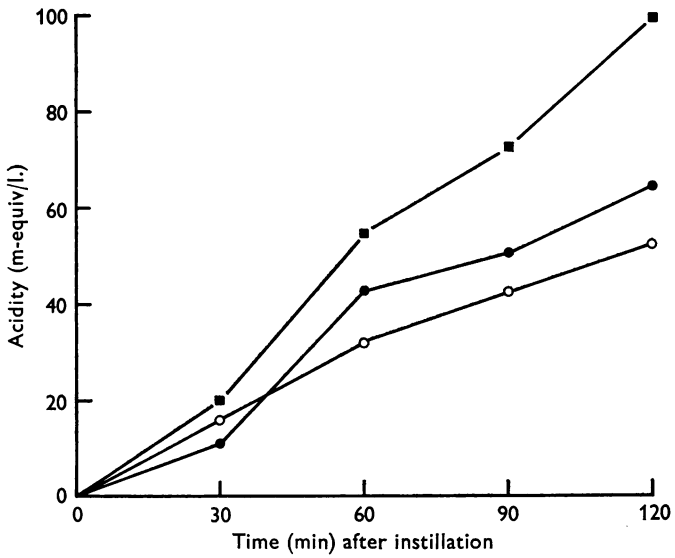

Fig. 3. The effect of glucose solutions instilled into the abomasum on acid production. In each case the same volume (1000 ml.) was instilled into the abomasum and the total acidity measured at intervals. Different concentrations of glucose solution were used (10% ○, 5% ● and 3% ■). Acid production is a continuous process which varies with the concentration of the glucose meal, low concentrations of meal being associated with greater output of acid.

Abomasal emptying. The results of serial test meals of glucose solution in a series of calves are shown in Table 1. Glucose solutions ranging from about 300 m-osmole/l. to more than 1000 m-osmole/l. show a progressive inhibition of abomasal emptying. With high concentrations of glucose the pH of the abomasal contents usually rises at the end of the test period because of inhibition of acid production and, as in calf 9 and calf 16, the progress of inhibition becomes variable.

To test whether alkalinity of the abomasal contents lessened the inhibitory effect of glucose, test meals were given serially but sodium bicarbonate was also added to the solution. In addition to the water control, the sodium bicarbonate solutions were tested as controls and the

results are illustrated in Table 2. Both control solutions of 0·5 and 2·0% sodium bicarbonate markedly increased the amount of fluid evacuated from the abomasum during the test period as in the human stomach (Hunt, 1956).

Following the instillation of the alkaline glucose test meals, the abomasal

TABLE 1. The influence of the concentration of glucose on the volume of abomasal contents after instillation of a test meal. The ratio of retention of meal/water is > 1·00 when glucose inhibits abomasal emptying and < 1·00 when activation occurs

Calf	Concn. glucose in meal (m-osmole/l.)	% meal remaining after 45 min	Ratio of retention meal/water	Final pH of meal
9	0 (water)	27	1·00	1·60
	290	32	1·19	1·65
	580	58	2·15	1·73
	870	50	1·85	6·35
15	0	56	1·00	1·75
	282	59	1·01	2·05
	604	70	1·25	1·70
	856	70	1·25	2·15
	1050	64	1·14	2·60
16	0	58	1·00	1·85
	290	43	0·74	1·80
	595	60	1·03	1·99
	900	74	1·28	2·18
	1080	53	0·91	4·60
	1760	72	1·24	5·90

TABLE 2. The influence of the test meals with sodium bicarbonate and glucose on abomasal emptying 45 min after instillation

