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DEVELOPMENT OF DIGESTIVE FUNCTIONS IN THE NEWBORN RUMINANT

Y. RUCKEBUSCH1, C. DARDILLAT2 and P. GUILLOTEAU3

1: Ecole Nationale Vétérinaire, 31076 Toulouse, France
2: INRA Theix, 63110 Beaumont, France
3: INRA Zootechnie, 65 route de Saint-Brieuc, 35042 Rennes, France

Abstract

To assess the progress of developing digestive functions accurately, it is necessary to evaluate the relative changes of certain variables. Observations have been reported on anatomical, biochemical and physiological changes that occur during the digestive adaptation of the neonatal lamb or calf to the extra-uterine life. For example, chymosin, a milk-clotting acid protease, is maintained by the milk diet at a high level until weaning in calves, as a result of the stimulation by casein of the rate of chymosin synthesis.

Development of motor functions: The behavioural maturity at birth of the ruminant species is accompanied by full differentiation of the gastro-intestinal tract motor activity during the last stage of foetal life in sheep. The digestive adaptation to the extra-uterine life involves sucking within a few hours after birth: the effect of ingestion of colostrum on gastro-intestinal motility and the interference of the early microbial contamination on the digestive tract being the main factors to be considered.

From motor responses to the ingestion of colostrum evaluated from e.m.g. records obtained in calves within 5 h after birth, increase in the number of the bursts of spike potentials along the whole intestine was the most striking feature. The first meal induced a pattern of continuous spiking activity at the expense of the periods of quiescence and of the phases of regular spiking activity. Within 2 to 3 h, the patterns of activity resembled those recorded before feeding. In germ-free calves, the absence of flora was accompanied by: 1. irregularities in the antral slow-wave frequency: the interval between the slow waves of low magnitude being 2-4 times as long as in a normal animal; 2. gastroduodenal hypomotility characterized by the disappearance of any strong burst of spike potentials; and 3. the absence of motor responses to feeding as well as patterns of activity resembling those seen in the foetal lamb.

Enzymatic activities: Digestibility usually increases during one month after birth for both milk and milk replacers but subsequently evolved very little in the calf maintained at a preruminant stage. The evolution of digestive secretions has been studied to a great extent for gastric and pancreatic secretions. The daily quantities of gastric juice collected from an abomasal pouch increased up till six weeks and then decreased. Chymosin activity also decreases in the preruminant calf according to age, while pepsin activity tends to increase slightly. Circadian changes in abomasal secretion were related to feeding in calves fed twice daily at 8.00 and 19:00. As expected, the amount of chymosin and pepsin collected from an abomasal pouch during 7 h following the morning meal represented 35.7 and 33.7 % of the 24 h output instead of 31.1 and 29.9 % for the evening meal.

The secretory potentialities of the pancreas which were minimal during the first week in the newborn lamb, seemed then mainly influenced by the age of the animal. In the calf, lactase activity declined with age although it was still at eight weeks ten times that in the adult. Conversely, maltase and isomaltase activities increased during the first 1-4 weeks of life, the values being later similar to those in adult animals. The notion of diet-induced adaptive changes of both intestinal monosaccharide transport and metabolism could be emphasized by the total absorptive capacity of the small intestine: the rate of disappearance of glucose in lamb less than one week of age decreased by 75 % within 2-3 months.
Gastro-intestinal and pancreatic hormones: The responsiveness of insulin secretion to milk ingestion in the newborn clearly indicates that this hormone is of major importance in determining adaptive changes in nutrient utilization. A good example is given by the differences in the postprandial stimulation of insulin secretion when diets were switched from a milk to a fish diet. The blood levels of somatostatin and secretin which are both involved in the abomasal acid secretion were obviously lower in weaned calves than in unweaned controls of the same age. In contrast, the rise in the concentration of vasoactive intestinal peptide (VIP) and cholecystokinin (CCK) after weaning, might represent the counterpart of a considerable increase in the flow of digesta along the digestive tract. Feeding was accompanied by immediate but transient increase of the blood concentration of CCK and pancreatic polypeptide and by a sustained increase in the blood concentration of gastrin and secretin.

