

The effect of nutrients on feed intake in ruminants

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The purpose of the present review is to examine the role played by nutrients in controlling feed intake in ruminants, in light of their particular anatomical, physiological, nutritional and behavioural characteristics. The ration is first digested in the rumen for several hours by microbial fermentation. Volatile fatty acids, which constitute 50–75 % of a ruminant's energy supply, considerably depress feed intake when administered by short-term infusion into the rumen. However, this effect seems to be largely due to osmolarity problems. Only propionate seems to have a specific action, unrelated to osmolarity, in the mesenteric or portal veins. Nitrogenous nutrients have little short-term effect on feed intake, except when there is excess NH₃ in the rumen. Metabolic cues from intestinal digestion, particularly of glucose and starch, have very little short- or long-term influence in controlling feed intake, in comparison with rumen digestion cues. However, the short-term responses in feeding behaviour do not always reflect longer-term effects on feed intake control. The effects of volatile fatty acid infusion on feed intake are much less significant over the long term, except in the case of propionate. The nutrients required for good microbial activity (proteins in the rumen) generally promote feed intake, whereas nutrients that disrupt rumen functioning (lipids) reduce feed intake. After a learning period, preferences are always governed by a tendency toward optimum rumen functioning, rather than by animal nutritional requirements, although the two factors are not independent. Ruminants, due to their particular anatomical and nutritional characteristics, have, in the course of their evolution, developed specific feed intake control mechanisms based on nutritional cues.

Résumé

L'objet de cette revue est d'étudier le rôle des nutriments dans les mécanismes de contrôle de la prise alimentaire chez les ruminants, en tenant compte de leurs particularités anatomiques, physiologiques, nutritionnelles et comportementales. La digestion de la ration se déroule d'abord pendant de nombreuses heures dans le rumen par fermentation des aliments par des microbes. Les acides gras volatils, qui constituent 50–75 % des nutriments énergétiques d'un ruminant, présentent des effets rassasiants marqués lorsqu'ils sont perfusés dans le rumen. Cependant, ces effets semblent liés dans une large mesure à des problèmes d'osmolarité. Seul le propionate semble agir avec une action spécifique autre que l'osmolarité au niveau des veines mésentériques ou porte. Les nutriments azotés ont peu d'effet à court terme sur la prise alimentaire, excepté en cas d'excès d'ammoniac du rumen. Les signaux métaboliques provenant de l'absorption intestinale, en particulier le glucose ou l'amidon, ont très peu d'effet, à court ou long terme, dans le contrôle de la prise d'aliment comparativement aux signaux provenant de la digestion ruminale. Mais les réponses observées à court terme dans le contrôle de la prise alimentaire ne présagent pas toujours des effets à plus long terme dans la régulation des quantités ingérées. Les effets des acides gras volatils sur les quantités ingérées sont beaucoup moins nets à long terme, sauf pour le propionate. Les nutriments indispensables au bon fonctionnement de l'activité microbienne (protéines dans le rumen) ont des effets favorables sur l'ingestion alors que les nutriments qui perturbent le fonctionnement du rumen (lipides) diminuent les quantités ingérées. Après apprentissage, les choix alimentaires s'orientent toujours vers une recherche d'un fonctionnement optimal du rumen plus que vers une bonne adéquation des apports aux besoins de l'animal, même si les deux ne sont pas indépendants. Les ruminants présentent donc, de par leurs spécificités anatomique et nutritionnelle, des adaptations originales dans les mécanismes de régulation des quantités ingérées à partir des signaux nutritionnels.

Ruminants: Feeding behaviour: Volatile fatty acids

Abbreviation: VFA, volatile fatty acids.

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Ruminants play a significant role in ecosystems, since they mainly eat plants. To get the most benefit from roughage, the ruminant digestive system includes forestomachs known as the reticulum, rumen and omasum, which constitute a veritable continuous-process digester. Ruminants use the various fermentation products as their main source of nutrition. Feeding behaviour may be separated into two distinct components: feed intake and rumination (Jarrige *et al.* 1995), which are highly influenced by the fact that feed consists primarily of roughage. Feeding is generally of very long duration (from 5 to 11 h/d), particularly when ruminants are in a natural environment and must find food for themselves. This extensive use of roughage has resulted in various specific characteristics relating to eating behaviour, digestion and metabolism, which have implications for feed intake control mechanisms.

