

VISCERAL METABOLISM AND EFFICIENCY OF ENERGY USE BY RUMINANTS

METABOLISMO VISCERAL E EFICIÊNCIA DO USO DA ENERGIA PELOS RUMINANTES

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- REVIEW -

SUMMARY

The visceral system (liver and portal-drained viscera) represents an interface between diet and the animal, and it acts as the main site of regulation of nutrients that are used for maintenance, growth, lactation, reproduction, and physical activities of animals. However the functions carried out by visceral organs have, however, a significant energetic cost and are influenced by a variety of factors, such as the level of feed intake and diet composition, among others. As a result, variable quantities of substances are metabolized by them and, thus, the pattern and the quantity of nutrients available to the peripheral tissues can be quite different from those absorbed at the intestinal lumen. Probably, the major source of variation in the efficiency of utilization of metabolizable energy among feeds is associated mainly with visceral metabolism and it is unlikely that the ratio ketogenic/glucogenic of absorbed substances has determinant effect under physiological conditions.

Key words: portal- drained viscera, liver , metabolism, energy, efficiency.

RESUMO

O sistema visceral (fígado e vísceras drenadas pela veia porta) representa uma interface entre a dieta e o animal e atua como o principal local de regulação dos nutrientes utilizados para a manutenção, crescimento, lactação, reprodução e atividades físicas dos animais. Contudo, as funções desenvolvidas

por estes órgãos têm um custo energético significativo e são influenciadas por uma série de fatores, como o nível de consumo de alimento e a composição da dieta, entre outros. Como resultado, uma quantidade variável de substâncias são metabolizadas por eles e, deste modo, o padrão e a quantidade de nutrientes disponível aos tecidos periféricos pode ser amplamente diferente daquele absorvido do lúmen intestinal. Provavelmente a maior parte da variação na eficiência de utilização da energia metabolizável entre os alimentos está associada com o metabolismo visceral e é improvável que a relação entre as substâncias cetogênicas/glicogênicas absorvidas tenha um efeito determinante em condições fisiológicas.

Palavras-chave: vísceras drenadas pela veia porta, fígado, metabolismo, energia, eficiência.

INTRODUCTION

Digestion and absorption are the early steps of a complex process through which animals obtain from the environment energetic and constitutive components needed to maintain their living state. In subsequent steps absorbed nutrients enter the bloodstream and are transported to the liver by the portal venous system. Together with

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exogenous nutrients, endogenous circulating metabolites derived from peripheral tissues also reaches the liver. As a part of this system, the liver can be regarded as a central regulator that controls the levels of nutrients that will be distributed to the body and ensure the maintenance, growth, lactation, reproduction, and all the physical activities of animals (SEAL & REYNOLDS, 1993).

The functional role played by visceral tissues (liver and portal-drained viscera (PDV)) has a considerable energetic cost and a variable quantity of substrates are metabolized by them (HUNTINGTON & REYNOLDS, 1987). Thus, changes in the metabolism of visceral tissues can change the proportions and the absolute quantities of metabolites that become available to the peripheral tissues and consequently can influence the metabolism of the whole organism.

Critical considerations about techniques used on studies dealing with visceral metabolism and on visceral metabolism of important nutrients have been considered in previous reviews (SEAL & REYNOLDS (1993), REYNOLDS (1995) and HUNTINGTON (1999)). The objective of the present review is to consider some factors that associate the visceral metabolism with the energetic efficiency of the whole organism of ruminant.

VISCERAL FLUX OF ENERGY

The portal energy flux is the sum of enthalpy of combustion of metabolites absorbed plus the visceral heat production estimated from oxygen consumed by the system. It represents up to 92% of the metabolizable energy (ME) intake (LINDSAY, 1993). The net portal energy flux would be expected to account to 100% or more of the ME intake. The difference between obtained and expected values has been associated with metabolites not determined in blood samples, such as nitrogen bases, peptides, and phenols, with fermentation heat and metabolites absorbed through the lymph, such as lipids. The portal flux of volatile fatty acids (VFA) is linearly correlated and represent about 43% of ME intake (Figure 1). The others significant components of portal flux of energy are oxygen uptaked, amino acids, ketone bodies, and lactate.

