The use of energy by the splanchnic tissues and their metabolism of VFA, glucose and FFA in sheep fed high- and low-fibre diets*

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Ten Dohne merino wethers with an average mass of 50 kg were used to study differences in the use of energy by the splanchnic tissues and their metabolism of VFA, glucose and FFA when fed high- or low-fibre diets. Dietary carbohydrate was provided in either the structural (HF treatment) or readily fermentable form (LF treatment), while energy and nitrogen intakes were kept constant. The wethers were fitted with ruminal cannula and with catheters in the abdominal aorta, mesenteric, portal and jugular veins. All 10 sheep were subjected to two protocols, separated by at least 2 weeks to minimise carry-over of isotopes. Either (1-^{14}C)-acetate or (2-^{14}C)-propionate was continuously infused into the rumen concurrently with either (9,10 N-^{3}H)-FFA or (6-^{3}H)-glucose into the jugular vein. Blood and digesta samples were drawn simultaneously after plateau specific radioactivities of these metabolites had been achieved. The effective tissue energy use by the PDV was higher ($p < 0.05$) for the LF than for the HF diet (60.9% vs. 57.9%). The PDV used between 20 and 27% of digestible energy intake and differed ($p < 0.05$) between groups. The net flux of propionate and FFA across the PDV were higher ($p < 0.05$) for the LF than the HF treatment. PDV utilization and production differed ($p < 0.05$) between treatments for all metabolites. The net hepatic flux of acetate and FFA was higher ($p < 0.05$) on the HF than the LF treatment. Production by the liver differed ($p < 0.05$) between treatments for all metabolites. It appears that glucose and propionate metabolism shifted away from the liver to peripheral tissues when the LF diet was fed. In general, the peripheral metabolism of acetate and FFA differed significantly ($p < 0.05$). The net utilization of acetate and FFA, as well as the conversion of acetate to FFA, was higher ($p < 0.05$) on the HF than on the LF diet. The results of this study show that, while the PDV and liver play a central role in the partitioning of absorbed nutrients between various metabolic pathways, the difference in the efficiency of dietary energy utilisation remains to be fully explained.

Tien Dohne merino-hammels met 'n gemiddelde massa van 50 kg is gebruik om die verskil in ingewande-veselenergieverbruik en die metabolisme van vlugtige vetsure (VVS), glukose en vrye vetsure (FVS) wanneer hoë- of lae-veseldiëte gevoer is, te bepaal. Die dieetkoolhidrate is as struktureel (HF-behandeling) of maklik fermenteerbaar (LF-behandeling) aangebied, terwyl energie- en stikstof-innames konstant gebly het. 'n Kannula is in die rumen, en blywende kateters is in die

abdominale aorta, mesenteriese, portaal en hepatiese venas sowel as 'n tydelike kateter in die nekaar van die hamels ingesit. Die diëte is halfuurliks gevoer. Óf (1-C^{14})-asetaat óf (2-C^{14})-propionaat is deurentyd intra-ruminaal geïnfuseer gelyktydig met óf (9,10-^{3}H)-FVS óf (6-^{3}H)-glukose, onderskeidelik wat in die nekaar geïnfuseer is. Bloed- en digesta-monsters is gelyktydig geneem nadat 'n plato-spesifieke radioaktiwiteit behaal is. Die effektiewe veselenergieverbruik van die PDV was hoër ($p < 0.05$) vir die LF- as die HF-behandeling (60.9% vs. 57.9%). Veselenergieverbriuk deur die PDV was tussen 20 en 27% van verteerbare energie-inname en het tussen behandelings verskil ($p < 0.05$). Die netto-vloei van propionate en FFA oor die PDV was hoër ($p < 0.05$) vir die LF- as die HF-behandeling. PDV-verbruik en -produksie het verskil ($p < 0.05$) tussen behandelings vir alle metaboliete. Die netto hepatiese vloei van asetaat en FVS was hoër ($p < 0.05$) vir die HF- as die LF-behandeling. Produksie deur die lewer het verskil ($p < 0.05$) tussen behandelings vir alle metaboliete. Dit blyk asof glukose- en propionaat-metabolisme vanaf die lewer na die perifere vesels geskuif het in die LF- in vergelyking met die HF-behandeling. Die perifere metabolisme van asetaat en FVS het tussen behandelings verskil ($p < 0.05$). In die algemeen was die netto-verbruik van asetaat en FVS sowel as die omskakeling van asetaat na FVS hoër in die HF- as die LF-behandeling. Die resultate van die studie bewys dat die PDV en lewer 'n sentrale rol speel in die verdeling van geabsorbeerde nutriënte tusssen die verskillende metaboliese paaie.

