Ann Zootech (1995) 44, 321-346

Review

Responses of the splanchnic tissues of ruminants to changes in intake: absorption of digestion end products, tissue mass, metabolic activity and implications to whole animal energy metabolism *

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(Received 26 June 1994; accepted 7 January 1995)

Summary — This review focuses on the influence of intake on the availability of digestion end products, on splanchnic tissue weights and metabolic activity, and on the consequences of these changes on whole animal energy metabolism in ruminants. An increase in intake reduces diet digestibility and modifies the relative importance of the sites of digestion. Passive absorption of volatile fatty acids depends on changes in blood flow with intake, whereas active absorption capacity of nutrients such as glucose does not seem to be greatly modified by intake. Consequently, with most diets, excluding the maize-based diets, the amount but not the balance of digestion end products is altered. Weights of the gastrointestinal tract and of the liver are subsequently increased with intake, due to the effects of both bulk and nutrient supply. Response time is very rapid and probably results from changes in tissue protein degradation rates and, to a lesser extent, from changes in tissue protein fractional synthesis rates. Metabolic rate of gut tissue is lower than that of liver but much higher than that of hind limbs. Intake may alter splanchnic tissue metabolic rates over a very short time period; however, no effects have been noted in the longer term. The combination of splanchnic tissue weight changes with intake and of high metabolic rates has important implications on whole animal energy metabolism. The increment in whole animal energy expenditure with intake originating from the portal drained viscera is 17–61%; from the liver, 16-44%; and from the carcass, 5–7%.

splanchnic tissues / intake / absorption / tissue mass / energy metabolism

Résumé — Réponses des tissus splanchniques des ruminants à des changements de niveau d'alimentation : absorption de produits terminaux de la digestion, masse des tissus, activité métabolique et implications pour le métabolisme énergétique de l'animal entier. *Cette revue traite de*

* Report presented in the 9th Conference on Nutrition and Feeding of Herbivores, Clermont-Ferrand, France, 16–17 March 1994.

l'influence du niveau d'alimentation sur la disponibilité en produits terminaux de la digestion, sur le poids et l'activité métabolique des tissus splanchniques et les conséquences de ces changements sur le métabolisme énergétique de l'animal entier chez les ruminants. Une augmentation du niveau d'alimentation diminue la digestibilité et modifie l'importance relative des sites de digestion. L'absorption passive des acides gras volatils dépend des variations de débits sanguins avec l'ingéré, alors que la capacité d'absorption active de nutriments tels que le glucose ne semble pas fortement modifiée par le niveau d'alimentation. Par conséquent, avec la majorité des régimes, à l'exception des régimes riches en maïs, seules les quantités mais non l'équilibre entre les produits terminaux de la digestion varient. Les poids de tube digestif et de foie sont accrus avec l'ingéré, suite à des effets de masse de contenus digestifs et d'apport de nutriments. Le temps de réponse est très rapide et semble provenir de modifications des taux de dégradation des protéines tissulaires et peut-être, dans une moindre mesure, des taux de synthèse protéique fractionnels. L'activité métabolique du tube digestif est inférieure à celle du foie, mais largement supérieure à celle du train-arrière. Le niveau d'alimentation modifie sans doute l'activité métabolique des tissus splanchniques à très court terme, mais aucune modification n'apparaît à long terme. La combinaison de changements de poids des tissus splanchniques avec l'ingéré et de taux métabolique élevé a des conséquences importantes sur le métabolisme énergétique de l'animal entier. L'augmentation de production de chaleur de l'animal entier avec le niveau d'alimentation provient pour 17 à 61% du tube digestif, pour 16 à 44% du foie et pour 5 à 7% de la carcasse.

tissu splanchnique / niveau d'alimentation / absorption / poids de tissus / métabolisme énergétique

INTRODUCTION

The digestive tract plays a key role in the utilization of food by animals as it is the intermediate between the digestive processes which degrade feeds into relatively simple molecules and the metabolic utilization of these nutrients by all the different body tissues. Through its absorptive functions and with its own metabolic processes, it regulates the exogenous nutrient supply to body tissues. In ruminants, whether at maintenance, growing or in lactation, digestive tissues do not represent a large proportion of body weight (up to 12%); however, their metabolic activity is extremely high and they subsequently contribute greatly to the energy requirements of the animals, accounting for 16 to 29% of total energy expenditure (Ortigues, 1991).

The liver also plays a key role in the metabolism of the whole animal, as the centre for the intermediary metabolism. It represents a smaller proportion of body weight (1–2%), but its contribution to whole animal energy expenditure is similar to that of the digestive tract (17–31%) (Ortigues, 1991).

By comparison, energy expenditure of muscles (35–50% body weight) represent only 8 to 16% of total energy expenditure of the whole animal, while adipose tissues and skin represent 10% and up to 18% each (*in vivo* data by Harris *et al,* 1989; Lobley, 1990 and Symonds and Lomax, 1990, as well as conclusions from a modelling exercise by Gill *et al,* 1989). Other estimates for the whole carcass, which includes muscles, adipose tissues, skin and bones, are slightly higher at 45–60% (Ortigues and Durand, 1995; Ortigues *et al,* 1995). Other tissues such as kidneys, heart, brain and lungs each account for smaller proportions of total O_2 consumption (6–7, 5–11, 5 and 6–7%, respectively, as measured or estimated by Summers *et al,* 1988; Gill *et al,* 1989 and Reynolds *et al,* 1991). Consequently, any changes in the energy metabolism of the digestive tract and, to a similar extent, of the liver which might take place with intake, diet and physiological state could largely determine the variations in efficiency of energy utilization by the whole animal.

The objective of this review is to describe the changes in the energy expenditure of

the gut and liver with intake and the consequences of these changes on whole animal energy expenditure. The term *intake* is used here to imply a change in the total amounts of feed ingredients without any changes in diet composition. The influence of intake on the availability of the different digestion end products will first be examined in terms of digestibility and absorption. Nutrient supply influences both tissue growth and the intensity of tissue metabolic activity. These aspects will be reviewed. The consequences of intake on the energy requirements of gut tissues and liver will then be developed. Finally, the importance of splanchnic tissues in determining the changes in whole animal energy metabolism with intake is presented.

In this review, the responses of gut tissues and of liver in terms of energy metabolism are compared with those of other tissues, in particular muscles. This review is based mostly on *in vivo* results. *In vitro* data were used only when *in vivo* data were lacking.

RELATIONSHIPS BETWEEN INTAKE, AMOUNT AND NATURE OF DIGESTION END PRODUCTS AND ABSORPTION

The influence of intake on digestion and absorption of nutrients from the gut lumen is developed here. An attempt will be made to determine whether possible limitations to the absorption of nutrients are due to digestive processes or to the absorption capacity of digestive tissues.