In ruminants, the activity of eating occupies most of the daytime. Changes in feed intake kinetics and particularly in feed intake rate over time make it possible to study the development of satiation mechanisms. The presence of feed in the rumen is an essential phase of the satiation process. Removing boluses during feed intake almost doubles the size of a normal meal (Campling & Balch, 1961). Although rumen fill plays a role in the satiation process (Forbes, 1995), the biochemical cues produced by fermentation may also be used to control feed intake. Digestion products during the post-feeding phase may, in the short term, send signals to the central nervous system through various nervous, metabolic or hormonal channels, and may also contribute to the satiation process during feeding. Their long-term effect is more complex, since a nutrient may cause premature satiation, without however ultimately reducing feed intake. The stimulation of reward mechanisms or effects on the metabolism may also have a longer-term impact on the animal's appetite.

The purpose of the present review is to show how nutrients are involved in feed intake control mechanisms in ruminants, in light of their particular anatomical physiological, nutritional and behavioural characteristics. It will deal specifically with the effects of major macronutrients on feed intake, examining separately energy nutrients and nitrogenous nutrients. First, the short-term effects of nutrients on appetite will be examined in both feeding and post-feeding satiation processes. An attempt will then be made to study the medium- and long-term effects of nutrients on feed intake. These mechanisms are more complex, but more interesting since they modify overall feed intake and not only feed intake kinetics.

The effect of nutrients on short-term feed intake control

The reticulo-rumen forms a very effective fermenter capable of rapidly digesting the carbohydrate compounds found in plant fibre for which ruminants have no specific enzymic system. The rumen digestion of carbohydrates essentially produces short-chain fatty acids, or volatile fatty acids (VFA), with two to six C atoms, mainly acetic, propionic and butyric acids, and to a lesser extent valeric and caproic acids and their isomers. Substances that are not degraded in the rumen are digested in the abomasum and the intestine, essentially as they are in single-stomached animals. The

relative proportions of these final digestion products vary considerably according to the composition of the diet.

VFA are very quickly metabolized when they pass through the rumen wall. Acetic and butyric acids mainly form ketonic and acetate substances in the blood, whereas propionic acid is almost totally converted into lactate (in the ruminal epithelium) and into glucose (in the liver). In ruminants, unless they are given a special diet, there is little glucose digested in the intestine. Glucose is primarily produced by hepatic gluconeogenesis. Ruminant livers use virtually no blood glucose.

Energy nutrients

Carbohydrates (i.e. soluble sugars, starch, hemicellulose and cellulose) ingested by ruminants may either be converted into VFA, mainly in the reticulo-rumen (a little in the omasum and in the large intestine) or, to a lesser extent, into glucose in the intestine, when starch is not digested microbially in the rumen.

Volatile fatty acids. VFA are the main energy source for ruminants, generally accounting for 50–75 % of energy digested. Their production through fermentation increases very rapidly when feed arrives in the rumen. These two characteristics explain why VFA were soon considered to play an important role in satiation.

Many experiments have shown that intraruminal infusion of a VFA mixture with a composition similar to that normally found in the rumen causes a decrease in feed intake during the course of a meal. Feed intake is inversely proportional to the amount of VFA infused. Major infusion experiments have shown that feed intake response varies with the type of VFA infused (Faverdin *et al.* 1995), in the following decreasing order: acetate > VFA mixture > propionate > butyrate. For a given level of energy infused, feed intake response is inversely proportional to the size of the molecule. Osmolarity in the rumen, however, seems to be a major satiation factor, as salt infusion studies have shown (Ternouth & Beattie, 1971; Bergen, 1972). This observation suggests that the VFA action cue may be of an osmotic nature. Comparing the effects of osmolarity and VFA has revealed considerable similarities (Grovmum, 1995). In Baile's work (Baile & McLaughlin, 1970), which resulted in the highest intake responses, the authors also noted a significant effect on water consumption. The nature of the rumen receptors remains to be determined (Forbes & Barrio, 1992), and there is no biological proof of the existence of osmoreceptors in rumen walls that are sensitive to physiological variations in osmotic pressure (Carter & Grovmum, 1990). The role of an osmotic cue, however, would be very similar. The increase in osmotic pressure may harm both the ruminant and the functioning of the rumen, since microbial cellulolytic activity is considerably reduced when the osmotic pressure of the incubation medium is increased (Bergen, 1972).