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Introduction

The splanchnic bed is the intermediate between the source of nutrition and the animal. These tissues modulate the flow of nutrients by responding to both exogenous and endogenous effectors. After absorption from the tract into the bloodstream, the incoming supply of nutrients is immediately processed by the liver to accommodate the needs of the body (Stangassinger & Giesecke, 1986).

Owing to the extensive fermentation of carbohydrates in the rumen, gluconeogenesis is a continual process in ruminants, primarily occurring in the liver and kidneys (Brockman & Bergman, 1975). Propionate is a primary precursor for glucose in the body. Changing the fibre content of the diet from low to high fibre decreases propionate production in the rumen, and there is a subsequent decrease in the size of the glucose pool (Bauman, 1976). The tissues of the splanchnic bed play a primary role in both the qualitative and quantitative supply of nutrients to the animal. These tissues play a complex protective role and have a high energy requirement (Webster, 1980). Peripheral metabolism can be directly influenced through changes in nutrient partitioning by the splanchnic bed via altering the supply of nutrients (Eisemann, 1994). The VFAs are the primary sources of energy absorbed by the ruminant, and their subsequent metabolism, and efficiency with which they are used for maintenance and growth, can be profoundly influenced by the splanchnic metabolism.

In a previous study, Linington *et al.* (1996) showed that high- and low-fibre diets were used with different efficiencies by lambs. This difference could not be explained in terms of the digestion of the nutrients (Linington *et al.*, 1997). The purpose of this study was to determine whether these differences could be attributed to differences in splanchnic metabolism and tissue energy use.

Methods

Animals

Ten Dohne Merino wethers (47–53 kg), aged 1–2 years were used. The sheep had each been fitted with rubber ruminal cannula and were housed indoors in individual metabolism crates under continuous lighting. The sheep were randomly divided into two groups and assigned to groups HF and LF, as previously described.

The voluntary intake of the HF sheep was determined over a two-week period. Thereafter, to ensure consistent intake, the HF sheep were fed at 90% of their *ad libitum* intake. The amount of the LF diet equal to 90% of the *ad libitum* ME intake of the HF diet was calculated and this amount offered daily to the LF sheep. The HF sheep were thus fed 1500 $g.day^{-1}$ and the LF sheep 1260 $g.day^{-1}$, divided into equal portions and offered at half-hourly intervals. Feed refusals were determined daily. The nitrogen (N) and metabolizable energy (ME) intakes were thus the same for both groups of sheep, viz. 138 $gN.day^{-1}$ and 13.18 MJ $ME.day^{-1}$, respectively. Water was freely available.

Surgery

The rumen-cannulated sheep were fitted with indwelling catheters in the hepatic, portal and mesenteric veins, before they were fitted with a catheter in the abdominal aorta, as described by Linington *et al.* (1998). A temporary catheter in the jugular vein was inserted when required.

Catheters

Lengths of single lumen, medical grade, polyethylene tubing (I.D. 1.00 mm, O.D. 1.45 mm, Portex, U.K.) were used to catheterise a jugular vein (Linington *et al.*, 1998). Medical grade polyvinylchloride (PVC) tubing (I.D. 1.00 mm, O.D. 2.00 mm, Dural Plastics, Australia) was used as hepatic, portal and femoral catheters. Narrower PVC tubing (I.D. 0.75 mm; O.D. 1.15 mm) was used to prepare the mesenteric catheter. PVC cuffs were glued (using cyclohexanone) 100 mm from the tips of the mesenteric and hepatic catheters and 10 mm from the tips of the portal catheters, respectively. In addition, the portal catheter was fitted with 30 mm silastic rubber tip. The catheters were sterilised and rinsed as previously described (Linington *et al.*, 1998).

After insertion, the catheters were filled with saline containing heparin (750 $U.ml^{-1}$, Glaxo, U.K.) and plugged with a blocked hypodermic needle of suitable gauge. Catheters were serviced every 2 to 3 days by withdrawing 5 ml blood, flushing with sterile saline and filling with the saline-heparin mixture.