Digestive processes and production of nutrients

Increasing intake without modifying diet composition generally decreases the overall digestibility and particularly the ruminal organic matter (OM) digestibility (see the review of Sutton, 1980). The relationship between intake and digestibility, obtained from experiments principally carried out above maintenance requirements, appears to be linear (Leaver *et al,* 1969; Alwash and Thomas, 1971). This effect is due mainly to a reduction in the retention time of particles in the rumen with increasing intake (Colucci *et al,* 1990). Microbial capacity of degradation does not vary to a large extent with intake, although the activity of enzymes involved in cellulolysis is higher when animals are underfed (Kabré *et al,* 1994). The influence of intake on microbial activity is probably minor when compared to that on retention time (Kabré *et al,* 1995). The effect of intake on digestibility is larger with concentrate- than with forage-rich diets (Colucci *et al,* 1989): the influence of retention time of particles in the rumen on digestibility is probably highest when retention time is short and limits degradation, as with concentrate diets. As intake does not greatly affect the microbial ecosystem, the molar proportions of ruminal volatile fatty acids (VFA) remain unchanged or exhibit a slight increase in propionate with increasing intake, with diets based on forages as well as on concentrates (Doreau and Rémond, 1982; Kabré *et al,* 1995).

The decrease in ruminal digestibility when intake increases is generally compensated for by an increase in small and large intestine digestion, whatever the diet (Doreau and Rémond, 1982; Merchen *et al,* 1986). This increase is partial and is not always observed (review of Galyean and Owens, 1991). Consequently, VFA produced in the rumen are partially replaced by glucose produced in the small intestine (especially with diets rich in cereals of low ruminal degradability) and by VFA produced in the large intestine. Although direct experimental evidence is lacking, it can be assumed that the proportion of VFA produced in the large intestine is increased at high intakes since carbohydrate digestion in the large intestine results in VFA production. In addition, the molar proportions

between the main VFA produced in the large intestine are rather constant whatever the diet (Bergman, 1990) and similar to those observed in the rumen with forage-rich diets. Consequently, it can be postulated that intake does not modify to a large extent the proportions of total VFA produced.

Starch digestibility is high, whatever the intake. However, starch is the component of the diet which is the most able to modify the nature of the digestion end products, since it produces VFA in the rumen and glucose in the small intestine. Increasing intake above maintenance decreases the ruminal digestion of starch almost exclusively with sources of starch which are slowly degradable in the rumen, such as maize (review of Sutton, 1980; Doreau and Rémond, 1982). At intakes below maintenance, it is likely that starch ruminal digestion is not modified and remains very high; however, experimental evidence is lacking.

Starch digestion in the intestines is not complete, and amounts digested in the intestines are linearly related to amounts escaping the rumen. Different experimental data suggest that limitations of starch intestinal digestion at very high intakes may be due to limitations of enzymatic activity. In normal conditions of feeding, however, the increase in intake involves an increase in total alpha-amylase activity and perhaps disaccharidase activity (reviews of Nocek and Tamminga, 1991 and Harmon, 1992). These latter activities could, however, be the limiting factor of starch digestibility at high intakes.

Intestinal digestibility of nutrients other than starch seems to be independent of feed intake. Lipid intestinal digestibility appears to be unrelated to fatty acid flow in the duodenum (review of Doreau and Ferlay, 1994). Thus an increase in intake, even with diets rich in lipids, does not modify fatty acid digestibility. The increase in feed intake results in an increase in amino acid flow to the duodenum, due to a higher by-pass of dietary protein and to an increase in microbial protein synthesis (review of Clark *et al,* 1992), because of a faster rate of passage of feed residues and microbes out of the rumen. From an analysis of literature data, Clark *et al* (1992) showed that the increase in duodenal non-ammonia nitrogen flow is linear and of the same magnitude as the increase in intake. Only a few results relate intestinal nitrogen digestibility to nitrogen escaping the rumen. No experimental evidence has been obtained for a decrease in digestibility when intake increases (Tamminga, 1983; MacRae *et al,* 1985).

Absorption across epithelia

In this section, absorption is considered as the uptake of nutrients from the epithelia of the various sections of the gut, and not as the flow of nutrients entering the portal blood after metabolism by the gastrointestinal tract (GIT), which is generally called *net absorption.*

Studies on the effects of intake on absorption have been carried out mainly for VFA and glucose, the former being absorbed by passive diffusion according to a concentration gradient, the latter being absorbed by passive diffusion as well as by active transport systems. Both mechanisms respond to changes in intake (Karasov and Diamond, 1983).

Using various methods of isolated rumen or of isotopic dilutions, several authors have shown that absorption rate of VFA is linearly related to their ruminal concentration within physiological concentrations (up to 130 mM) (Hogan, 1961; Weigand *et al,* 1972; Thorlacius and Lodge, 1973; Oshio and Tahata, 1984; Peters *et al,* 1990, 1992). Only Dijkstra *et al* (1993) found, by the method of isolated rumen, some decrease in VFA absorbability when ruminal VFA concentration was increased. It can be concluded that in physiological conditions, the

passive diffusion of VFA across the rumen wall is not limited by their concentration.

Even if the theoretical rate of absorption is not limiting, the increase in liquid outflow rate towards the omasum due to increasing feed intake may reduce VFA absorption in the rumen (Owens and Goetsch, 1986; Tamminga and Van Vuuren, 1988). It can be assumed that VFA will be absorbed postruminally, so that total VFA absorption will not be modified by food intake: it has been shown that VFA absorption in the omasum increases with VFA concentration (Dardillat, 1973). Moreover, abomasal capacity for VFA absorption is similar to that of the rumen (Williams *et al,* 1968). According to Myers *et al* (1967), the efficiency of VFA absorption in the large intestine decreases when VFA concentration increases. In the same way, some experiments suggest that when OM digestion or VFA production in the large intestine is high, VFA absorption is not complete (Ørskov *et al,* 1970; Argenzio *et al,* 1975). However, the amount of VFA which escape absorption cannot be calculated.

It has recently been shown that the ability of rumen epithelium to absorb a given amount of VFA is reduced when animals are underfed for 1 month (Perrier *et al,* 1994). This effect is probably very rapid since a 2-d fast has the same effect, as suggested by observations of Pfander and Phillipson (1953) and demonstrated by Gäbel *et al* (1993). The practical importance of this result is not demonstrated yet since underfed animals produce less VFA and the absorptive capacity of the rumen may not be limiting then.

The lower VFA absorption capacity at low intakes can be related to a lower blood flow in digestive tissues (Mailman, 1982). In ruminants, portal blood flow is known to vary with metabolizable energy intake (reviews by Huntington, 1990 and Ortigues, 1991). More specifically, an increase in ruminal concentrations of VFA and CO_2 pressure enhanced arterial ruminal blood flow (Sellers *et al,* 1964; Dobson *et al,* 1971), even though recent data obtained by intragastric infusions modulated this conclusion (Gross *et al,* 1990). In nonruminants, systematic studies have been conducted which showed clearer effects. At intestinal level, micellar fatty acids and glucose, to a lesser extent, are vasodilators, whereas amino acids have little effect on intestinal blood flow. In addition, bile enhanced the glucose-induced hyperemia and rendered fatty and amino acids vasoactive (Gallavan and Chou, 1985). Conversely, in *in situ* studies, an increase in blood flow increased nutrient absorption in ruminants (Murray *et al,* 1987; Kohn *et al,* 1993).