REYNOLDS (1995), in a review of several studies carried out on cattle, observed that the energy released by the total visceral system in the form of metabolizable compounds corresponds to about 87% of ME intake. Visceral acetate release

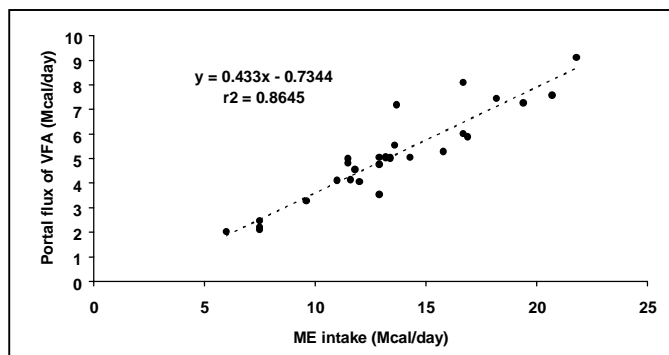


Figure 1 – Relation between ME intake and net portal flux of energy as volatile fatty acids (VFA: acetate + propionate + butyrate). Data were taken from experiments with steers and heifers conducted by HUNTINGTON & PRIOR (1983), HARMON & AVERY (1987), HARMON *et al.* (1988), GROSS *et al.* (1988), REYNOLDS & HUNTINGTON (1988), THEURER *et al.* (1991), KREHBIEL *et al.* (1992), SEAL *et al.* (1992), SEAL & PARKER (1994), TANIGUCHI *et al.* (1995) and HUNTINGTON *et al.* (1996). The combustion heat used to calculate the energy of VFA was 209, 365 and 552kcal/mol of acetate, propionate and butyrate, respectively.

normally represents about 24%, β -OH-butyrate 16%, glucose 23%, and amino acids 5% of the ME intake .

The forage:concentrate ratio in the diet or the site of starch digestion does not seem to change the total quantity of energy released by the visceral system for a fixed level of ME intake. However, the metabolizable components of this energy are different. A higher proportion of net visceral energy flux is represented by acetate on forage-based diets or when starch is fermented into the rumen, but on concentrate-based diets or when starch digestion occurs in the small intestine, a higher proportion is represented by glucose (TANIGUCHI *et al.*, 1995; HUNTINGTON *et al.*, 1996).

The site of protein digestion affected neither the quantity of net visceral energy flux nor the proportion of metabolites components of this energy (TANIGUCHI *et al.*, 1995). However, the increase of protein intake decreased the net visceral energy release in the form of aminoacids by steers (REYNOLDS *et al.*, 1992).

ENERGY CONSUMPTION BY VISCERAL SYSTEM

The visceral metabolism alters the pattern and the amount of available nutrients to the peripheral tissues but also spends a significant part of energy consumed by the whole organism. The increase of feed or energy intake increases both the mass of these organs in relation to total body mass (BURRIN *et al.*, 1990) and the

metabolic activity of these tissues (REYNOLDS, 1995).

Data compiled by HUNTINGTON (1999), from experiments with cattle and sheep fed up to about two times their energy maintenance requirement, demonstrated that the oxygen uptake by visceral tissues is linearly related to whole body oxygen uptake (about 40%). However, GOETSCH (1998) analysed data from experiments with sheeps fed forage-based diets ad libitum and observed that the efficiency of energy metabolism of visceral tissues increased as the level of ad libitum intake increased, i.e., the oxygen uptake by visceral tissues decreased when compared to whole body oxygen uptake. Similarly, portal and liver aerobic heat production (estimated from oxygen uptake) in cattle were linearly related to ME intake (SEAL & REYNOLDS, 1993, REYNOLDS, 1995). Thus, considering that the efficiency of utilization of ME by the whole body decreases as the level of ME intake increases, i.e., the whole body heat production increases in relation to ME intake (KETELAARS & TOLKAMP, 1996), it also indicates that the efficiency of energy metabolism of visceral tissues increases as level of ME intake increases. The difference between the above studies (HUNTINGTON, 1999 vs. SEAL & REYNOLDS, 1993, REYNOLDS, 1995, GOETSCH, 1998) about oxygen consumption and energetic efficiency of visceral system can be related to difference on level of fed intake of experimental animals. REYNOLDS *et al.* (1994) observed a biphasic response in the portal-drained viscera of cattle, where the increase in portal heat production with increasing metabolizable energy intake appears to be reduced at intakes greater than twice maintenance.

The forage: concentrate ratio of the diet can affect the energy expenditure by the visceral system. REYNOLDS *et al.* (1991) fed heifers with pelleted diets containing 75% alfalfa or 75% concentrate, at equal ME intake and at two levels of intake. Some results of this study are summarized in table 1. They observed a greater production of heat by the whole body and a lower retention of tissue energy for the diet containing more forage, which resulted from differences in visceral tissues metabolism, mainly the PDV.

The characteristics of forage is another factor that may affect visceral energy consumption. In studies with sheep, the visceral energy consumption in relation to digestible energy intake

Table 1 – Intake of ME and oxygen uptake by tissues of heifers fed 75% alfafa or 75% concentrate diet at two levels of intake (REYNOLDS *et al.*, 1991)¹.