Surgical procedures

The sheep were prepared for surgery as previously described (Linington et al., 1998). The catheters were inserted using a modification of the method described by Katz & Bergman (1969a). The surgical objectives were to expose and catheterise the common trunk of the portal vein, a superficial branch of the mesenteric vein and the hepatic vein via the left lobe of the liver.

Experimental design

All 10 sheep were subjected to two protocols, separated by at least 2 weeks to minimise carry-over of isotopes. In one protocol, the metabolism of acetate and FFA was traced by continuously infusing (1-^{14}C)-acetate into the rumen concurrently with (9,10 N-^{3}H)-FFA into the jugular vein. In the other protocol, propionate and glucose metabolism were estimated by infusing (2-^{14}C)-propionate

into the rumen concurrently with (6-^{3}H)-glucose into a jugular vein. The protocols were otherwise identical, and were identical to that previously described (Linington *et al.*, 1998). Two sheep from each group (2 × 2) were infused at a time, and the procedure repeated with another four sheep one week later. The sheep in the first group were selected on the basis of catheter patency. The rectal temperatures of the sheep were taken before and after the infusions.

Infusions

Protocol 1: (1-^{14}C)-acetate (Amersham, U.K) was made up in sterile water and was continuously infused (19.12 KBq.l^{-1}, 0.5 ml.min^{-1}) into the anterior section of the rumen, starting 16 h before sampling commenced. No priming dose was administered. The ^{3}H-FFA infusate (30 KBq^{-1}, 0.8 ml.min^{-1}) was made up of equal mixtures of (9,10(N)-^{3}H)-oleic and (9,10(N)-^{3}H)-palmitic acids (New England Nuclear, U.S.A.). The labelled FFA mixture was adsorbed to endogenous plasma albumin previously extracted from each individual sheep and was then diluted to the appropriate volume by sterile saline. The rate of blood flow across the splanchnic bed was determined using the dye-dilution method (using p-aminohippuric acid (PAH; Sigma, USA) as marker) of Katz & Bergman (1969a). The PAH was dissolved (2% (m/v)) in sterile saline (Sabax, S.A.) and, after a 12 ml priming dose 1 h before sampling, was continuously infused at a rate of 52 ml.h^{-1} into the mesenteric vein.

Protocol 2: (2-^{14}C)-propionate (Amersham, U.K.) was dissolved in sterile water and continuously infused (19.12 KBq.l^{-1}, 0.5 ml.min^{-1}) into the rumen starting 16 h before sampling. D-(6-^{3}H)-glucose (Amersham, U.K.) was dissolved in sterile saline containing 20 mg.l^{-1} unlabelled glucose as inert carrier. The glucose was infused (30 KBq.l^{-1}, 0.8 ml.min^{-1}) continuously via the jugular vein after a priming dose of 75 ml was administered and the infusion was started 5 h before sampling commenced. The PAH solution was also infused into the mesenteric vein as described in Protocol 1.

Sampling

Rumen and blood samples from the arterial, portal and hepatic catheters ($n = 4$) were drawn simultaneously at half-hourly intervals. Three ml of blood was used for blood gas, haemoglobin and haematocrit determinations as well as for the estimation of CO_2 specific activity. A further 3 ml whole blood was used for VFA analysis, while 10 ml blood was used to obtain plasma, which was stored cold (4°C) for the remainder of the analyses.

Analyses

Total VFA were extracted from deproteinised blood by ether distillation (Neish, 1952; van der Walt & Briel, 1976). The VFA were separated by HPLC on a reverse-phase, C-18 column (Bush *et al.* 1979) after being reconstituted in 2 N phosphoric acid. The peaks were detected via a refractive index detector (Du Pont, USA). VFA concentrations were determined from peak areas. Radioactivity of each peak sample was measured using a liquid scintillation spectrometer (LKB, Sweden). The specific activity of carbon dioxide in blood was determined as $BaCO_3$ according to the method of Hinks *et al.* (1966).

Glucose concentrations in plasma were colorimetrically determined using a commercially available diagnostic kit (Boehringer-Mannheim, Germany). The glucose penta-acetate derivative was used to determine the specific activity of both ^{3}H- and ^{14}C-glucose according to the method of Jones (1965).