As far as glucose is concerned, the intestinal absorption capacity is very high: in sheep, up to 300 g of glucose can be infused in the abomasum daily without saturation of the absorptive capacity of the intestine (Ørskov *et al,* 1971). In addition, Kreikemeier *et al* (1991) showed, in the small intestine of steers, that glucose absorption capacity is higher than glucose production from starch. However, in the distal small intestine, the glucose absorption rate could be lower than the starch hydrolysis rate; indeed when large amounts of starch are given, free glucose is found in ileal digesta. Any limitations in glucose absorption in the distal small intestine, when glucose flow is very high, could be due either to the very rapid transit time or to limitations of absorption capacity.

Generally, however, the activity of transport systems is considered to be non-limiting for the absorbability of nutrients (Seal and Reynolds, 1993). Among the enzymes involved in the active transport systems, the Na^+, K^+-ATPase has been the most studied (McBride and Kelly, 1990). The *in vitro* activity of this enzyme in gut tissues has tended to be enhanced by an increase in intake even if statistical significance was not always reached (McBride and Milligan,

1982, 1985; Rompala *et al,* 1987; Kelly and McBride, 1990). An increase in dietary bulk also increased Na^+, K^+-ATPase activity (Rompala *et al,* 1988).

All this different information indicates that a change in intake results mostly in quantitative changes in the production of digestion end products. Significant changes in the balance of nutrients absorbed may also occur, but in very specific situations such as with high maize diets. Since absorption seems to be directly related to the production of nutrients in most nutritional situations, similar changes will be noted in terms of absorbability of exogenous nutrients by the GIT. It should be remembered, however, that tissues of GIT have another source of nutrient supply through arterial blood.

EFFECT OF FEEDING LEVEL ON GASTROINTESTINAL TRACT AND LIVER WEIGHTS

An increased supply of nutrients to splanchnic tissues with intake alters the mass of total and individual tissues of the splanchnic bed through changes in hyperplasia, hypertrophia and, consequently, in tissue protein turnover. These aspects are discussed here.

Influence of intake on total weights

Several experiments have shown a positive effect of intake on the weight of the digestive tract, when differences in intake were applied at the same empty body weight (Murray *et al,* 1977; Butler-Hogg, 1984). From 6 experiments in which intake and the nutritive value of the diet before slaughter were recorded, Johnson *et al* (1990) found that total weights of GIT and liver increased by 52 to 79 g for the former, and by 23 to 39 g for the latter, when dietary metabolizable energy intake increased by 1 MJ, irrespective of species (ovine or bovine) and physiological state (growth or lactation). The effect of intake on GIT and liver has first been shown on growing lambs by Wallace (1948): the influence of different intake levels applied over a 50-d fattening period was highly significant and almost independent of the previous feeding level. It has been clearly shown in this experiment that an increase in the proportion of GIT in empty body weight can be reverted by a subsequent low intake. Weight of GIT can even decrease in the course of growth, when intake is low. Moreover, there is no carry-over effect of previous nutrition on GIT weight; only a moderate carry-over effect can be noted on liver weight. This phenomenon has since been confirmed with different types of animals: ovines or bovines, growing or mature, both for the GIT and the liver (Schake and Riggs, 1972; Winter *et al,* 1976; Koong *et al,* 1982; Ferrell *et al,* 1986; Varga and Tyrrell, 1989; Taylor and Murray, 1991). All these results show that changes in GIT and liver weights are not proportional to changes in total body weight: when animals are first underfed and then refed, proportional loss or gain of splanchnic tissues is of higher magnitude than the proportional loss and gain of body weight (Kabbali *et al,* 1992).

The adaptation to a given intake occurs very rapidly. The most demonstrative result is that of Rompala and Hoagland (1987), who showed that intake in the 5 d just preceding slaughter has a higher influence on the weight of the digestive tract than previous intakes. Similarly, the adaptation of liver to changes in feed intake appears to be very rapid (Richmond *et al,* 1988). In growing animals, the effect of intake is proportional to the duration of a given plane of feeding: the weight of GIT and liver of lambs of the same age can be more than 2-fold higher when animals have been fed at high intake for 16 weeks than when they have been fed at low level for the same period. In adult animals, the length of application of a given intake could have a lesser influence on the

weight of GIT (Hight and Barton, 1965), except in the case of a very long and very severe undernutrition (Butler-Hogg, 1984). The short-term adaptation of GIT had been suggested previously by an experiment of Fell *et al* (1972) on sheep in which variations in GIT weight closely followed those in feed intake throughout lactation. In several experiments, it is clear that variations with physiological state are due to variations of feed intake rather than to physiological state by itself or body condition (Cowan *et al*, 1979, 1980; Doreau *et al*, 1985). However, Butler-Hogg *et al* (1985) showed in cows that, for the same feed intake, weight of the intestine (but not of the rumen) tended to be higher in late pregnancy than in dry non-pregnant state.

The increase in feed intake of a diet of constant composition implies an increase in both energy and protein intake. These 2 factors can be involved in variations of GIT weight so that their respective effects must be disconnected. The dietary protein content of the diet, at similar dry matter (DM) intake, did not modify the weight of GIT in trials by Sykes and Field (1972) and Cowan *et al* (1981). In contrast, Drouillard *et al* (1991) showed that energy or protein restriction have the same effects on total GIT and liver weights.

The rapid adaptation of GIT and liver weight to variations of intake has some consequences on the interpretation of slaughter data. Indeed, when animals are slaughtered at different body weights, it is not possible to establish with accuracy allometric equations for GIT or liver weights if they have not been managed in similar nutritional conditions.

Comparative effects on the different parts of the digestive tract and on the liver

Table I summarizes the effects of intake on the weights of different portions of the digestive tract. The degree of variation in tissue weight is mainly related to the magnitude of differences in feed intake. Within each portion of GIT, however, no consistent response is observed. The relative increase in the weights of rumen, intestine and liver with intake does not seem to depend on the species, ovine or bovine, nor on the physiological state, growth or lactation.