Calf	Composition of test meal	Meal (m-osmole/l.)	% meal remaining after 45 min	Ratio of retention meal/water	Final pH of meal
15	Water	0	56	1·00	1·75
	2·0% $NaHCO_3$ (approx.)	446	16	0·29	6·60
	2·0% + 5% glucose	787	34	0·61	8·00
	2·0% + 10% glucose	971	74	1·32	8·10
	2·0% + 15% glucose	1110	70	1·25	8·50
	2·0% + 20% glucose	1270	71	1·27	8·70
	2·0% + 30% glucose	2000	87	1·55	8·80
23	Water	0	58	1·00	1·95
	0·5% $NaHCO_3$ (approx.)	115	16	0·28	2·05
	0·5% + 5% glucose	389	40	0·69	5·30
	0·5% + 10% glucose	678	22	0·38	3·65
	0·5% + 15% glucose	960	65	1·12	5·90
	0·5% + 20% glucose	1200	70	1·21	6·25
	0·5% + 30% glucose	1800	62	1·07	6·80

contents at the end of the meal showed high pH levels. There is no associated additive effect on the stimulus produced to abomasal evacuation by hypotonic sodium bicarbonate solution and glucose solution. The stimulatory effect of sodium bicarbonate overrides the inhibitory effect of glucose solutions on abomasal emptying. The result is probably due to the strong osmotic effect of sodium bicarbonate ions and not a change in the potency of glucose nor in the increased alkalinity of the glucose test meal.

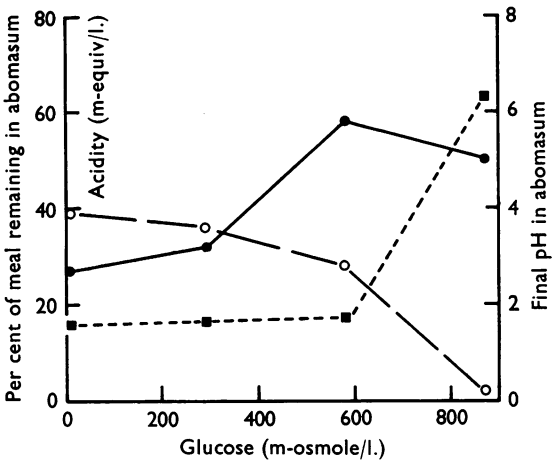

Fig. 4. The results of glucose serial test meals on abomasal emptying (●), acid production (○) and the pH (■) of abomasal contents. In each case the 950 ml. glucose test meal was instilled into the abomasum and the data plotted in the Figure was obtained from analysis of abomasal chyme 45 min later. Increasing concentration of glucose solution inhibits gastric emptying and acid secretion. Strong solutions of glucose are associated with a rise in pH when in some cases the inhibition of emptying is less marked.

Acid secretion. The aliquots of abomasal contents used to estimate abomasal volume change were used to measure the pH of the abomasal contents and, by titration, the acid content. Hypertonic glucose solutions inhibit acid production much more than do weaker solutions of glucose (Figs. 4 and 5).

With increased osmolarity of glucose solution the pH remains about the level of pH 2·0 until about 600 m-osmole/l. is reached when there is a sharp break and the pH rises quickly. With this rise in pH there may be a small degree of reversal in the rate of abomasal emptying (Fig. 4).

In Fig. 4 are combined the results of serial meals of different concentrations of glucose solutions which summarizes the effects on abomasal emptying, acid secretion and pH of abomasal contents at the end of the meal. It can be seen that rising concentrations of glucose inhibits abomasal emptying but at 600 m-osmole/l. there is no further increase in effect and

sometimes the effect is reversed so that abomasal emptying is improved. At the time of this reversal of the delaying effect of high concentrations of glucose, acid secretion is inhibited and the pH of the abomasal contents rises.