The FFA were determined colorimetrically according to the method of de Villiers *et al.* (1977). The ^{3}H- and ^{14}C-FFA specific activities were determined after extracting the FFA from plasma

(Dole, 1965) and binding these to resin according to the method of Kelly (1968). Radioactivity was measured using a liquid scintillation spectrometer (LKB, Sweden). The haemoglobin content of blood was determined according to the cyanmethemoglobin method (A.O.A.C., 1990). The pO_2, pCO_2 and pH of blood was determined within 30 min of sampling using a blood gas analyser (Radiometer, Denmark). The concentration of PAH in plasma was determined colorimetrically using the method of Katz & Bergman, 1969b.

Calculations

The glucose irreversible loss (GIL) rate and FFA entry rates were determined from the ratio of the infusion rate and plateau specific activity and corrected for PDV production and hepatic label uptake according to the method of Bergman *et al.* (1966, 1970, 1974) and Bergman & Wolff (1971). The proportion of CO_2 from ruminal acetate or propionate was determined from the ratio of the mean arterial carbon dioxide specific activity and the plateau acetate or propionate specific activity. The method of Leng *et al.* (1967) was used to estimate the ruminal quantities of acetate or propionate converted to FFA or glucose, respectively.

The plasma flow in the portal and hepatic vein was calculated from the dilution of infused PAH, (Bergman *et al.*, 1966). Blood flow was calculated from the plasma flow by compensating for the haematocrit. Flow in the hepatic artery was determined as the difference between the hepatic and portal vein blood flow values.

Oxygen concentration was calculated from the pO_2, pH and haemoglobin concentration, after a correction of pO_2 for the Bohr effect (Oddy *et al.*, 1984). Carbon dioxide concentrations were calculated from the Henderson-Hasselbach equation (Oddy *et al.*, 1984). Tissue energy use (TEU) was calculated from tissue oxygen uptake and carbon dioxide output (Oddy *et al.*, 1984). Energy lost as heat (HE) in the PDV, liver and splanchnic bed was calculated from the oxygen consumption of each respective system [460.2 KJ HE produced per mol O_2 consumed (Huntington & Reynolds, 1987)].

The metabolite net flux in each tissue was determined as the product of blood flow and the veno-arterial concentration difference of each metabolite. The extraction ratio was calculated as the fraction of metabolite presented to the tissue that was taken up by the tissue. The hepatic utilization ratio was determined as the fraction of metabolite absorbed into portal blood that was taken up by the liver (Peters *et al.*, 1983). The unidirectional uptake of a metabolite was calculated as the product of the extraction ratio of the radioactive marker for that metabolite in passage across the tissue and the total amount of metabolite flowing through the tissue. Metabolite absorption and hepatic production rates were determined from the sum of the net flux and utilization rates (Bergman *et al.*, 1970). The interconversion of metabolites was calculated from the respective metabolite entry rates and their specific ^{14}C-activities.

Statistics

The statistical significance of differences between the two groups was calculated using the Statgraphics 6.0 (Manugistics, Inc., Maryland, USA) personal computer package in which the two-sample test with pooled variance provided a t-statistic for unpaired samples with equal variances. All data in the form of ratios were first transformed to log (base 10), tested for normal distribution, before being subjected to the above test. The mean values for four blood samples were taken as representative of the plateau value, once linear regression had shown that the slope of the line drawn through the four points was not different from zero (i.e. horizontal). The blood metabolite concentrations thus obtained during the whole body, tissue energy use and organ experiments were used to calculate the mean results for each group.

Results

Blood flow

The mean blood flow in the portal and hepatic veins as well as the estimates of hepatic artery flow are given in Table 1. There were no significant differences in the rate of portal or hepatic venous blood flow between groups. There was no effect of group on the derived hepatic artery values or on the percentage contribution of portal flow to the flow in the hepatic vein (approximately 80%). These values are similar to those reported by Bergman *et al.* (1970) and Lomax & Baird (1983) but are higher than the values reported by Burrin *et al.* (1989).

Table 1 Blood flow through the splanchnic bed ($l.min^{-1}$; $n = 8$ per group; mean ± s.e.m.)