The effect of feed intake on the weight of the digestive tract can be due either to a bulk effect of food or to the availability of nutrients, either of digestive or of endogenous origin. The first hypothesis was tested by Rompala *et al* (1988), who introduced 10% of inert bulk in the diet. Bulk caused a small increase in stomach (+6%) and large intestine (+13%) weight, but not in small intestine weight. Rompala *et al* (1990) confirmed this effect with polyethylene, but not with polyurethane of the same volume, suggesting a mechanical effect on the epithelium rather than a fill effect. This absence of fill effect is consistent with the low variations in total rumen contents when intake is modified, whereas DM rumen contents vary in the same way as intake (Grimaud and Doreau, 1995). Rompala *et al* (1990) observed that bulk caused an increase in Na^+, K^+-ATPase activity, which could enhance glucose absorption. Moreover, in experiments in which forage or concentrate diets were compared at similar digestible energy intake (Bailey, 1986; Johnson *et al*, 1987), rumen, intestines and liver weight did not vary: only omasum weight was higher when fibre content increased. Jones *et al* (1985), Gibb *et al* (1992) and Sun *et al* (1994) fed animals either with forage- or with concentrate-rich diets given *ad libitum* so that digestible energy intake was higher for concentrate-rich diets. For these latter diets, large intestine weight was not modified, rumen weight was increased in 1 of 3 trials, small intestine weight was increased in 2 of 3 trials and liver weight was increased in all 3 trials. Among the experiments sum-

Table I. Relative variations in the weights of the different parts of the digestive tract consecutively to variations in feed intake.

Authors	*Type of animal*	*F:C ratio*	*Stomach*				*Intestine*			*Liver*
			Rumen [a]	*Omasum*	*Abomasum*	*Total*	*Small*	*Large* [b]	*Total*	
Wallace (1948)	Lambs	0–10:90–100	130	86	88	115	56	49	53	118
Palsson and Vergès (1952)	Lambs	?	58	54	85	62	38	64	47	115
Schake and Riggs (1972)	Cows	94:6	35	--------32----------		34	–	–	26	20
Smith and Baldwin (1974) [c]	Cows	–	20	6	35	30	–	–	31	25
Murray *et al* (1977)	Steers	10:90	16	5	14	13	26	3	17	31
Robinson *et al* (1978)	Ewes	40:60	–	–	–	18	–	–	13	10
Slezacek and Murray (1978)	Lambs	80:20	10	35	13	12	67	29	52	–
Koong *et al* (1982)	Lambs	?	–	–	–	43	72	34	53	63
Butler-Hogg *et al* (1985)	Cows	10:90	–	–	–	12	–	–	41	21
Ferrell *et al* (1986)	Lambs	45:55	–	–	–	129	147	59	107	165
Ferrell and Koong (1987)	Lambs	?	–	–	–	39	59	–	–	89
Rompala and Hoagland (1987)	Lambs	100:0	–	–	–	10	15	15	15	21
Johnson *et al* (1987)	Steers	10:90	36	39	–	–	24	–	–	42
Burrin *et al* (1990)	Lambs	10:90	–	–	–	59	60	59	59	109

Differences in feeding level corresponded to differences in amounts of food offered at the same forage:concentrate (F:C) ratio. The magnitude of splanchnic tissue weight changes depends on the difference between intakes, and for growing animals on the duration of this difference. Values represent the proportion of weight increase of each compartment between the 2 extreme feeding levels of each experiment: (highest–lowest)/lowest. [a] Rumen + reticulum; [b] caecum + colon; [c] variable ratio but no effect of ratio on relative weight of components.

marized in table I in which the increase in small intestine weight was higher than that of the rumen, several were obtained with diets rich in concentrates (Koong *et al,* 1982; Butler-Hogg *et al,* 1985), but this trend was not general since it has also been observed with forage-based diets (Slezacek and Murray, 1978). In conclusion, liver weight seems to be related to the available nutrients. In addition, even though it is likely that bulk increases rumen weight, it is not clear from experimental data whether the amount of nutrients available influences only small intestine weight, as suggested by Drouillard *et al* (1991).

Specific effects on epithelium and muscular layers of the digestive tract

Weights of rumen or intestines are generally considered regardless of the histological and functional differences which exist between the epithelium and the muscular layers. The word *epithelium* or *mucosa* generally represents the sum of epithelial layers, basal lamina and connective tissues; the word *muscular* represents the 2 muscular layers and the serosa. The mass ratio between epithelium and muscular parts is about 40:60 for the rumen (Barnes *et al,* 1983); the effect of the proportion of dietary concentrate on this ratio has given contradictory results (Harrison *et al,* 1960; Stobo *et al,* 1966; Johnson *et al,* 1987). The effect of intake on the partition between epithelium and muscle has only been studied by Johnson *et al* (1987), who observed that increasing intake resulted in a similar increase in the epithelial and muscular parts of the rumen, whereas the higher weight of small intestine was only due to an increase in the weight of the epithelium, the weight of muscular layers remaining constant. The development of rumen muscular weight may be related to an increased strength required to mix rumen contents when the fill is higher; however, frequency of contractions is not modified to a large extent by intake (Ulyatt *et al,* 1984). The influence of intake on intestinal epithelium could be due to the increase in the amount of available nutrients arising from lumen or blood (see later).

In addition to the effect of intake on epithelial weight, morphology and histology of the epithelium could also be modified. Very few studies have focused on this aspect. In lambs, Drouillard *et al* (1991) did not observe any changes in the size of rumen papillae with feed restriction. On the contrary, there were morphological changes in intestinal mucosa consecutively to feed intake: height of villi was decreased when food intake was restricted (Rompala and Hoagland, 1987).

The increase in epithelial weight can be due either to an increase in area or in thickness. For the rumen as well as for the intestines, area seems to be increased.

Tulloh (1966) found a higher rumen water-filled volume, a higher length and circumference of the intestines in lactating than in dry cows. Palsson and Vergès (1952), Kreikemeier *et al* (1990) and Gibb *et al* (1992) also observed a positive relationship between intake and length of small intestine, for concentrate-rich as well as for forage-rich diets. However, the increase in length is not sufficient to explain variations in weight: an increase in thickness probably occurs. Such an observation has been made by Kreikemeier *et al* (1990) with a concentrate-rich diet but not with a forage-rich diet.

Variations in composition of digestive tract and liver

In early lactation, females generally mobilize their body reserves to cover milk production when their intake capacity is limiting. Various authors (table II) have shown that

between the 1st and the 5th to the 8th week of lactation, females lost carcass lipids and proteins; they also lost lipids in the GIT, but gained (especially when food intake was increased), or at least did not lose (when feed intake remained constant), proteins in the GIT. Similarly, Champredon *et al* (1990), comparing dry and early lactating goats, showed that lactation involved a gain in GIT proteins and a loss in GIT lipids. These experiments show that protein balance differs between GIT and the rest of the body. Protein weight gain in early lactation is more marked for rumen than for omasum, abomasum, small or large intestine (Cowan *et al,* 1980). It can be noted that, in these 2 experiments, total GIT weight did not vary, the decrease in lipids being compensated for by the increase in protein. In the trial of Gibb *et al* (1992), the effects of intake on liver protein weight was the same as for GIT, but liver protein weight did not vary in the trial of Cowan *et al* (1980), perhaps in relation with a moderate increase in DM intake.

Contrarily to these experiments, growing lambs submitted to a severe undernutrition lost high amounts of protein but no visceral lipids at all (Butler-Hogg, 1984; Drouillard *et al,* 1991). Moreover, in this latter experiment, non-visceral and visceral protein varied in the same way consecutively to energy or protein restriction or refeeding. Loss of protein was shown with protein restriction but not with energy restriction.