Minimal blood concentrations of somatostatin and VIP have been recorded in calves fed twice daily, either in fasted or fed animals, at midday while the blood concentration of secretin and CCK-PZ showed a tendency to decrease during daytime with superimposed hourly variations.

To assess the progress of developing digestive functions accurately, it is necessary to evaluate the relative changes of certain variables. Observations have been reported on anatomical, biochemical and physiological changes that occur during the digestive adaptation of the neonatal lamb or calf to extra-uterine life. For example, the relative size of the bovine stomach compartments at various ages (fig. 1) and the weight of the total digestive tract, from 5.2-5.8 % of the empty body weight whatever the calf’s liveweight, show that only relative development takes place as far as the preruminant stage is maintained (fig. 2). Similarly, among the digestive secretions, chymosin, a milk-clotting acid protease, is maintained by the milk diet at a high level until weaning in calves (see Garnot et al., fig. 3).

Contribution to existing knowledge also came from studies of the development of post-prandial motor and secretory responses using non-invasive methods in conscious animals. Radiography has produced much information (Bell and Mostaghni, 1975), but the actual flow of radio-opaque medium is difficult to assess (fig. 4). A notable advance was achieved with the record of electromyograms (e.m.g.) from multiple sites (Ruckebusch et al., 1972). However, the use of abomasal pouches provided the most interesting data related to the effects of feeding on gastric secretions and concerning the daily outflow of gastric juice which increased after birth in the neonatal calf (Guilloteau and Le Calve, 1977; Guilloteau et al., 1981).
When the gastric juice was collected at hourly intervals from calves fitted with an innervated abomasal pouch and milk fed twice daily, the influence of the morning meal was always more marked than that of the evening meal (Guilloteau and Toullec, 1983).

Finally, a significant advance in alimentary tract methodology has been the introduction of radio-immunoassay which now permits precise measurement of fluctuating endogenous hormone levels in the blood during the evolution of digestive processes. The coupling of radio-immunoassay with measurements of secretory and absorptive capacities as well as of motor functions will permit a discrimination between and quantification of nervous and humoral component actions.

This study will be restricted to the data of interest in the evaluation of the perinatal development of 1. motor functions, 2. digestive processes including secretions, absorption and disordered carbohydrate and protein digestion, 3. gastro-intestinal and pancreatic hormones levels in the blood.

1. Motor functions

The digestive adaptation to the extra-uterine life firstly involves sucking within 4 h after birth for 90 % of lambs, and within 6 h after birth for 66 % of calves (Edwards, 1982). Early sucking ensures 1. the energy to resist hypothermia brought on by fleece drying; 2. cellular gut immunity, 3. a direct supply of absorbable proteins which modify plasma smotic pressure, and 4. supply of antibody activity. The effect of ingestion of colostrum on gastro-intestinal motility and the interference of the early microbial contamination on the digestive tract are thus the two main factors to be considered. On the other hand, it has been established that the behavioural maturity at birth of the ruminant species is accompanied by full differentiation of the gastro-intestinal tract during the last stage of foetal life in sheep (Ruckebusch and Grivel, 1974).

1.1. Foetal alimentary tract

In the foetal lamb, stimulation of the peri-oral region at 0.8 of term was accompanied by gastric filling, a phenomenon that corresponded to swallowing of amniotic fluid (Duncan and Phillipson, 1951). The spontaneous contractile activity of the smooth muscles from the ovine complex stomach undergoes appreciable development during ontogenesis. It appears firstly in the abomasum at the end of two months, when the stomach has completed its differentiation. The contractile activity of the abomasum increases gradually from low-amplitude and un rhythmic during the first half of pregnancy to regular phasic activity near term. At 0.6 of term, the reticulum manifests stable spontaneous phasic contractile activity which disappears after delivery, while the rumen manifests no regular contractile activity before and after birth. It is suggested that inhibitory non-adrenergic nerve structures are involved (Milanov and Stoyanov, 1980). Full development of the ovine intestinal mucosa has been observed when the foetus is growing rapidly beyond 16-week gestation and seemed to be coincident with the existence of orally and aborally propagated contractions (Toofanian, 1976). In the foetal lamb, both slow waves and bursts of spike potentials were recorded from the gastro-duodenal junction and the small intestine.