Diet	Portal vein	Hepatic vein	Hepatic artery	%(Pv/Ha)
HF	3.16	4.11	0.94	76.9
LF	3.52	4.55	1.04	77.4
s.e.m.	±0.161	± 0.289	± 0.247	
p	NS	NS	NS	

s.e.m. = standard error of the mean; NS = not significant.

Tissue energy use (TEU) and heat production (HE) by the splanchnic bed

The carbon dioxide and oxygen concentrations in the aorta, portal and hepatic veins are shown in Table 2. Carbon dioxide concentrations in the aorta and portal vein were higher in the HF than in the LF group.

Arterial oxygen concentrations of the HF group were higher than the LF group. The arterial values of both groups were, as expected, significantly higher ($p < 0.05$) than either of the corresponding venous values. The ratio of carbon dioxide to oxygen did not differ significantly between diets.

Blood flow (Table 1) and CO_2 and O_2 concentrations (Table 2) were used to calculate the net O_2 uptake and CO_2 output of the PDV, liver and splanchnic bed as a whole (Table 2). Oxygen uptake by the PDV and liver did not differ between the two groups. About 60% of the O_2 utilization by the splanchnic bed was taken up by the PDV. This ratio was not affected by diet. The liver extracted more of the O_2 that was presented than did the PDV. However, the liver consumed significantly less ($p < 0.05$) O_2 than the PDV, accounting for approximately 40% of the O_2 consumption of the splanchnic bed.

There was no dietary effect on either the hepatic or the splanchnic flux of oxygen or carbon dioxide. However, carbon dioxide production by the PDV was significantly higher ($p < 0.05$) in the HF than in the LF group, while the CO_2 production in the liver of the HF group tended to be lower ($p < 0.1$). The CO_2 production by the splanchnic bed also tended to be lower ($p < 0.1$) in the LF group. In the HF group, CO_2 production by the PDV was significantly higher ($p < 0.05$) than by the liver and accounted for 60% of splanchnic CO_2 output, whereas this trend was not clear in the LF group, where CO_2 output accounted for only 42% of total splanchnic CO_2 output.

The O_2 uptake and CO_2 output by the PDV and liver were used to calculate the amount of energy used (TEU), the quantity of energy lost as heat (HE) as well as the energy used, and not lost as heat (TEU_e) by these tissues. The heat energy was expressed as a percentage of TEU, and TEU was expressed as a percentage of digestible energy intake (DEI). These values are given in Table 3.

The energy use, heat production and effective energy use by the PDV, differed significantly between diets. Although the total energy use and heat production of the PDV were lower on the HF

Table 2 Oxygen and carbon dioxide concentrations in the different blood vessels including their uptake and output by the PDV, liver and splanchnic bed (n = 8 per group; mean ± s.e.m.)

		HF	LF	s.e.m.	p
O_2 mM	Pv	4.14	3.50	± 0.202	NS
	Hv	3.93	3.21	± 0.177	NS
	Ha	5.19	4.61	± 0.141	0.05
CO_2 mM	Pv	21.1	16.8	± 0.812	0.05
	Hv	21.7	17.8	± 1.28	NS
	Ha	18.9	15.6	± 0.619	0.05
$CO_2 : O_2$	Pv	5.15	4.80	± 0.177	NS
	Hv	5.72	5.56	± 0.266	NS
	Ha	3.70	3.39	± 0.125	NS
PDV					
O_2 uptake mM.h^{-1}		190	232	± 26.6	NS
CO_2 output mM.h^{-1}		427	253	± 30.9	0.05
O_2 extraction		12.2	14.7	± 0.496	NS
$CO_2 : O_2$		2.25	1.09	± 0.221	0.05
Liver					
O_2 uptake mM.h^{-1}		130	151	± 18.1	NS
CO_2 output mM.h^{-1}		284	349	± 31.7	NS
O_2 extraction		19.6	23.9	± 0.938	NS
$CO_2 : O_2$		2.14	1.57	± 0.229	NS
Splanchnic bed					
O_2 uptake mM.h^{-1}		329	383	± 44.5	NS
CO_2 output mM.h^{-1}		711	602	± 63.7	NS

s.e.m. = standard error of the mean; NS = not significant.

than the LF diet, heat production was a greater percentage of tissue energy use (42.0%, HF; 39.1%, LF). Consequently, the effective tissue energy use (TEU_e) by the PDV was significantly higher for the LF than for the HF diet (60.9% vs. 57.9%). The PDV used between 20 and 27% of DEI and the groups differed significantly.