This discrepancy between growing and lactating animals can be explained either by the fact that total viscera including internal fat was taken into account only in the 2 experiments on growing animals, or by the different hormonal patterns in growth and lactation. The common observation between all these experiments is that protein weight in GIT varies with DM and more probably with protein intake. Further experiments would be necessary for a better understanding of the regulation of accretion or loss of protein in the GIT.

Components of tissue growth

Hyperplasia and hypertrophia

The increase in GIT weight mentioned earlier can be obtained either by hyperplasia or by hypertrophia. It has clearly been shown that the presence of the 3 main VFA stimu-

Table II. Changes in protein and lipid weight of the carcass and of the gastrointestinal tract in early lactating females.

Authors	*Species*	*Changes between weeks 1 and 5–8*				
		Intake (%)	*Carcass*		*GIT*	
			Lipids	*Protein*	*Lipids*	*Protein*
Cowan *et al* (1980)	Ewe	+10	↘	↘	↘	↗
Chilliard and Robelin (1983) Doreau *et al* (1985)	Cow	+11	↘	↘	↘	→
Gibb *et al* (1992)	Cow	+5	↘	↘	↘	↗

lates *in vivo* epithelial cell proliferation (estimated by the mitotic index) in adult ruminants at the ruminal (Sakata and Tamate, 1978, 1979) and intestinal (Sakata and Yajima, 1984) levels. It can be noted that the reverse effect is observed *in vitro* (Galfi *et al,* 1991), so that the effect observed *in vivo* is thought to be mediated by the influence of VFA on hormonal pattern. This effect is very rapid, 2 to 3 d, and temporary, it lasts no more than 1 week. *In vivo*, the variations of mitotic index with feed intake are probably of a low magnitude, as shown by Moon and Campbell (1973), because level of intake only slightly modifies ruminal VFA concentrations.

Hyperplasia in an organ can be exhibited by the increase in DNA content in this organ. When intake increases, the concentration in DNA in the ruminal epithelium does not vary and DNA content increases (Moon and Campbell, 1973; Burrin *et al,* 1992). Ruminal growth could then be due to hyperplastic and probably to hypertrophic mechanisms. At the intestinal and liver levels, DNA content does not vary with intake (Burrin *et al,* 1992) so that growth is due to hypertrophia.

Tissue protein turnover

Tissue growth implies some changes in tissue protein metabolism. Among the components of tissue protein turnover, only synthesis rates have been studied so far in ruminants in relation with intake. Besides, only a limited number of reliable results have been obtained on *in vivo* protein synthesis in ruminant splanchnic tissues. These data are based on the use of the large dose technique (Attaix, 1988; Lobley *et al,* 1992).

In growing sheep, the *in vivo* fractional synthesis rates of the different component parts of the gut tended to increase with intake (Lobley *et al,* 1994). The majority of the responses, however, eluded statistical significance. These trends were not confined to the mucosa, which had the highest synthesis rates (in relation with the high turnover rate of villi cells), but were also generalized to the serosa (Lobley *et al,* 1994). The magnitude of response did not vary consistently with the type of tissue considered. In addition, even though the synthesis rate of secretory proteins was not directly measured, there were indications that this rate was enhanced in parallel to that of constitutive proteins (Pain *et al,* 1978; Lobley *et al,* 1994). This is important since 30% of the overall protein synthetic activity of the small intestinal mucosa of pigs was attributed to the secreted proteins (Reeds *et al,* 1993). Combining the previously mentioned results with those noted in terms of tissue mass raised the assumption that changes in gut mass with intake might be regulated through both protein degradation and protein synthesis (Attaix *et al,* 1992).

Similarly, the fractional synthesis rate of ovine liver proteins seemed insensitive to chronic alteration of intake (Lobley *et al,* 1994), altough small changes were observed by Lobley *et al* (1992) when less effective tracer flooding conditions were met. Since liver mass varied with intake, this again suggested that liver constitutive protein mass is primarily regulated by alterations in protein degradation. No direct evidence, however, is available in ruminants.

Other *in vivo* studies based on a continuous tracer infusion technique and dealing with the comparison of dry and lactating goats have shown similar non-significant trends (Champredon *et al,* 1990; Baracos *et al,* 1991). In these studies, the effect of intake was confounded with that of the physiological state. Nevertheless, the effect of intake might be predominant in the same way as intake appeared to be predominant in altering gut and liver tissue mass in lactating cows.

The lack of large effects of intake on the fractional protein synthesis rates in splanchnic tissues of sheep reported earlier are in

agreement with the data obtained in 11–12 week old rats during phase I of starvation using a large dose technique (Attaix, 1988; Chérel *et al,* 1991). Indeed, the response to changing nutritional conditions depends on age (Lobley, 1993) as well as duration or severity of underfeeding. The most significant effects were noted for very young rats after a 2-d fast (McNurlan *et al,* 1979, 1982; Burrin *et al,* 1991). For older animals, a much longer fasting period was necessary for the fractional synthesis rates of both gut and hepatic tissues to be modified (Attaix, 1988; Chérel *et al,* 1991). This limited effect of intake on splanchnic protein synthesis rates is consistent with the observation that the precursor amino acid pool used for *in vivo* intestinal protein synthesis may be of plasmatic rather than of intraluminal (dietary) origin (Egan and Rennie, 1986, cited by Attaix, 1988). In addition and similarly to ruminants, indirect evidence has been obtained in rats that intestinal mass was partly regulated through changes in protein degradation rates (Attaix, 1988). For the liver, direct evidence exists in rats (Waterlow *et al,* 1978).

TISSUE METABOLIC ACTIVITY

Changes in splanchnic tissue mass subsequent to altered nutrient supply with intake may be accompanied by changes in tissue metabolic activity. The latter refers here to the general oxidative activity of tissues, measured as the quantity of O_2 consumed per unit tissue weight and per unit time. The oxidative metabolism of tissues is known to sustain a variety of metabolic processes. In gut tissues, protein turnover and active transport systems could contribute in total for approximately 50% of the energy expenditure (Lobley, 1991). The other thermogenic components, such as smooth muscle tone and activity, substrate cycling, nucleic acid turnover, lipid synthesis, mitochondrial transport and so on (Summers *et al,* 1988; Lobley, 1991), have not yet been quantified in gut tissues. In the liver, Lobley (1991) estimated that tissue energy expenditure originated mainly from protein turnover (12%), active transport systems (35%), substrate cycles (24%), gluconeogenesis (20%) and urea synthesis (15%).

Unfortunately, information on the effect of intake on *in vivo* gut and liver tissue metabolic activity is limited to that obtained in a study by Burrin *et al* (1989, 1990). Consequently, recently obtained knowledge on tissue metabolic activity is reviewed and indirect evidence for changes with feeding level is considered on the basis of blood flow through tissues.