The effects of VFA mixtures are sometimes greater than those of an iso-osmotic saline (9 g NaCl/l) control sample (Engku Azahan & Forbes, 1992; Faverdin *et al.* 1992; Faverdin & Peyraud, 1994). It is possible that the effect of the VFA is not merely osmotic in nature. Among the various VFA, propionate seems to play a major and special role

(Baile & Mayer, 1969; Frobish & Davis, 1976; Farningham & White, 1993). The injection of local anaesthetics into the rumen eliminates the effects of acetate and butyrate infusions, but not those of propionate infusions (Martin & Baile, 1972). Infusion into the liver seems to reduce appetite whereas infusion into the jugular vein has no effect (Anil & Forbes, 1980). Furthermore, lesions of the nerves of the hepatic plexus eliminate the effect of propionate infused into the portal vein. Strangely, the response in the mesenteric veins seems to be greater than that in the portal vein (Leuvenink *et al.* 1995). The most recent work shows clearly that this effect is independent of the osmotic effects related to the infusion (Farningham & White, 1993; Leuvenink *et al.* 1995).

With more physiological doses or with saline control solutions, the effect of VFA infusions tends to disappear (De Jong, 1981; Quigley & Heitmann, 1991; Grovum, 1995). It seems, however, that animals become increasingly sensitive to VFA infusions with higher feed intake levels and therefore higher internal VFA production (Faverdin, 1990; Faverdin *et al.* 1992).

These various satiation cues may combine and, at least partially, have a cumulative effect over the short term. Thus, ruminal infusions of propionate and acetate result in a greater decrease in feed intake than each of the nutrients infused alone (Mbanya *et al.* 1993). This finding is in keeping, as with a dose effect, with detection by osmoreceptors. However, the same cumulative effect may be seen with different types of satiation cues such as rumen fill and VFA infusion (Adams & Forbes, 1981).

Far from controlling feed intake according to needs, short-term VFA satiation mechanisms, above all, make it possible to evaluate the size of the meal and prevent excesses that could be detrimental to the proper functioning of the rumen or even the ruminant's health. It is probable, however, that propionate plays a special role among the various VFA as a feed intake control cue. Thus, it could help limit the intake of diets rich in feed concentrates.

Glucose. Intestinal glucose represents a relatively minor energy source in normal ruminant diets. Only the presence of a large amount of starch with low rumen degradability would result in large amounts of glucose. Given the important roles that glucose and insulin play in rats and human subjects, many authors have tried to detect similar effects in ruminants. In the late 1950s, Manning *et al.* (1959) infused glucose intravenously into adult ewes for 2 h and observed no changes in feed intake or in eating behaviour. These results were rapidly confirmed (Dowden & Jacobson, 1960). Since then, intravenous or intraperitoneal infusions performed on various ovine and bovine species at various doses and times (Holder, 1963; Simkins *et al.* 1965; Frobish & Davis, 1976; Hikosaka *et al.* 1979) have revealed no effect of glucose on feed intake.

Intravenous infusions of insulin increase the use of glucose by tissues in ruminants as in single-stomached animals. This phenomenon also often causes a slight decrease in glycaemia during meals, since glucose use increases more rapidly than its arrival during the meal as a result of digestive absorption or gluconeogenesis. Intravenous infusion of insulin induces a slight decrease in feed intake during the 30 min following the injection (the phase

during which glucose is most rapidly used). However, this very short-term effect is generally compensated for during the following 1 h by an increase in feed intake (Faverdin, 1985; Bareille & Faverdin, 1996). Conversely, large injections of insulin result in prolonged hypoglycaemia that increases feed intake to some extent (Haupt, 1974). These side-effects of insulin and glucose (Dulphy & Faverdin, 1987) in ruminants are similar to effects observed in single-stomached animals, but are much less severe (Le Magnen, 1985). However, it is probable that the low variations in glycaemia and exogenous glucose under actual feeding conditions limit the effect of these mechanisms.