	75% alfafa diet		75% concentrate diet	
	low intake	high intake	low intake	high intake
ME intake (Mcal/day)	10.7	18.4	10.6	18.4
Oxygen uptake (liters/h):				
PDV ²	21.0	31.7	16.8	25.0
Liver	16.1	27.0	13.9	26.7
Total visceral ³	37.2	59.7	31.9	51.9
Whole body	80.0	116.0	73.6	108.0
Oxygen uptake by visceral system as % of whole body	44.8	53.4	45.8	43.6

¹ Heifers were multicatheterized for visceral measurements and were placed in respiratory chambers for measurements of whole body energy and nitrogen balance.

² Probability of diet effect: P<0.01

³ Probability of diet effect: P<0.07

was higher to bermudagrass than ryegrass-wheat hay (GOETSCH & FERRELL, 1995; PATIL *et al.*, 1995; GOETSCH *et al.*, 1997). The time of intake and digesta mass in sheep fed bermudagrass (a more fibrous forage) is higher compared to ryegrass-wheat hay (SUN *et al.*, 1994). A larger digesta mass may cause a greater energy consumption due to a higher metabolic activity of epithelial cells and to a higher contractile activity of muscle cells in the digestive tract. In addition, although the mechanisms are unknown, there is a high flow of sodium ions in the saliva when animals receive high fiber diets, which have been suggested to increase energy use by the gut (KETELAARS & TOLKAMP, 1996).

Increased crude protein intake increased oxygen consumption by the portal system and by the liver in steer (REYNOLDS *et al.*, 1992) and sheep (GREANEY *et al.*, 1996). In addition, infusions into the mesenteric vein of an amino acid mixture stimulated oxygen uptake by these organs in sheep (LOBLEY *et al.*, 1998). In these studies, the increased uptake of oxygen by the liver was associated with urea synthesis. Indeed, there is a significant correlation ($r^2=0.70$) between oxygen uptake and urea N production by liver when data from various experiments with steers are compared (Figure 2). However, ammonia infusion into the mesenteric vein of sheep (LOBLEY *et al.*, 1995) or amino acid infusion into the mesenteric vein of dry dairy cows (WRAY-CAHEN *et al.*, 1997) increased hepatic urea synthesis but had no effect on oxygen

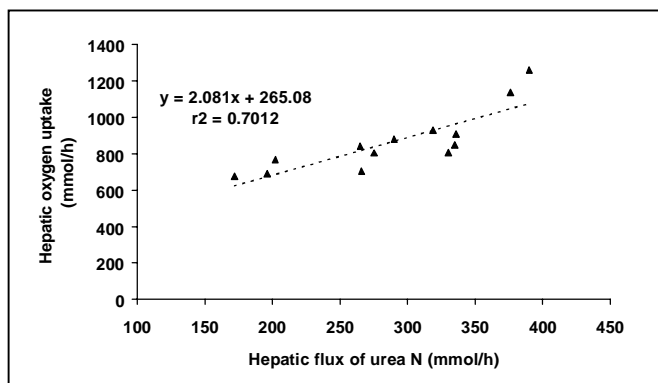


Figure 2 – Relation between hepatic production of urea N and hepatic oxygen uptake. Data were taken from experiments with steers conducted by GUERINO *et al.* (1991), REYNOLDS *et al.* (1992), BAUER *et al.* (1995) and TANIGUCHI *et al.* (1995).

uptake by visceral system. Urea synthesis had a cost estimated from 1 to 4 mol of ATP for mol of urea (LEHNINGER *et al.*, 1993), depending on whether fumarate production in the urea cycle is considered in energetic calculations or not. However, as more amino acids are deaminated to support the increase in urea synthesis, more gluconeogenic substrates will be available in the hepatocytes. The main amino acids used as precursors of glucose in ruminant liver, in fed state, are alanine and glycine (REYNOLDS, 1995) enter into the gluconeogenic pathway as pyruvate (LEHNINGER *et al.*, 1993). The glucose synthesis from these substrates had an estimated cost of 12 mol of ATP for mol of glucose synthesized (LEHNINGER *et al.*, 1993) and, thus, it is certainly associated with a significant increase of ATP consumption by the hepatocytes when protein-rich diets are fed.

The energy expenditure by the visceral system is also affected by the site of starch digestion. TANIGUCHI *et al.* (1995) infused starch into the rumen or abomasum of steers fed alfalfa hay and observed that the oxygen uptake by the portal system and the liver was higher in the animals that received infusion into the abomasum. However, the net visceral flux of energy, as metabolizable nutrients for use by peripheral tissues, was also higher in this treatment compared with starch infusion into the rumen. Thus, the net availability of energy for use by peripheral tissues, as a proportion of energy intake, was similar to corn starch digested in the rumen or in the lower gastrointestinal tract of steers. Although there is a loss of starch energy when it is fermented in the rumen, giving origin to VFA, this loss is counterbalanced by the energy consumed in the small intestine to absorb glucose

when starch is digested by the enzymes of ruminants at this site (McBRIDE & KELLY, 1990).