Metabolic rate

An increasing number of published studies have now reported the *in vivo* mass specific metabolic rates of tissues (table III) based on *in vivo* measurements of tissue O_2 consumption, followed by slaughter of the animals, and removal and weighing of the tissues. These data confirm that large differences exist between the portal drained viscera, the liver and other tissues such as the limbs. The *in vivo* metabolic rates were highest for the liver (2.8–9.3 mmol O_2 consumed/d/g wet tissue), intermediate for the portal drained viscera (1.3–3.1 mmol O_2 consumed/d/g wet tissue) and lowest for the hind limbs (0.22–0.43 mmol O_2 consumed/d/g wet tissue).

Published results are still too scarce to detect any systematic changes in tissue metabolic rate with the nutritional status of the animals. A few studies (Webster and White, 1973; Ortigues *et al,* 1995) suggested that over a 24-h period, metabolic rates of the portal drained viscera and of the liver increased postprandially probably in response to changes in specific nutrient supply (Ortigues *et al,* 1995) and in hor-

Table III. Published daily averages of *in vivo* oxygen consumption by portal drained viscera (PDV), liver, hind limb and skin (mmol O_2/d/g wet tissue).

Authors	*Animal*	*PDV*	*Liver*	*Hind limb*	*Skin*
Boyle *et al* (1992); Boyle *et al* (1990) Wilkening *et al* (1988)	Fetal lambs (130 d)	–	–	0.22–0.30	–
	Newborn pigs				
Nowicki *et al* (1983); Mayfield *et al* (1989)	Preprandial	1.28–1.35	–	–	–
Mayfield *et al* (1989)	Postprandial	2.38	–	–	–
Edelstone and Holzman (1981);	Newborn lambs				
Holzman *et al* (1985)	Fasted	3.08	2.83–6.36	–	–
Ortigues *et al* (1995)	Preruminant calves	1.56	3.02	0.36	–
Burrin *et al* (1990)	Growing lambs				
	Maintenance	1.42	6.96	–	–
	2.6 x maintenance	1.44	9.31	–	–
Domanski *et al* (1974)	Sheep				
	Standing quietly	–	–	0.77 [a]	–
Lobley (1991)	Sheep (lying)				
	Maintenance	–	–	0.18 [a]	–
	1.8 x maintenance	–	–	0.27 [a]	–
Lobley (1990)	Sheep	–	–	0.33–0.37 [a]	–
Harris *et al* (1989, 1993)	Sheep	–	–	–	0.03–0.21
Harris *et al* (1994)	Sheep				
	0.6 x maintenance	–	–	–	0.13
	1.4 x maintenance	–	–	–	0.38
Oddy *et al* (1984)	Ewes	–	–	0.22–0.42	–
Ortigues and Durand (1995)	Ewes 0.5 x maintenance	1.65 [b]	4.89	0.27	–
Pethick *et al* (1987)	Ewes				
	Standing quietly	–	–	0.25 [a]	–
	Exercise	–	–	1.37[a]	–
Symonds and Lomax (1990)	Pregnant ewes				
	Fed	–	–	0.43	–
	Underfed	–	–	0.40	–

[a] Values expressed per g muscle, rather than per g hind limb tissues. [b] Values expressed per g of adipose tissue free PDV.

monal balance (Christopherson and Brockman, 1989). In the longer term, however, it is not certain that the mass specific metabolic activity of splanchnic tissues is modified. Burrin *et al* (1990) showed that after 3 weeks of adaptation, the *in vivo* metabolic rates of the portal drained viscera and of the liver were not significantly affected by intake, suggesting that the changes in total energy expenditure of these tissues arose only from changes in tissue weights. By contrast, intake appeared to modify the *in vivo* metabolic rate of the hind limbs (Harris *et al*, 1989).

In vitro data might have cast further light on these effects. However, *in vitro* metabolic rates of gut and liver tissues have not been clearly altered by intake (see Ortigues, 1991, for review). Additionally, some discrepancies exist between the published *in vivo* and *in vitro* metabolic rates, suggesting some caution in the interpretation of the *in vitro* data. The principal discrepancy pertained to the liver whose metabolic rate was 2 to 6 times higher *in vivo* than *in vitro* (Johnson *et al*, 1990; Ortigues, 1991). Concerning the portal drained viscera, it may be questioned whether the *in vitro* metabolic rate of the epithelium is also underestimated. Indeed, the epithelium is very active metabolically because of its absorptive function and its high turnover rate; nevertheless, its *in vitro* metabolic rate (Ortigues, 1991) was similar to the average *in vivo* metabolic rate of the whole portal drained viscera. Finally, higher metabolic rates were measured *in vitro* for muscle alone than *in vivo* for hind limb preparations, which generally include muscles, adipose tissues, bones and skin (Lobley, 1990).

Relationships between energy expenditure and blood flow

It has been suggested that a close relationship exists between O_2 consumption and blood flow through a tissue (Coulson, 1986). Lindsay (1993) found some correlation between total portal blood flow and total O_2 consumption by the portal drained viscera of ruminants. Different correlations probably exist for each tissue. Indeed, blood flows are highly correlated with O_2 flows to the tissues, whereas the O_2 extraction capacity of tissues differs. For example, the portal drained viscera extract from 21 to 30% of the O_2 flow; a similar extraction capacity has been noted for the liver (17–36%), whereas much higher values are obtained in the hind-limbs (36–64%) (Eisemann and Nienaber, 1990; Huntington *et al*, 1990; Symonds and Lomax, 1990; Reynolds *et al*, 1991, 1992; Ortigues and Durand, 1995).

In addition, the relationship between blood flow and oxygen consumption for each tissue may vary with the nutritional conditions. For example, in an experiment with adult ewes fed at 1 and 0.5 times the maintenance metabolizable energy (ME) requirements, the reduction in energy expenditure of splanchnic tissues with undernutrition was greater than the reduction in blood and O_2 supply, leading to some decrease in the O_2 extraction rates as a percent of supply (Ortigues and Durand, 1995). In contrast, the energy expenditure of the hindquarters was maintained constant due to an increase in O_2 extraction rates which partly counterbalanced the drop in supply. Consequently, changes in O_2 supply (and thus in blood flow) explained 40% (portal drained viscera) or 50% (liver, hindquarters) of the changes in O_2 consumption of tissues with intake (Ortigues and Durand, 1995).

Blood flow per unit tissue weight

On the basis of the previously mentioned relationships between tissue energy expenditure and blood flow, changes in blood flow per unit tissue weight with intake were inves-

tigated as possible and partial indicators of changes in tissue metabolic rates with intake. Only short-term responses could be examined from the available data.

First and similarly to metabolic rates, blood flow measured in conscious animals using dilution or ultrasonic techniques and expressed per unit tissue weight varies according to the specific tissue considered. In sheep, blood flow in the portal drained viscera is only 10 to 30% that of the liver, and 3 to 10 times higher than that of leg tissues (table IV). These proportions are similar to those noted in terms of metabolic rates between the 3 tissue beds.