Fig. 3. — Chymosin and pepsin activities in gastric content in milk-fed calves, weaned between 59 and 82 days of age (from Garnot et al., 1977).

Fig. 4. — Abomasum of a 10 day-old milk-fed calf. The non-secretory stomach (reticulum and omasum) is undeveloped. A prominent feature, the torus pyloricus, separates the antrum from the duodenum. Below, lateral radiograph from standing conscious calf following installation of a 1.5 l radio-opaque test meal and showing waves passing over the antrum in sequence (from Bell and McLeay, 1978).
Fig. 5. — Development of gastro-intestinal motility in foetal lamb and neonate. (a) Diagram showing placement of pairs of electrodes in the foetus one month before birth. (b) Electrical spiking activity of the jejunum 7 days before birth showing direct and retrograde propagation. (c) Slow-wave frequency before and after birth. Broken lines indicate intermittent presence of slow waves. (d) Percentage of the recording that spiking activity was present. (e) Velocity of passage of spike bursts with ratio of direct versus retrograde propagation in the foetus and recurring intervals between migratory complexes in the neonate (from Bueno and Ruckebusch, 1979).
but during less than 20% of the recording time at 90 days of foetal life. The subsequent development of the motor profile consisted of an increase of slow-wave frequency as a prerequisite of the duration of the spiking activity and its aboral propagation.

The results obtained in foetal lambs (Bueno and Ruckebusch, 1979) suggest that the patterns of electrical activity seen in the last third of foetal life can be related to their function of mixing and absorbing but not expelling intestinal contents (fig. 5). The electrical phenomena of the gastrointestinal tract recorded a few days before birth resembled that of myoelectric complexes seen in the adult. According to the relationships between the migration of these complexes and the propulsion of intraluminal contents, the stimulation of this pattern of motility by hypoxia may explain the elimination of meconium considered as a sign of foetal distress (Meis et al., 1982).

It must also be emphasized that if the newborn ruminant digestive system continues to develop with the breakdown of nutrients in the abomasum (Juhasz et al., 1976), the closure of the reticular groove permits, in the neonate like in the foetus, the direct passage of liquids into the abomasum. This pattern of activity partially persists when abomasal activity is progressively altered by its association to the microbial digestive activity of the forestomach.

1.2. Neonate motor functions

The unfed newborn calf shows the main motor patterns of activity seen in the lamb: regular occurrence of slow waves, intermittent bursts of spike potentials, propagation along the intestine as migrating myoelectric complexes. The number of bursts is variable but on the average, low until the first meal. From motor responses to the ingestion of colostrum evaluated from e.m.g. records obtained in calves within 5 h after birth, increase in the number of the bursts of spike potentials along the whole intestine was the most striking feature. The motor profile of the small intestine which consisted, like in lambs, of migrating complexes occupying 20-30% of the recording time (versus 49% in lambs) was modified. In both species, the first meal induced a pattern of continuous spiking activity at the expense of the periods of quiescence and of the phases of regular spiking activity (RSA). Within 2 or 3 h, the patterns of activity resembled those recorded before feeding with a transient period during which phases of quiescence alternated with phases of high amplitude regular spiking activity: such a profile is roughly mimicked by the excitatory effects of the i.v. administration of a high dose of 5-hydroxytryptophan (fig. 6).