VISCERAL METABOLISM AND WHOLE ENERGY EFFICIENCY

The differences on efficiency of ME use by ruminants have generally been attributed to ketogenic/glycogenic ratio of digestion and absorption products (ØRSKOV, 1977; REYNOLDS, 1995). However, in studies on sheep (ØRSKOV *et al.*, 1979) and steers (ØRSKOV *et al.*, 1991), no significant differences were detected on nitrogen retention or on the efficiency of energy utilization from different VFA mixtures infused into the rumen, above the maintenance level. Moreover, in studies “in vitro” with ovine adipocytes, the variation in glucose concentration within the physiological range (2 to 5mM) in the incubation media had no effect on acetate metabolism. In addition, acetate oxidation and conversion to lipid increased with acetate concentrations in the media, also within the physiological range (0.5 to 1.5mM), even though glucose concentrations were low (YANG & BALDWIN, 1973; SCOLLAN & JESSOP, 1995). Yet, in these studies, the lack of glucose oxidation limited acetate incorporation into lipid but only at concentrations of acetate above physiological range. Another important aspect to be considered, is that visceral metabolism greatly modifies the pattern and quantity of available nutrients to peripheral tissues in relation to those that disappear from the intestinal lumen. Thus, even in the most different dietary conditions, the ratio of the ketogenic/glycogenic substrates (on an energetic basis) released by the visceral system to peripheral tissues is about two times (REYNOLDS, 1995), which is unlikely to limit acetate utilization. Indeed, differences in efficiency of utilization of ME among feeds are likely to be associated with metabolism of visceral tissues and not with metabolism of peripheral tissues. REYNOLDS *et al.* (1991) observed in steers that most of the increase in heat generated by increasing intake of a roughage-based-diet was aerobically generated in the visceral system and not in peripheral tissues. In addition, SUSENBETH *et al.* (1998) verified that the energy requirement for eating and ruminating is high and different among feeds. When untreated straw was fed to steers, approximately 30% of ME provided by the feed was used to supply energy demanded for eating and

ruminating. In turn, when a high-quality roughage was fed, only 10% of ME was used for these physiological functions.

In the other hand, LENG (1990) observed that supplementation of roughage-based-diets with urea and protein sources of low degradability, greatly increased the efficiency in the utilization of the ME provided by roughage and that this would be due to a higher utilization of acetate for synthetic processes and to a decrease in the production of futile heat by the ruminant. Indeed, SCOLLAN & JESSOP (1995) verified a higher incorporation of acetate into lipid on adipocytes of sheep fed diets containing high protein compared with low protein content. However, alternatively to that stated by LENG (1990), it is possible that higher aminoacids supply led to a higher glucose production from gluconeogenic aminoacids by the liver. Thus, the increased glucose supply could have a sparing effect on acetate oxidation by the peripheral tissues, increasing its incorporation into lipid (BALCELLS *et al.*, 1995). In addition, a higher aminoacids supply can lead to low oxidation of aminoacids present into the cells of peripheral tissues. Consequently, the protein renewal in these tissues decreases and the deposited/synthesised protein ratio increases, lowering ATP expenditure by protein turnover (ABDUL-RAZZAQ & BICKERSTAFFE, 1989). KREHBIEL *et al.* (1998) supplemented ewes fed low-quality forage "ad libitum" with soybean meal and observed that this supplementation increased the net portal flux of α -amino nitrogen but did not increase the total net visceral flux. The additional aminoacids flux from portal blood in these supplemented ewes was uptaken by the liver and did not reach peripheral tissues. Moreover, the hepatic uptake of lactate, mainly of peripheral origin, was higher in no supplemented ewes, suggesting a change of glucose precursors from lactate in no supplemented to aminoacids in supplemented ewes.

CONCLUSIONS

The portal-drained viscera and the liver metabolism have a profound impact on the availability of nutrients and energy to the peripheral tissues, which is influenced by several factors, such as level of feed intake and diet composition. Probably, the major source of variation in the efficiency of utilizing metabolizable energy among feeds is associated mainly with visceral metabolism and it is unlikely that the ratio ketogenic/glucogenic of absorbed substances has determinant effect under

physiological conditions. However, excepting few experiments with sheep fed forage "ad libitum", these conclusions are obtained, for the most part, from results of experiments with sheep and growing cattle fed near or slightly above maintenance levels. There are few data and, thus, more research is necessary to describe visceral metabolism of high yielding dairy cow and of ruminants with high levels of intake.

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Ciência Rural, v. 31, n. 5, 2001.