More specific information on tissue differences is obtained from measurements using radioactive microspheres. For the portal drained viscera, the epithelium of the reticulorumen is 10 to 60 times more irrigated than the smooth muscles (table V). Among the other gut tissues, other but smaller differences could be noted, in particular the slightly lower mass specific blood flow in the large than in the small intestine. The pancreas is highly irrigated, whereas mesenteric and omental adipose tissues present a much reduced blood flow.

By comparison, blood flow through individual tissues of the limbs ranged from 1.9 to 65.6 ml/min/100 g wet tissue in skeletal muscle, from 2.2 to 47.2 ml/min/100 g in adipose tissues, from 0.3 to 22.2 ml/min/100 g in skin, and averaged 3 and 5 ml/min/100 g in connective tissues and bones, respectively (Hales, 1973; Bell *et al,* 1976; Gregory and Christopherson, 1986; Gregory *et al,* 1986; Rhodes *et al,* 1991; Hales and Fawcett, 1993). These wide ranges show that very large differences exist among indi-

Table IV. Mass specific blood flow through portal drained viscera, liver and leg tissues (ml/min/100 g wet tissue) measured in conscious animals.

Authors	*Tissue*	*Animal*	*Mass specific blood flow*
	Portal drained viscera		
Burrin *et al* (1989, 1990)	Stomachs + intestine	Growing lambs	72–83
Ortigues and Durand (1995)	Adipose tissue free	Ewes	109
Ortigues and Durand (1995)	Total	Ewes	51
Ortigues *et al* (1995)		Preruminant calves	74
	Liver		
Burrin *et al* (1989, 1990)		Growing lambs	348–427
Ortigues and Durand (1995)		Ewes	453
Ortigues *et al* (1995)		Preruminant calves	223
	Leg		
Harris *et al* (1992)	Whole	Growing lambs	2.6–9.1
Oddy *et al* (1984)		Standing ewes	7.0–13.2
Ortigues and Durand (1995)		Standing ewes	5.8
Ortigues *et al* (1995)		Preruminant calves	9.6
Teleni *et al* (1986)	Muscles	Sheep	7.4
Domanski *et al* (1974)		Standing sheep	24
Pethick *et al* (1987)		Sheep	7.2
Pethick *et al* (1981)		Ewes	24
Pethick and Vernau (1984)		Ewes	14.2

vidual muscles, as well as among the individual anatomical sites of adipose tissues and skin.

It should first be noted that diet composition and thus partition of digestion along the tract may influence the mass specific blood flows. For example, in sheep fed at similar metabolizable energy intakes (167 to 251 kJ.kg^{-1} live weight [LW]), blood flow through tissues of the omasum down to the large intestine was much higher with concentrate-rich than with forage-rich diets. Unfortunately, no direct comparison could be obtained for the reticulorumen (table V).

Within this context, short-term effects of intake on blood flow through specific tissues were measured but they seemed to vary with the type of diet considered. Blood flow through tissues appears to be relatively similar at zero intake regardless of previous diet (table V). However, with forage-rich diets, feeding increased blood flow mainly through the reticulorumen with little changes from the abomasum down to the large intestine (Barnes *et al,* 1983). With concentrate-rich diets, on the other hand, feeding also increased blood flow through the omasum, abomasum and small intestine even though

Table V. Mass specific blood flow (ml/min/100 g wet tissue) through individual tissues of the portal drained viscera measured using microspheres in sheep.

	Forage-based diet [a,b]		*Concentrate-based diet* [c,d]	
	2 h post-feeding	*> 18 h post-feeding*	*2 h post-feeding*	*18 h post-feeding*
Reticulorumen				
Epithelium	229–353	59–130	–	–
Muscles	6	3–9	–	–
Overall	–	–	61–112	18–22
Omasum	67	57	175–227	54–66
Abomasum	67	98	147–204	110–140
Small intestine				
Duodenum	74	93	115–128	82–101
Jejunum	70	74	–	–
Ileum	48	72	–	–
Large intestine				
Caecum	51	59	93–105	68–75
Colon	32	31	–	–
Pancreas	335	381	288–340	223–290
Adipose tissues				
Mesenteric	3.6	6.5	4.6–10.7	6.1–14.9
Omental	2.0	6.0	9.3–23.1	9.4–32.5

[a] Engelhardt and Hales (1977); [b] Barnes *et al* (1986); [c] Gregory and Christopherson (1986); [d] Gregory *et al* (1986). Intakes were estimated to range from 171 to 251 kJ ME/kg live weight (LW) in [a], from 175 to 188 kJ ME/kg LW in [b] and to an average of 176 kJ/kg LW in [c] and [d].

the rise was not as marked as in the forestomatchs (Gregory *et al,* 1986). A tendency also existed for reduced blood flow through adipose tissues with feeding (Barnes *et al,* 1983; Gregory and Christopherson, 1986).

Consequently, it can be concluded that the extent to which the portal drained viscera and the liver are sollicited for digestive and absorptive functions may potentially determine their average mass specific blood flow and/or metabolic activity in each nutritional condition. Concerning the specific effect of intake, the limited evidence did not suggest any definite modifications in the metabolic rates of splanchnic tissues after a few weeks of adaptation to the new intakes. This agrees with the observations that the rates of the 2 major components of energy expenditure in these tissues (ion transport and protein synthesis) were only slightly affected by intake. It could only be inferred from blood flow data that a few changes may occur in a very short time period after the change in feed allowances. Such a response would probably last only a few days until tissue weights have stabilized to a new level.

INCREMENT OF TISSUE ENERGY EXPENDITURE WITH INTAKE

From the previous discussion, it appears that because of the very high metabolic rate of splanchnic tissues by comparison with that of other tissues, the changes in tissue mass will have important consequences in terms of their total energy expenditure whether no or only short-lived modifications in metabolic rates are noted. It is thus of interest to quantify for each tissue the increase in energy expenditure with intake. Using results obtained in experiments where 2 different intakes were applied, the increase in tissue energy expenditure was calculated for each multiple of maintenance ME intake (taken at 481 kJ.kg $LW^{-0.75}.d^{-1}$). It ranged from 25 to 142 kJ.kg $LW^{-0.75}.d^{-1}$ for the portal drained viscera, and from 25 to 134 kJ.kg $LW^{-0.75}.d^{-1}$ for the liver (table VI). The lowest values generally refer to high concentrate-rich diets, whereas the highest values were obtained with silages or grass hays. In addition, the increase in energy expenditure might be proportionally larger at high than at low intakes (Webster *et al,* 1975). In contrast, the increment in energy expenditure due to the total musculature measured at low intakes was extremely small. Higher increments would probably be obtained at higher intakes, but it is still likely that the discrepancy between muscle and splanchnic tissues would remain.