Hepatic values for TEU, HE and energy used, but not lost as heat (TEU_e) were similar for both groups, approximately 4 MJ.day^{-1}. Hepatic heat production was similar to the PDV in that it was approximately 38% of tissue energy use. TEU was about 25% of DEI for both groups.

Since the energy use and heat production of the liver did not significantly differ between diets, the splanchnic bed metabolism reflects that of the PDV. The TEU of the splanchnic bed as a whole was 7.3 and 8.09 ± 0.16 MJ.day^{-1} for the HF and the LF groups respectively ($p < 0.05$), representing 44.8 and 53.3 ± 1.20% of DE intake (HF and LF groups, respectively; $p < 0.05$). The PDV contributed more than the liver to total splanchnic TEU only in the HF group. Less energy was lost as heat in the splanchnic bed of the HF than of the LF group; the PDV and the liver contributing equal

Table 3 Tissue energy use (TEU) and energy lost as heat (HE) in MJ.day^{-1} as well as HE expressed as a percentage of TEU and TEU as a percentage of digestible energy intake (DEI) by the PDV, liver and splanchnic bed (n = 8 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	p
PDV				
TEU	3.38	4.07	± 0.146	0.05
HE	1.42	1.59	± 0.035	0.05
TEU_e	1.96	2.48	± 0.071	0.05
HE/TEU %	42.2	39.1	± 1.47	NS
TEU/DEI* %	20.8	26.8	± 0.600	0.05
Liver				
TEU	3.92	4.02	± 0.141	NS
HE	1.48	1.55	± 0.090	NS
TEU_e	2.44	2.47	± 0.056	NS
HE/TEU %	37.8	38.6	± 1.20	NS
TEU/DEI* %	24.1	26.5	± 0.666	NS
Splanchnic bed				
TEU	7.3	8.09	± 0.160	0.05
HE	2.8	3.14	± 0.056	0.05
TEU_e	4.4	4.95	± 0.056	0.05
HE/TEU %	38.4	38.8	±0.742	NS
TEU/DEI* %	44.8	53.3	± 0.849	0.05

* DEI (MJ.day^{-1}) determined previously (HF, LF = 16.28 & 15.18 ± ?? MJ.day^{-1}, respectively; NS); s.e.m. = standard error of the mean; NS = not significant.

amounts of the energy lost. The PDV contributed 44.6% and 50.1 ± 0.95% ($p < 0.05$) of the TEU_e in the HF and LF groups, respectively. HE as a percentage of TEU was similar for the LF and the HF group (38.4 and 38.8 ± 0,74%, respectively). These results suggest that energy utilization by splanchnic tissue was more efficient in the HF than in the LF group.

The splanchnic bed comprises a small percentage of the whole body mass, but utilizes proportionately far more energy. In the present experiment, the ME intake was the same (13.20 MJ.day^{-1}) for the two diets. Consequently, the splanchnic bed is responsible for between 55% and 62% of the utilization of the ME intake, while heat loss accounts for 21% to 24% of ME utilization. Net energy use by this organ is between 33% and 38% of ME intake.

Blood metabolite concentrations

The concentrations of the metabolites in the various blood vessels are shown in Table 4. FFA, haematocrit, pH and haemoglobin concentrations did not differ between groups in any of the blood vessels and were all within the normal physiological range.

Propionate concentrations in the portal vein did not differ between groups. However, propionate concentrations were higher in the hepatic vein and lower in the artery of the LF than the HF group.

Table 4 Metabolite concentrations in the artery, hepatic and portal veins (n = 4 per group; mean ± s.e.m.)