A more detailed analysis of the flow rate in relation with the e.m.g. records (Dardillat, 1977) and of the propagation of spike bursts potentials in the calf (Dardillat and Bueno, 1979) indicated expulsion into the duodenum of boluses of 5-10 ml in volume by the antral contractions and their propulsion along the intestine on the short distance of about 1 metre at a mean velocity of a few cm per
second. The increased motility recorded after feeding concerned mainly the first third of the small intestine and then within about 120 min its whole length. More important was the occurrence during the first week after birth of a progressive development of the motor responses to feeding which consisted of a hyperactivity of the whole small intestine immediately after and even during feeding.

Besides the role of colostrum, that of microbial contamination has been questioned (Dardillat et al., 1977). In germ-free calves, the absence of flora was accompanied by 1. irregularities in the antral slow-wave frequency: the interval between two slow waves of low magnitude being 2-4 times as long as in a normal animal (fig. 7); 2. gastroduodenal hypomotility characterized by the disappearance of any strong burst of spike potentials; and 3. the absence of motor responses to feeding as well as patterns of activity resembling those seen in the foetal lamb. Accordingly, microbial contamination of the digestive tract was followed within 24 h in a 4-day-old calf by the patterns of activity seen in control animals.

1.3. Motor disturbances

The postnatal development of the motor functions is impaired during neonatal diseases. The motor disturbances of ten calves which exhibited transient hyperthermia, anorexia and diarrhoea or constipation (Dardillat, 1976) consisted of antral hypomotility followed by the disorganization of the small intestine spiking activity in a pattern of series of unpropagated spike bursts. Another pattern, recorded before the clinical signs of illness have developed, is oral propagation of some spike bursts. The outcome of the disturbances was in the case of death an irreversible "silent bowel" syndrome.

One could speculate that surgery performed within 2 h after birth might interfere with the absorption efficiency which decreases from birth, a reduction occurring at the same time as the renewal of the intestinal epithelium from 36 to 48 h after birth and apparently triggered by cortisol. Experiments performed in both operated and control colostrum-fed calves show in both cases rapid antibody absorption (fig. 8). The amount of immunoglobulins absorbed was similarly reduced in unoperated and operated calves exhibiting clinical signs of abomasal atony and distension, suggesting inhibition of the propulsive discharge of fluid from the terminal antral segment to the duodenum and possibly the accumulation of gas (or air) in the abomasal body above the fluid contents (Dardillat, 1982).

When newborn calves were subjected to cold stress and made hypothermic by immersion in...
water at 15 to 17 °C, cold stress delayed the onset and significantly decreased the rate of absorption of immunoglobulins (IgM, IgG1 and IgG2) up to 15 h after first feeding of pooled colostrum. However, the net absorption of colostral immunoglobulins was not affected (Olson et al., 1980). The deleterious effect of cold stress on absorption of colostral immunoglobulins by newborn calves might be related to a delayed gastric emptying of colostrum.

Diet and feeding techniques, especially milk replacers which increased the rate of abomasal emptying probably affect the digestive motor functions which in turn influenced protein and fat digestibility (Guilloteau et al., 1979).

2. Digestive processes

The evolution of digestive potentialities depends mainly on secretions, flora (at least in the case of some carbohydrates) and absorption. Estimates can be made either at the blood and lymphatic levels or by measuring digestibility.

2.1. Digestive secretions

The evolution of digestive secretions has been studied to a great extent for gastric and pancreatic secretions but not for salivary secretions. Different measurements made on parotid and submaxillary glands did not indicate in fact any evolution since the weight of the parotid glands in the calf decreased from 37 to 28 g/100 kg liveweight between the ages of 2 and 13 weeks (Sasaki, 1968). Gastric secretions: The amount of enzymes found in the gastric mucosa of newborn lambs did not seem to be related to birth weight and/or sex (Guilloteau et al., unpublished data). The quantity of chymosin decreased with age whereas that of pepsin did not change significantly in both preruminant lamb and calf. As expected, weaning was accompanied by lower chymosin and higher pepsin contents (Guilloteau et al., 1983, unpublished results). No changes with age occur in the distribution of enzymes in the fundus of the calf between the parietal and visceral surfaces or between the proximal, median and distal plicae. In contrast, an increased amount of the enzymes provided by