More generally, for the portal drained viscera, Seal and Reynolds (1993) estimated by regression using results from different published experiments that its energy expenditure increased by an average of 52 kJ.kg $LW^{-0.75}.d^{-1}$ for each multiple of maintenance ME intake. These authors also noted a tendency for the increment in energy expenditure by the portal drained viscera to be higher with silage than with dried forage- or concentrate-rich diets. The lowest values had been obtained in experiments where animals were fed intragastrically. These differences probably reflect the changes in the work of digestion with the physical and chemical nature of the diet, gut fill as well as the nature of the components absorbed, since gut tissue mass was not clearly influenced by diet composition.

CONTRIBUTION OF TISSUES TO THE INCREASE IN WHOLE ANIMAL ENERGY EXPENDITURE WITH INTAKE

The efficiency with which ME can support maintenance and production depends on the energy expenditure at different intakes. An increasing number of studies have shown that a large proportion of this incre-

Table VI. Increment in tissue energy expenditure with intake (per multiple of maintenance ME requirements, taken at 481 kJ ME • kg live weight$^{-0,75}$•d^{-1}).

Authors	*Animals*	*Diets*	*Intake (kJ.kg LW$^{-0.75}$.d^{-1})*	*Increase in tissue energy expenditure (kJ.kg LW$^{-0.75}$.d^{-1})*		
				Portal drained viscera	*Liver*	*Muscles*
Huntington *et al* (1988)	Steers	Orchard grass silage	715 *vs* 879	140	–	–
		Lucerne silage	795 *vs* 1 096	67	–	–
Reynolds *et al* (1991)	Heifers	75% lucerne hay	586 *vs* 1 130	54	56	–
		75% concentrate	586 *vs* 1 130	43	60	–
Reynolds *et al* (1992)	Steers	75% concentrate	594 *vs* 1 071	26	25	–
Ortigues and Durand (1995)	Ewes	Orchard grass hay	180 *vs* 326	97	103	4*
Symonds and Lomax (1990)	Pregnant ewes	75% straw	113 *vs* 356	–	–	14
Burrin *et al* (1989)	Growing lambs	80% concentrate	389 *vs* 816	36	136	–

* Carcass.

ment in energy expenditure was not directly associated with productive functions in tissues of economic importance (*eg* muscle deposition in growing animals), but rather with support functions by other tissues. The digestive tract, in particular, is the first to be challenged by modifications in the availability of digestion end products. From these studies, it may be assumed that its mass specific absorption activity and metabolic rate will be altered probably only transiently, but that changes in mass will occur very rapidly. Because of its high metabolic rate, the subsequent contribution of the portal drained viscera to the increase in total energy expenditure with increments of intake is quite important. It has been measured that 17 to 61% of the increase in whole animal energy expenditure with intake originated from the portal drained viscera (Webster *et al,* 1975; Huntington *et al,* 1988, 1990; Reynolds *et al,* 1991, 1992; Ortigues and Durand, 1995) (table VII). This contribution varied with the composition of the diet. The lowest contributions were generally obtained with concentrate-rich diets (17–20%). Intermediate values were obtained when legumes (lucerne) were used as the main forage in forage-rich diets (28–31%) and the highest contributions were obtained with grasses (39–46%).

These contributions should be compared with those from other tissues (table VII). Changes in hepatic metabolism with intake will also contribute greatly to the increase in energy expenditure, by 14 to 44% (Huntington *et al,* 1990; Reynolds *et al,* 1991, 1992; Ortigues and Durand, 1995). Similarly to the portal drained viscera, the contribution of the liver in fed conditions seems to be more important with forage-rich (32–44%) than with concentrate-rich diets (16–24%).

In contrast to the splanchnic tissues, the other components of the increment in energy expenditure are of much smaller magnitude. The skeletal muscles or the carcass contributed only 5 to 7% to the increase in whole animal energy expenditure with intake (table VII; Symonds and Lomax, 1990; Ortigues and Durand, 1995), which is disproportionately small considering the importance of these tissues in terms of weight. Eating also contributed up to 9% (Webster *et al,* 1975; Ortigues and Durand, 1995), whereas renal function did not seem to be greatly altered (Reynolds *et al,* 1991). As a consequence of the previously mentioned changes, contributions of splanchnic tissues to total energy expenditure of the whole animal increased with intake, whereas that of the carcass decreased (Ortigues, 1991; Ortigues and Durand, 1995).

CONCLUSION

A general understanding of the relationships between feed intake and digestion in the different compartments of the GIT, as well as between production of nutrients and their absorption, is obtained from a large number of experiments. However, it is not possible as yet to evaluate with accuracy the amount of nutrients absorbed by the GIT. Further research on digestion in the large intestine and on the stoichiometric relationships between ruminally degraded OM and VFA production is necessary to improve knowledge in this area.

It has been shown that the rate of adaptation of GIT tissues to variations in intake is very rapid. Some aspects remain unclear, such as the influence of the nature of the diet on changes in GIT tissue weight: no effect is shown by experimental data, whereas the increase in energy expenditure of GIT with intake clearly varies with the forage:concentrate ratio. A better understanding of GIT metabolism should be gained from the knowledge of which nutritional factors determine proteolysis and proteosynthesis of the digestive tract, as well as the contribution of the different metabolic

Table VII. Contribution of tissues to the increment in total energy expenditure with intake.

Authors	*Animals*	*Diets*	*Intake* ($kJ.kg\ LW^{-0.75}.d^{-1}$)	*Contribution (%)*		
				Portal drained viscera	*Liver*	*Muscles*
Huntington *et al* (1988)	Steers	Orchard grass silage	715 *vs* 879	45.7	–	–
		Lucerne silage	795 *vs* 1 096	27.7	–	–
Huntington *et al* (1990)	Steers	60% lucerne hay	0 *vs* 966	29.5	14.0	–
Reynolds *et al* (1991)	Heifers	75% lucerne hay	586 *vs* 1 130	31.4	43.6	–
		75% concentrate	586 *vs* 1 130	20.0	23.5	–
Reynolds *et al* (1992)	Steers	75% concentrate	594 *vs* 1 071	17.3	16.6	–
Ortigues and Durand (1995)	Ewes	Orchard grass hay	180 *vs* 326	39.0	32.0	5.0*
Symonds and Lomax (1990)	Pregnant ewes	75% straw	113 *vs* 356	–	–	6.8
Burrin *et al* (1989)	Growing lambs	80% concentrate	389 *vs* 816	61.3	–	–
Webster *et al* (1975)	Wether sheep	Dried lucerne	Below *vs* above			
		Chopped	maintenance	23.1	–	–
		Pelleted		35.4	–	–
		Dried grass				
		Chopped	Idem	28.3	–	–
		Pelleted		46.3	–	–
		Barley	Idem	56.6	–	–

* Carcass.

pathways to total energy expenditure of the GIT.

The figures stress the predominant role of the splanchnic tissue in determining the efficiency of energy utilization for maintenance and production. The energy expended at splanchnic levels will partly depend on the supply of exogenous nutrients to other tissues and thus their metabolic utilization. The development of *in vivo* studies on the relationship between energy expenditure and intake appears necessary, taking into account the possible difference of mechanisms involved when animals are either fed at high levels, as high-producing dairy cows, or at levels below maintenance.

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