Metabolite	n	HF	LF	s.e.m.	p
Artery					
Acetate (mM)	8	1.41	1.20	± 0.041	0.05
Propionate (mM)	8	0.16	0.12	± 0.004	0.05
FFA (mM)	4	0.288	0.332	± 0.010	NS
Glucose (mM)	4	3.60	4.39	±0.181	0.05
Haematocrit %	8	26.0	24.4	± 0.991	NS
pH	8	7.33	7.33	± 0.035	NS
Haemoglobin (g%)	8	9.35	8.70	± 0.266	NS
Portal vein					
Acetate (mM)	8	2.13	1.79	± 0.056	0.05
Propionate (mM)	8	0.44	0.45	± 0.004	NS
FFA (mM)	4	0.285	0.335	± 0.021	NS
Glucose (mM)	4	3.55	4.34	± 0.189	0.05
Haematocrit (%)	8	26.0	24.3	± 1.06	NS
pH	8	7.27	7.23	± 0.071	NS
Haemoglobin (g%)	8	9.29	8.87	± 0.270	NS
Hepatic vein					
Acetate (mM)	8	2.05	1.58	± 0.056	0.05
Propionate (mM)	8	0.17	0.18	±0.002	0.05
FFA (mM)	4	0.262	0.317	± 0.015	NS
Glucose (mM)	4	3.69	4.49	±0.142	0.05
Haematocrit %	8	26.9	24.2	± 0.424	0.05
pH	8	7.26	7.26	± 0.035	NS
Haemoglobin (g%)	8	9.59	9.19	± 0.195	NS

s.e.m. = standard error of the mean; NS = not significant.

Although these differences were small, they were significant. Acetate concentrations were significantly higher in the blood of the HF than of the LF group. Glucose concentrations were lower in the arterial ($p < 0.05$), portal and hepatic venous blood ($p < 0.05$) of the HF group compared to the LF group.

Differences in metabolite concentration between blood vessels were similar for both groups. For example, arterial acetate concentrations were significantly lower ($p < 0.05$) than the hepatic and portal venous values, probably owing to low hepatic utilization and extensive peripheral use. Hepatic uptake of propionate in both groups resulted in the portal vein propionate concentrations being significantly ($p < 0.05$) higher than those in the hepatic vein and artery. In neither group of sheep was there a significant difference between blood vessels in glucose or FFA concentrations. Haemoglobin concentrations and pH did not differ between vessels.

The blood flow values (Table 1), the mean blood metabolite concentrations (Table 4) and the specific radioactivities (Table 5) were used to calculate the organ and tissue metabolism data in Tables 6 to 9.

Table 5 Specific radioactivity concentrations in the artery, hepatic and portal veins of sheep fed either the HF or LF diets (n = 4 per group; mean ± s.e.m.)

	Radioactivity KBq.mmol^{-1}							
	^{14}C				^{3}H			
Metabolite	HF	LF	s.e.m.	p	HF	LF	s.e.m.	p
Artery								
Acetate	2.29	3.28	± 0.256	NS				
Propionate	11.7	9.76	± 0.628	NS				
FFA	8.70	4.64	± 0.812	0.05	171.7	303.1	± 24.1	0.05
Glucose	6.93	5.43	± 0.493	NS	14.08	12.06	± 1.20	NS
$^{*}CO_2$ (a)	0.234	0.271	± 0.038	NS				
$^{*}CO_2$ (p)	0.847	0.821	± 0.083	NS				
Hepatic vein								
Acetate	1.84	3.63	± 0.219	NS				
Propionate	3.75	1.38	± 0.070	0.05				
FFA	9.08	4.29	± 0.476	0.05	175.4	281.4	± 16.9	0.05
Glucose	6.88	5.36	± 0.576	NS	14.02	11.54	± 1.08	NS
$^{*}CO_2$ (a)	0.189	0.180	± 0.025	NS				
$^{*}CO_2$ (p)	0.088	0.123	± 0.018	NS				
Portal vein								
Acetate	2.89	3.35	± 0.226	NS				
Propionate	10.46	4.21	± 0.232	0.05				
FFA	8.98	4.31	± 0.494	0.05	177.4	280.3	± 19.7	0.05
Glucose	6.90	5.19	± 0.576	NS	13.98	11.92	± 1.11	NS
$^{*}CO_2$ (a)	0.199	0.255	± 0.023	NS				
$^{*}CO_2$ (p)	0.076	0.119	± 0.013	NS				

*CO_2 (a) is the ^{14}C radioactivity of CO_2 when ^{14}C acetate was infused; CO_2 (p) is the ^{14}C radioactivity of CO_2 when ^{14}C propionate was infused.. s.e.m. = standard error of the mean; NS = not significant.

Metabolism in the portal-drained viscera

Values for the net flux, unidirectional utilization and production of nutrients in the PDV are presented in Table 6. Net flux of each metabolite is calculated from the blood flow through the PDV and the corresponding arteriovenous difference and represents the balance between use and production by the PDV (i.e. that flowing to the liver). While acetate and propionate appeared in significant amounts in portal blood, more glucose was used by the PDV than was absorbed from the small intestine.