Fig. 9. — Effect of feeding on the secretion of gastric juice (a) in a calf fed once daily (from Hill, 1968) and (b) in calves fed twice daily — mean and SEM for 6 days (from Guilloteau and Toullec, 1983). The first meal caused a considerable increase in the secretion of electrolytes and enzymes. For H+ chymosin and pepsin, the values during the first postprandial hour were 4.2.4 and 2.1 times higher respectively than previously. The influence of the second meal was less marked. Variations in the amount secreted were larger for H+ ions than for the enzymes, with a ratio between maximum and minimum of 4.6 for H+ ions and of 2.8 for chymosin.
the ventral surface (along the greater curvature) was recorded with age meanwhile the part of enzymes provided by the dorsal surface along the small curvature decreased (Guilloteau et al., 1982).

The daily amount of gastric juice secreted by an abomasal pouch decreased with age on a body weight basis like that of chymosin in the preruminant calf. The amount of pepsin and H⁺ which remains unchanged after birth increased at the time of weaning, a phenomenon paralleled by an important increase in the secretion of gastric juice (Guilloteau et al., 1980). According to Ternouth and Roy (1973), the outflow of acid beyond the pylorus could be doubled during the first month and tripled during the second month of age without changes in the amounts of Na⁺, K⁺ and Cl⁻ ions. This acid secretion decreased with soyabean protein instead of milk protein and increased with fish protein; the amount of chymosin decreased likewise when the casein content of milk was reduced (Williams et al., 1976). The coagulating activity of samples of abomasal mucosa taken in 24-day-old calves was half that measured 5 days after birth (Hagyard and Davey, 1972).

Pancreatic secretions: The development of pancreatic enzymes undergoes a reverse pattern of that recorded for chymosin in the lamb and the calf, except for colipase activity which did not increase at weaning (Guilloteau et al., 1983). The colipase/lipase ratio was always higher than 1 in the lamb, suggesting that lipase activity was always saturated. The potentialities of pancreatic enzyme digestion appeared to be influenced mainly by age or weight of the newborn ruminant. Accordingly, a low activity persisted for about 7 days after birth (fig. 10), especially when not enhanced by enzymatic adaptation to the amount of the ingested substrate. Finally, the pancreas seemed to take over progressively the secretion of abomasal proteolytic enzymes.

In the calf, lactase activity declined when age increased although it was still at 8 weeks ten times that in the adult. Conversely, maltase and isomaltase activities increased during the first 1–4 weeks of life, the values being later similar to those in adult animals (Toofanian et al., 1974). The notion of diet-induced adaptive changes of both intestinal monosaccharide transport and metabolism could be emphasized by the total absorptive capacity of the small intestine: the rate of disappearance of glucose in lamb less than 1 week of age decreased by 75% within 2–3 months. In addition, these changes in the active intestine monosaccharide (and amino-acid) transport were independent of the rumen development, at least for their control by insulin (Sharrer, 1975).

2.2. Absorption and digestibility

The postprandial evolution of the plasma concentration of triglycerides was similar in the neonate receiving milk substitute immediately after birth, to that observed in 2.5 month-old calves (fig. 11). This indicated that the dietary fat was absorbed at about the same rate in the two groups of animals. The blood glucose level which increased during 6.5 h after a meal in the newborn, decreased immediately after 30 min in older calves. Since the gastric emptying of lactose was more rapid than that of fat, it seems that the metabolic utilization of glucose is not so fast in the newborn than in older calves (Edwards, 1970). The blood free α-amino-nitrogen level was always higher in the newborn than in the 2.5 month-old calves. However, differences in the postprandial evolution probably reflect important changes with age in the amino-acid metabolism.