Lipids. Lipids form a small proportion of the energy nutrients ingested by ruminants, since roughage tends to contain relatively little lipid. Most lipids are hydrolysed in the rumen and the long-chain fatty acids thus released are largely hydrogenated when they are not protected by special treatments. Fatty acids are absorbed by the intestine in quantities similar to those ingested, but they have a very different composition (following hydrogenation and conversion to microbial lipids). Their short-term effects can be studied by intravenous infusion, since any rapid increase in lipids is primarily due to the mobilization of body reserves. Studies related to this subject (Vandermeersch-Doize & Paquay, 1984; Bareille & Faverdin, 1996) have revealed that lipid infusion depresses feed intake. This response is very fast and synchronous with infusion, but it remains limited. The response to exogenous lipids, such as Intralipid infusion, is different however from that observed by the mobilization of body lipids using such lipolytic substances as β -adrenergic agonists (Bareille & Faverdin, 1996). This response is due to the fact that during the lipolysis phase caused by the lipolytic agents the concentration of free fatty acids increases very rapidly, with no effect on appetite. It is only several hours later that feed intake decreases, this decrease possibly continuing after the mobilization phase. The effect of free fatty acids on appetite, therefore, does not seem to be direct, and the mechanisms involved have not been clearly identified in ruminants.

Nitrogenous nutrients

The microbial population is able to digest all nutrients in relatively large proportions. This is the case for protein, which forms NH_3 . Microbes, however, can also use NH_3 to make their own amino acids and proteins; thus the amino acids arriving in the cow's duodenum are different in proportion and in nature from those in the ingested protein. This adaptation of N and the ability to use non-protein-N are therefore major points of difference from single-stomached animals. This process means that proteins arrive in the intestine much later than the time of ingestion, and may be considered to have a more medium-term action.

Rumen degradation on the other hand rapidly causes NH_3 to form in the rumen, and this may constitute a major short-term cue. NH_3 in the rumen enables microbes to carry out protein synthesis, but it is absorbed very rapidly through the rumen wall and may become toxic in large doses when the liver's detoxification capacity is exceeded. This process may explain the decrease in feed intake observed after infusion of ammonium salts into the goat rumen (Conrad *et al.* 1977).

However, large doses must be administered to obtain these responses and adding NH_3 to grass silage in doses near those observed in practice causes no modification in behaviour and no decrease in feed intake in sheep (Van Os *et al.* 1995).

Short-term response limits

Experimental feeding of final digestion products to ruminants poses many methodological problems due to the short length of the C chains, which means that substantial amounts must be provided to reach a significant energy level. When biosystem conditions are not disrupted, there is generally no effect on feed intake (De Jong, 1981).

To avoid problems associated with infusion methodology, another possibility is to add directly into the rumen a feed that ferments rapidly (using an artificial saliva to replace that which would have normally accompanied ingestion) for a short period. Using this methodology, no effect on the satiation response for the meal studied was observed, either during the meal or during the 4 h preceding the meal (Faverdin *et al.* 1999). However, more than 12 h after this treatment, cows increased the intensity of their satiation response during main meals of their usual diet, although no further treatment was administered. The cows assimilate the characteristics of a particular diet after analysing all the consequences of a meal's post-digestive characteristics. After one or more experiences, diets are evaluated according to their sensory characteristics at the start of the meal and animals anticipate the expected consequences by satiation responses of varying intensity. They cannot do this rapidly when the feed is added directly to the rumen (Baumont *et al.* 1994).

Recent work by Provenza and his team (Provenza, 1995) clearly shows the important role that post-ingestive cues play in the learning of diet preference, and how the diet's sensory characteristics are used to identify it, as had been observed in single-stomached animals (Booth, 1992). Experiments performed over a period of only a few hours have been unable to account for these learning mechanisms, which control feed intake or diet preference over a longer period. A treatment that has no effect over the very short term may modify the animal's feed intake over the long term through a learning process. Conversely, a nutrient's very high short-term impact on feed intake, due to a disruption of the animal's equilibrium, may disappear after several days of treatment if the animal succeeds in adapting to this disequilibrium. In ruminants, the satiation process seems to be largely determined at the start of the meal, once the diet has been identified. Associations between nutrients and hormonal secretions certainly play a decisive role in the memorization and learning of the necessary behavioural response to a given diet. The role of cholecystokinin in these processes has already been clearly observed (Farningham *et al.* 1993; Berthelot *et al.* 1996). After learning, feed intake control responses to different nutrients may therefore be different from responses observed over the short term.