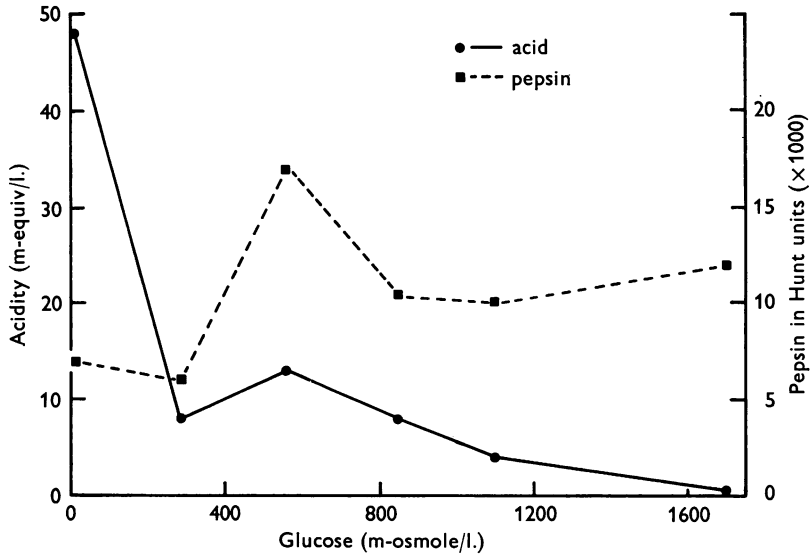

Fig. 5. The effect of glucose serial test meals (950 ml.) on acid and pepsin secretion in the abomasum. Glucose solutions inhibit acid secretion but pepsin is unaffected during the test period of 45 min.

Pepsin secretion. Pepsin secretion in three calves in response to the stimulation of glucose solutions was examined in the serial test meal situation and compared with the effect of a control test meal of water. In all calves pepsin was secreted during all glucose test meals but without any obvious correlation with the concentration of sugar. Certainly pepsin output was as great at high glucose concentrations as in the water control meal. It was noted that usually acid secretion was low when pepsin secretion increased and sometimes a decrease in pepsin output coincided with a rise in acid secretion.

Serial test meals with lactose

Abomasal emptying. Experiments were made on three calves using the serial test meal technique.

In isotonic and hypertonic solutions lactose delayed abomasal emptying when compared with a control water test meal. Hypotonic solutions of lactose had less effect in delaying abomasal emptying and in one calf abomasal emptying was enhanced (Table 3).

Acid secretion. In calf 23 only slight inhibition in acid secretion occurred

with the hypotonic concentrations of lactose incorporated in the test meals but at higher concentrations acid output was clearly reduced. This was seen also in calf 24 but in calf 30 there was little effect on acid secretion as the concentration of lactose was increased in the test meal. This effect is reflected in the pH of the abomasal contents at the end of the meal.

Pepsin secretion. There was no clear correlation between the concentration of lactose in the test meal and pepsin secretion.

TABLE 3. The influence of the concentration of lactose on the volume of abomasal contents after instillation of a test meal. There is little effect on acid secretion

Calf	Concn. lactose in meal (m-osmole/l.)	% meal remaining after 45 min	Ratio of retention meal/water	Final pH of meal
23	0 (water)	58	1·00	1·95
	50	27	0·47	1·90
	130	49	0·84	1·90
	170	42	0·72	1·80
	250	62	1·07	1·70
	360	86	1·48	1·80
	570	67	1·16	1·90
	730	90	1·55	1·90
24	0	50	1·00	1·90
	60	53	1·06	1·70
	160	66	1·32	1·70
	360	72	1·44	1·80
	510	65	1·30	1·90
	800	63	1·26	2·05
30	0	68	1·00	2·00
	200	82	1·21	1·95
	300	92	1·35	1·90
	370	72	1·06	1·80
	620	88	1·29	1·90

DISCUSSION

Using phenol red as a marker in simple solutions instilled through cannulae it was possible to determine the volume of the contents of the abomasum accurately at any given time. From these measurements the basic pattern of abomasal emptying in the young milk-fed calf has been established to be exponential in character for most of the evacuation period. This pattern of emptying remains whether larger or small volumes of the same concentration or when similar volumes of different concentrations of solute are added to the abomasum. This pattern of emptying demonstrated in the milk-fed calf is very similar to the pattern of emptying seen in the stomach of man (Hunt & Spurrell, 1951; Hunt, 1960).