Digestibility usually increased during a month after birth for both milk and milk substitutes, but subsequently evolved very little in the calf maintained at a preruminant stage (Roy and Stobbo,
1975). The nitrogen and lipid digestibility decreased more especially as coagulation was modified but the modification or the suppression decreased when the calf got older (Toullec et al., 1974). In the preruminant lamb, the daily quantities of starch digested in the whole gut were 10.7 and 14.3 g/kg P<0.05 respectively in germ-free and holoxenic animals (Peyraud et al., 1981); thus, flora could digest 3.6 g starch almost exclusively in the hindgut.

In the milk-fed calf, the amino-acid composition of faeces became more different of that of meconium and more similar to that of faecal bacteria, as age increased (Grongnet et al., 1981); these observations showed that in faecal protein, the proportion of endogenous protein decreased and that of bacterial protein increased.

The importance of abomasal digestion was demonstrated by substituting to skim-milk other sources of protein (fish diet) which increased the abomasal emptying rate. As a result, the metabolic utilization of the diet components could be unfavorably affected by very rapid absorption of lipids and amino-acids (fig. 12). When food was given by tubing into duodenum thus bypassing the abomasum, no significant effect on animal health was observed but the apparent digestibility of each diet decreased for an infusion into the duodenum at the gastric emptying rate of its protein (slow infusion of the control diet, rapid infusion of fish). Infusion at a higher rate (rapid infusion of the fish diet) increased this effect, while infusion at a lower rate (slow infusion of the fish diet) suppressed it, thus indicating a role of paramount importance of the time spent in the abomasum for the digestion of proteins and fats.

2.3. Disordered carbohydrate and protein digestion

Starch digestion is limited in the calf less than 60-day-old when given in the milk at a level exceeding 15% on a dry matter basis. Nevertheless, the calf's ability to adapt to starch utilization is quite spectacular on the basis of the growth rate with milk substitutes containing various proportions of starch products. A calf could be maintained in the preruminant state, at least from 60 days of age on, by replacing all the lactose in milk substitutes by starch products. Feed efficiency and carcass characteristics remain unaltered by this substitution (Thivend et al., 1980). Impaired carbohydrate absorption from stomach and small intestine can occur as a result of pancreatic insufficiency, from generalised enterocyte malfunction and as a result of genetically determined enzyme and transport system defects. Isolated amylase deficiency has not been detected but lactose deficiency occurred as a consequence of diarrhea. The predictable consequences of malabsorption are that the contents of the small and large bowel are maintained at an isotonic concentration achieved by the absorption of a large volume of water accompanying the absorption of solutes which include...
monosaccharides. For example, the ingestion of half a litre of milk containing 20 g of lactose will result in the osmotic retention of 200 ml of water within the jejunum which in turn stimulates peristalsis, and in some subjects abdominal pain and diarrhoea.

The use of milk substitute proteins that do not coagulate accelerated gastric emptying of protein and fats without diarrhoea, except in the case of inflammatory reactions of the intestinal mucosa to feed antigens of some soya bean products. When the ingested proteins came exclusively from milk, the amino-acid composition of the ileum contents differed greatly from that of the milk and resembled that of endogenous proteins, suggesting a complete digestibility. When casein was replaced by fish or soya bean protein, the proportion of dietary protein in the ileum contents increased when the digesta flow rate was high. However, no protein losing enteropathy associated to protein malabsorption has been described.

A point of interest is the part taken by the digestive processes in the high mortality associated to low birthweight in ruminants. The digestibility of a milk substitute was compared in 1 week-old lambs weighing from 1.8 to 5.5 kg (Houssin and Davicco, 1979). A lower digestibility of dry matter, energy, crude protein was evidenced for the small size lamb. The digestibility of the saturated long-chain fatty acids was markedly decreased. These acids have poor solubility in the micellar solution of bile salts necessary for their absorption and form insoluble calcium soap excreted in faeces. This suggested that low birthweight lambs may suffer from an insufficient bile salts pool also found in premature infants (Watkins et al., 1973) and leading to an increased formation of calcium soap.