Short-term effects of nutrients on the control of feed intake may be found in ruminants, but they seem to be minor. Nutrients have a direct feedback effect on feed intake primarily when they disrupt the animal's homeostasis. The main mechanisms seem to involve osmotic pressure

equilibrium, rumen distension, homeothermy and acid–base equilibrium in the blood and the rumen. These mechanisms work to preserve the animal's short-term equilibrium. When they are triggered minimally or not at all, there is generally little effect on feed intake. However, short-term cues may be involved in the learning mechanisms that enable diet evaluation, and thus have a lasting effect on feed intake.

The effects of nutrients on medium- and long-term control of feed intake

Medium- and long-term feed intake responses always involve complex mechanisms. In ruminants they are even more complex, since there are two types of nutritional equilibria: the equilibrium of the rumen ecosystem and the metabolic equilibrium of the ruminant itself.

Energy nutrients

Volatile fatty acids. VFA infusions administered in order to study effects on feed intake have generally been designed to favour short-term response. However, infusions of a VFA mixture for 2 weeks show that the substantial effects observed during the first few days in lactating animals tend to disappear after 2 weeks of infusion (Faverdin *et al.* 1992).

Thus, after experience, responses to repeated VFA infusions may evolve. When excess propionate in the rumen is associated, through learning, with a particular smell applied to a particular diet, the conditioned preference for this diet decreases in comparison with the same diet with a different smell (Ralphs *et al.* 1995). This aversive response only occurs with large amounts of propionate. Furthermore, the same response is obtained with excess salt (Villalba & Provenza, 1996). It is possible that the negative effects of the disequilibrium caused by hyperosmotic infusions are associated with a state of discomfort, perhaps a 'nauseous' feeling. When antiemetic drugs are used to treat a LiCl-induced aversion, they neutralize the effect of LiCl on the appetite (Provenza *et al.* 1994). It would be interesting to study the effects of these drugs during ruminal infusions of high VFA doses. However, lambs show a clear preference for diets associated with low-propionate doses in the rumen (Villalba & Provenza, 1996). The mechanisms of this preference are not yet known, but they allow the ruminant to select diets containing the most gluconeogenic substances.

Glucose. Extended infusions of glucose into the duodenum have no effect on feed intake in dairy cows (Faverdin *et al.* 1992). Unlike single-stomached animals, glucose receptors could not be found in the ruminant duodenum. Adapting the diet to increase glucose in the intestine therefore has no effect on feed intake. The same is true for large doses of starch when the intestinal enzymic system is present. Over the long term, a starch-rich diet that is not degraded in the rumen is generally more readily ingested than a diet with an equivalent energy value but which is primarily and rapidly degraded in the rumen. This finding is consistent with the assumption that ruminants are more sensitive to satiation cues from the rumen than to those from intestinal digestion, particularly with respect to glucose.

Furthermore, it seems that ruminants detect and develop a preference for sweetened diets. For example, among several

types of feed additives or control samples, cows show a preference for diets to which sucrose has been added (15 g/kg DM content; Nombekela *et al.* 1994). Similarly, after a period of learning, sheep prefer a diet when it is associated with the force-feeding of glucose, even though glucose is highly fermented in the rumen (Ralphs *et al.* 1995). The mechanisms of this preference for sugar in ruminants have yet to be understood. There are few practical applications, since this preference for sweetness does not enable feed intake to be increased over the long term (Nombekela & Murphy, 1995).

In ruminants, intestinal glucose does not seem to have a satiation effect. It is undoubtedly by modifying the area of the digestive system where energy is digested, rather than by modifying palatability, that diets rich in intestinal glucose may contribute to increasing feed intake, even if ruminants show a preference for sweet feeds when they can choose.