Negative starting indices were obtained in the calf showing that the onset of emptying of the abomasum is rapid like the human stomach (Hunt & Spurrell, 1951). The rapid emptying of a test meal from the abomasum seen in our experiments corroborates the results of radiological examination (Benzie & Phillipson, 1957; Bush, Schuh, Tennille & Waller, 1963) and duodenal flow, which have indicated that some abomasal contents are evacuated within minutes of feeding (Otterby, Ramsey & Wise, 1964; Ash, 1964; Mylrea, 1966). The negative starting index, which is indicative of rapid onset of flow, occurs with different concentrations and volumes of sugar test meals and suggests that it is the first rapid flush of abomasal chyme which may set up a situation in the duodenum which controls subsequently the exponential form of abomasal evacuation.

The effects of test meals on calves suggest that the varied forms of duodenal receptors controlling gastric emptying in the simple stomach discussed by Hunt & Knox (1968) may also be effective in the milk-fed calf. The clear-cut stimulatory effect of low concentrations of sodium bicarbonate is directly comparable with the osmotic effect of sodium chloride and sodium bicarbonate demonstrated in man (Hunt, 1960).

There is some difference of opinion with regard to the effect of sugar solutions on gastric emptying in the simple stomach. In man glucose solutions inhibit gastric emptying (Hunt, 1956) although earlier Shay & Gershon-Cohen (1935) were unable to see any effect, and in the dog (Carnot & Chassevant, 1905*b*), and cat (Gianturco, 1934) glucose is said to hasten gastric emptying. Singleton (1951) showed that when 20–30 % solutions of glucose were instilled into the duodenum of the adult goat, abomasal motility was depressed although isotonic glucose solutions were ineffective. Our results in the milk-fed calf show that isotonic glucose solutions actually inhibit emptying of the abomasum and that the inhibition increases with rising concentration of glucose in the test meal. The abomasum of the adult goat and the suckling calf, however, receive vastly different forms of food input and there is no reason why the control mechanisms should be the same. In man glucose is more inhibitory to gastric emptying than lactose and, since this is also the case in the milk-fed calf, the duodenal mechanism discussed by Elias, Gibson, Greenwood, Hunt & Tripp (1968) may be similar in both species.

In the simple stomach sugar solutions inhibit acid secretion as well as motility (Miller, Bergeim, Rehfus & Hawk, 1920; Hunt, McDonald & Spurrell, 1951; Sircus, 1958). In the calf fractional meals with low concentrations of both glucose and lactose (up to 700 m-osmole/l.) produce a continuous output of acid in the abomasum. Hypertonic glucose solutions (higher concentrations of lactose could not be used because of supersaturation) have less effect on acid production, and in serial test meals high

concentrations of glucose hardly stimulate acid secretion at all so that the abomasal contents remain alkaline. It is possible that the duodenal factor which, with high concentrations of glucose, causes inhibition of gastric motility also causes inhibition of acid secretion. Another possibility is that low concentrations of sugars, especially disaccharides, stimulate acid secretion in the abomasum which, by depressing the pH, stimulates abomasum motility directly from within the viscous itself or indirectly via duodenal 'acid' receptors. Another possible explanation is that the rise in abomasal pH is brought about by reflux of duodenal contents when the abomasum is almost immobile, for in ruminants, as well as simple animals, considerable volumes of chyme can be refluxed into the stomach (Singleton, 1961).

The difficulty of assessing the multiple controlling mechanisms of gastric emptying in a way comparable to the cardiovascular and pulmonary systems has been stressed (Hunt, 1959; Hunt & Knox, 1968). This is true of man because of the intimate physiological interaction of stomach effluent on duodenal receptors. The difficulty is even greater in the complex ruminant stomach but the results of our experiments on abomasal emptying of the milk-fed calf show that at this stage the ruminant stomach is controlled by mechanisms similar to those demonstrated in the simple stomach. The effect of some molecules and ions on abomasal emptying reported by Bell & Razig (1973) adds weight to this view and suggests that the conscious milk-fed calf may be a valuable experimental subject for examination of gastro-duodenal physiological interrelationships.

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