3. Gastro-intestinal and pancreatic hormones

The responsiveness of insulin secretion to milk ingestion in the newborn clearly indicates that this hormone is of major importance in determining adaptive changes in nutrient utilization (Grizard et al., 1979). The postprandial stimulation of insulin secretion in 50 versus 65 day-old calves when diets were switched is also of interest (fig. 13). The role in the postnatal maturation of the digestive processes of the hormones of the alimentary tract is highly questionable. These hormones (both of the pancreas and GI tract) comprised two distinct groups of similar structural homology and related endocrine function. The first group which contains cholecystokinin (CCK), gastrin as well as motilin, somatostatin and pancreatic polypeptide are peptides predominantly stimulating gastro-intestinal motor activity (Bueno et al., 1982). The second group has a structure like that of secretin and contains many newer hormones such as pancreatic glucagon, enteroglucagon, vasoactive intestinal peptide (VIP) and gastric inhibitory peptide (GIP). The older omnibus inhibitory hormone enterogastrone may prove to be a cocktail of some of the secretin group of hormones, and is predominantly inhibiting the gastrointestinal motor activity.

3.1. Perinatal sensitivity to insulin

The infusion of arginine and of glucose stimulated a release of insulin in the sheep fetus from 119 to 142 days of gestational age (Fowden, 1980b); the infusion of adrenaline abolished the response to both glucose and arginine (Fowden, 1980a). The intravenous injection of insulin induced severe hypoglycaemia in the calf at different ages (Edwards, 1970); however, the resistance to hypoglycaemia was higher from birth to four days of...
age than from one to four weeks. The intravenous administration of 1.25 mIU insulin/kg produced a prolonged hypoglycaemia accompanied by an increased continuous pattern of activity along the whole digestive tract of the 10 day-old calf (Ruckebusch, 1981).

In lambs, ingestion of milk before weaning was followed by a pattern of continuous activity which was of longer duration if the animal was fasted. In both animals a good correlation was found between the IRI level (mean maximal increase 98 ± 17 μU/ml) and the duration of the pattern of continuous activity (4-5 h). Toward the end of the weaning period, the IRI increase was halved (mean maximal increase 50 ± 13 μU/ml), and the continuous pattern of activity lasted only about 3 h. The mean maximum IRI level after milk increased to 70 ± 20 μU/ml) after a 24 h-fast, and the continuous activity lasted 1 or 2 h longer (Bueno and Ruckebusch, 1976). After weaning, motor responses to feeding disappeared. Other factors, such as gastrin and/or motilin, somatostatin, pancreatic polypeptide (Bueno et al., 1982) might be involved in the motor response of the neonate to feeding. However, the major part seemed played by insulin release in response to glucose in the neonate and experimentally by the infusion of a volatile fatty acid mixture which are potent insulin-releasing stimuli after weaning (Bueno et al., 1977). The part played by the automatic nervous system remains largely unknown. Also a vagal reflex mechanism may be involved, similar to that suggested for the release of vaso-active intestinal peptide from the gastro-intestinal tract in response to autonomic stimulation in the calf (Edwards et al., 1978; Bloom et al., 1979).

3.2. Postnatal evolution of hormone blood levels

In the newborn calf fasted from birth to 28 h, the plasma level of somatostatin increased from birth to 5 h, decreased from 5 to 16 h and then did not change; the plasma levels of secretin, CCK and

![Graphs showing hormone blood levels](image)

*Fig. 13.* Postprandial immunoreactive insulin concentrations and related glycaemia of 50 and 65 day-old calves receiving skim milk powder. The area under the curve of blood insulin was reduced with age. This effect was not significant for the diet fish (from Grizard et al., 1982).
VIP did not show any modification (Guilloteau et al., unpublished results). The first colostrum meals involved large increases in the levels of secretin, CCK and VIP but not in that of somatostatin. Thus, the first meals probably initiated the departure of many regulatory digestive mechanisms.