Lipids. There are few lipids in ruminant feed. However, adding lipids directly to feed or by extended infusion has been widely studied for dairy cows, in order to increase the diet's energy supply and reduce the mobilization of reserves. Indeed, lactating animals release large quantities of lipids into milk (over 1 kg/d at the start of lactation) which are mostly synthesized from VFA produced in the rumen and long-chain fatty acids produced by the mobilization of adipose tissue.

Lipids added to the duodenum by extended infusion generally reduce feed intake (Hagemester *et al.* 1988; Gagliostro & Chilliard, 1991; Chilliard *et al.* 1993; Doreau & Chilliard, 1997). These responses are significant for rather low doses of 300–500 g lipids/d, with a reduction in intake of about 2 kg DM, or about 10 % of daily intake. Although effects are consistent with the results obtained from intravenous infusions of Intralipid over the short term, these infusions had no effect beyond 3 d in sheep (Vandermeerschen-Doize & Paquay, 1984). However, generally speaking, decreases in feed intake are greater than the energy equivalent infused.

When lipids are ingested or directly infused into the rumen, the decrease in feed intake is even greater (Chilliard *et al.* 1993). These negative effects are proportional to the polyunsaturated fatty acid content of the lipids. These effects on feed intake have long been attributed to the negative effects of lipid infusion on rumen digestion (Michalet-Doreau *et al.* 1997) or to palatability problems associated with high-fat diets. However, very great decreases in feed intake (–18 %) are observed during intraruminal infusion of fish oil (Doreau & Chilliard, 1997), although indices of digestion may even be improved. It is possible that the hydrogenation of fats forms substances that have specific effects on feed intake control, but no such substances have yet been identified.

Nitrogenous nutrients

Nitrogenous nutrients are, over the long term, just as important for rumen microbes as for the ruminant itself. Very generally speaking, feed intake increases with the amount of crude protein ($N \times 6.25$) in the diet. For cows starting lactation, feed intake increases by 0.4 kg DM (about 2–2.5 %) for each g crude protein/kg DM added to the diet

(Journet *et al.* 1983). There are many mechanisms that can explain this increase. These mechanisms may involve digestive aspects, particularly those relating to the rumen, nutritional aspects related to the ruminant, or a combination of the amount and type of protein intake (i.e. palatability and amino acid equilibrium).

Increase in nitrogen that is degradable in the rumen. The first explanation, and that most frequently advanced, concerns the effect of the crude protein on microbial activity and the digestion of N in the rumen. Many studies have shown an improvement in feed digestibility and microbial activity when crude protein that is degradable in the rumen is added. Faster and more complete digestion of the feed by microbes apparently reduces the fill of the feed in the rumen, and thus enables an increase in feed intake. Unfortunately, this hypothesis, which seems plausible with very poor roughage, is not totally convincing for other diets. There seems to be a greater response to adding crude protein when diets are rich in concentrates (5 % increase or more in feed intake for each g crude protein/kg added to the diet) than with high-roughage diets (Cowan *et al.* 1981; Faverdin *et al.* 1998), although rumen fill problems are less severe with these diets. Effects on rumen functioning may stimulate appetite independently of effects on rumen fill. Ruminants rapidly learn to prefer diets that improve the functioning of the rumen. For example, after a conditioning period, lambs always prefer diets associated with the presence of casein in the rumen, whereas this is not always the case with high doses of urea, which may result in excess NH_3 (Villalba & Provenza, 1997).

The effect of protein degradability. It is also possible that the appetite of ruminants is stimulated by a larger intake of digestible protein. By using protein sources of varying degradability in the rumen, the use of protein may be divided between the rumen microbial population and the ruminant itself. Many studies have been performed with dairy cows by comparing diets with identical amounts of crude protein but of different degradability. The variations in degradability caused by the usual treatments (i.e. heating, protein type and substitution with non-protein-N) have no effect on feed intake (Vérité & Journet, 1975; Mielke & Schingoethe, 1981; Netemeyer *et al.* 1982; Kung & Huber, 1983; Annestad *et al.* 1987; Robinson & Kennelly, 1988; Broderick *et al.* 1990; Scott *et al.* 1991; Grummer *et al.* 1996). In some tests, where proteins are protected from degradation in the rumen by formaldehyde tanning, feed intake is increased (Vérité & Journet, 1977; Lundquist *et al.* 1986; Baker *et al.* 1996). Fish and certain animal meals which contain a large amount of protein that is not easily degraded may not appeal to ruminants (Spain *et al.* 1990; Atwal & Erfle, 1992), and their effect on feed intake cannot be directly related to an increase in protected protein intake.