The levels of somatostatin and CCK increased from birth to two weeks of age, but that of VIP and secretin did not show any significant trend (fig. 14). The prefeeding levels of somatostatin and secretin were obviously lower in weaned calves than in unweaned controls of the same age (fig. 14); by contrast, the levels of VIP and CCK tended to be higher in weaned calves. One hour after the morning meal, the differences between weaned and unweaned animals did not change for somatostatin and VIP but were reversed for secretin. The concentration of CCK recorded before or after feeding tended to decrease between 9 and 13 weeks in weaned calves.

3.3. Diurnal and postprandial changes of hormonal plasmatic levels

In preruminant calves, a diurnal rhythm characterized by minimal values at midday has been recorded for somatostatin and vasoactive intestinal polypeptide (fig. 14). The plasma level of secretin and CCK showed a tendency to decrease during daytime with superimposed hourly variations. This evolution was recorded either in faster or fed ani-

Fig. 14. — (a) Changes in the hormone plasma levels of preruminant calves from birth to 13 weeks of age and effect of weaning finished at 8 weeks on both somatostatin and secretin blood levels. — (b) Circadian variations of cholecystokinin and secretin in more than 30 day-old preruminant calves. Full lines (n = 8) correspond to fasted animals which have got their last meal 16 h before the beginning of blood sampling. Dotted lines (n = 35) correspond to animals fed at 8 and 15 h 45 (from Guilloteau et al., unpublished data).
mals. Feeding was accompanied for both the morning and evening meals by immediate and transient increase of the plasma concentrations of cholecystokinin and pancreatic polypeptide (Davicco et al., 1979). As suggested by McLeay and Bell (1981), cholecystokinin might be a potent stimulus for gastric acid secretion in the calf. The sustained increase in the blood concentration of gastrin and secretin which occurred from 4 to 7 h after feeding was accompanied by low blood levels of somatostatin, hence the long-lasting changes in abomasal secretions (Guilloteau and Toullec, 1983). The maximum secretion of pancreatic (Davicco et al., 1979) or gastric (Guilloteau and Toullec, 1983) juices did not seem to occur when the plasma levels of gastrin and CCK are maximum and that of somatostatin is minimum. These observations suggest that other mechanisms (other hormones, autonomic nervous system,...) were involved in the control of gastric and pancreatic secretions. According to Bell et al. (1981) the complete inhibition of gastric function which ensued on acidification of the duodenum and which continues after splanchno-vagotomy, is not mediated by autonomic nervous system. This inhibitory process appears to involve the endocrine system only, with somatostatin (but not gastrin) fulfilling a main enterogastrone role.

In weaned calves, the levels of secretin, CCK and VIP observed 1 h after the distribution of the diet were not different from prefeeding levels (Guilloteau et al., unpublished results): that might be due to staggering of ingestion along the day, hence a more regular flow rate of digesta.

Conclusions

Many studies of the development of the alimentary tract have been discussed in terms of changes limited to the inductive role of various nutrients. Accordingly, patterns of motor activity resembling those of the adult are fully developed only after birth (Ruckebusch and Bueno, 1973). Similar changes occurred only after weaning for digestive functions (Toullec and Mathieu, 1973). However, recently designed studies showed that not only sucking behaviour (Titchen and Newhook, 1975) but also secretory (chymosin) and absorptive (proteins) capacities are already well developed at birth. In fact, the important development of gastric acidity and pancreatic enzyme secretions after birth indicates that the digestive functions of the neonate could be easily impaired. Many of the factors involved in the adaptive changes to nutrient utilization before weaning are still ignored, especially those related to the neuro-hormonal control of the increased postnatal digestibility of milk and milk substitutes.

A real peculiarity for ruminants as a group of mammals which deliver young that are agammoglobulinaemic, is that their newborn are dependent upon colostrum not only for nutrients but also for antibodies. The subsequent postnatal changes in gut motility and enzyme activities are triggered by intermittent enteral feeding via specific hormonal surges. These effects will progressively decrease with postnatal age until the transition to the ruminant pattern of digestion associated with a considerable increase in the volume of digesta.

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