The effect of post-rumen infusion of protein. Adding protein directly to the abomasum or to the duodenum by continuous infusion generally has no significant effect on feed intake (Broderick *et al.* 1970; Vik-Mo *et al.* 1974; Spires *et al.* 1975; Clark *et al.* 1977; Barry, 1980; Rogers *et al.* 1984; Seymour *et al.* 1990; Choung & Chamberlain, 1993 *a,b*). Only a few tests with very poor roughage (Egan, 1965), grass or grass silage show positive effects (even very short-term effects) which sometimes

seem to be due to hydromineral equilibrium problems (Bryant *et al.* 1970).

The effect of amino acid equilibrium. The specific effects of amino acids on feed intake in ruminants seem to be much fewer than those in single-stomached animals (Forbes, 1995). Although there is variation in the composition of intestinal amino acids (Rulquin & Vérité, 1993), this variation is less than that in single-stomached animals, due to the large proportion of microbial protein in intestinal protein flows. It is therefore difficult to increase the proportion of an amino acid other than by duodenal or intravenous infusion, or by providing protection against rumen degradation. The availability of protected methionine and lysine now makes it easy to increase the intake of these two amino acids. However, at the levels at which they are usually used (i.e. 6–30 g/d for a lactating dairy cow), there is generally no significant effect on feed intake (Broderick *et al.* 1970; Yang *et al.* 1986; Xu *et al.* 1998), no more than that with duodenal or intravenous arginine infusions (Vinci *et al.* 1988). On the other hand, increasing methionine intake in sheep seems to stimulate appetite in many cases (Barry, 1976). In general, the effects of post-rumen additions of protein and the intestinal amino acid equilibrium do not explain the effects of feed protein content on feed intake.

Studies of feed preferences have shown that single-stomached animals are able to balance their diet to meet their amino acid requirements when they are offered a choice between several feeds containing different amounts of amino acids. The protein requirements of a dairy cow change considerably during lactation. When cows are offered the choice between two diets with different protected-protein contents throughout their lactation, they prefer the high-protein diet, but the proportion ingested of each of the two diets offered does not change (Tolkamp *et al.* 1998). Similarly, ewes prefer high-N diets independently of their protein requirements (Cooper *et al.* 1994). There are no studies that currently indicate specific appetites related to amino acid equilibrium in ruminants.

Ruminants mainly select feed based on the amount of crude protein, generally showing a preference for diets high in high-quality degradable N. Controlling feed intake through N apparently serves to meet the animal's requirements primarily by optimizing the functioning of the rumen.

Conclusion

In ruminants, feed intake is mostly controlled by cues triggered by the presence of feed in the rumen. Cues sent from subsequent digestion stages (abomasum and intestines) are undoubtedly less important, as Baile & Mayer's (1967) experiments have shown. The distension of the rumen and the various chemical or biochemical cues triggered by rumen digestion enable ruminants to control their short-term feed intake. Nutritional signals perceived over the short term are not directly related to the control of energy consumption. Over the longer term, ruminants seem able to select feed both to optimize the functioning of their rumen and to satisfy the nutritional equilibrium the organism requires. The energy consumption of ruminants may greatly exceed their requirements, and very rapid weight gains are possible with diets rich in feed concentrates. This finding tends to

contradict energy control theories which assume that energy consumption does not increase when requirements are satisfied. The mechanisms that specifically control a ruminant's nutrient flows are not clearly understood, but new theories propose some interesting possibilities (Tolkamp & Ketelaars, 1992; Illius & Jessop, 1996). It is possible that annual variations in the nature of the availability and quality of roughage serve naturally to limit nutrient intake over the year.

The preference of ruminants for nutritional equilibria that facilitate rumen digestion may explain the good correlation between rate of feed intake and digestibility. In addition to the mechanical view of rumen fill that is associated with this improved digestibility, what may be most important in determining ruminant preferences and the feed intake levels of various diets is probably this adjustment to achieve rumen equilibrium.

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