FFA was used in net amounts by the PDV in the HF group and produced in the LF group. Net appearance of acetate did not differ significantly between diets and represents between 62% and 57% of acetate production in the rumen. Propionate appearance across the PDV was significantly lower ($p < 0.05$) in the HF than in the LF group. However, when expressed as a percentage of ruminal production rate, there was no significant difference (51.0% and 58.3 ± 3.5%; HF and LF, respectively), while the difference in net flux is a reflection of the different ruminal production rates.

Table 6 Metabolism of nutrients by the PDV ($mmol.h^{-1}$; n = 4 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	p
Net PDV flux				
Acetate	136.7	124.6	± 10.5	NS
Propionate	52.4	69.5	± 3.41	0.05
FFA	–0.569	0.634	± 0.053	0.05
Glucose	–10.1	–10.6	± 0.625	NS
PDV Utilization				
Acetate	73.3	41.1	± 5.81	0.05
Propionate	4.28	12.1	± 0.715	0.05
FFA	1.78	2.24	± 0.122	0.05
Glucose	16.2	21.2	±1.082	0.05
PDV Production				
Acetate	210.0	165.7	± 7.041	0.05
Propionate	56.7	81.9	± 4.36	0.05
FFA	1.22	2.87	± 0.250	0.05
Glucose	6.09	10.64	± 0.540	0.05

s.e.m. = standard error of the mean; NS = not significant; A '–' sign indicates net utilization.

Although the net flux of FFA across the PDV was small (5.4% and 10.3 ± 0.25% of FFA entry rate; HF and LF, respectively), it differed significantly between diets.There was a net utilization in the HF group and a net production in the LF group. Since fats are absorbed from the digestive tract via the lymphatic system, production does not represent absorption from the lumen but *de novo* synthesis. Although substantial amounts of glucose disappeared from the lumen of the small intestine, there was a net utilization of glucose by the PDV representing between 28% and 25% of the GIL rate.

Diet affected PDV utilization of all metabolites significantly, being generally greater for the LF than the HF group. However, acetate utilization by the PDV was significantly ($p < 0.05$) lower in the LF group, representing 33% and 19 ± 3% of ruminal acetate production in the HF and LF groups, respectively. Although little propionate is utilized by the PDV, the LF group utilized more ($p < 0.05$) than the HF group. Propionate utilization by the gastrointestinal tract tissues was 4.16% and 10.15 ± 1.1% (p < 0.05; HF and LF, respectively) of ruminal production rate.

FFA utilization was greater ($p < 0.05$) in the HF than in the LF group. As a result, net production was thus lower ($p < 0.05$) in the HF group. As for the FFA, glucose utilization by the PDV was significantly ($p < 0.05$) higher in the LF group, and accounted for 45 and 50 ± 1.3% of the GIL rate in the HF and LF groups, respectively.

Actual production by the PDV is calculated from the difference between net flux and utilization. These production rates differed significantly between groups, as follows. The total acetate appearance rate across the PDV was significantly greater ($p < 0.1$) for the HF than for the LF group and was 95% and 76 ± 3% ($p < 0.05$) of the respective ruminal production rates. Propionate production was significantly lower in the HF than the LF group ($p < 0.05$). This was not, however, as a result of different ruminal production rates since PDV production as a percentage of ruminal propionate production also differed significantly ($p < 0.05$) between groups (55% and 69 ± 3% for the HF and LF

groups, respectively.

FFA production by the PDV was lower ($p < 0.05$) in the HF than in the LF group and represented 12 and 47 ± 2.1% of the whole body FFA entry rate for the HF and LF groups, respectively. Glucose production by the PDV was lower ($p < 0.05$) in the HF than in the LF group but, when expressed as a percentage of glucose disappearing from the small intestine, it was higher ($p < 0.05$) for the HF than for the LF group (84% and 69 ± 3%, HF and LF, respectively.

Metabolism in the liver

Values for the net flux, unidirectional utilization and production of nutrients in the liver are presented in Table 7. Despite a greater flow of propionate from the PDV (Table 6) in the LF group, the net hepatic uptake of propionate as well as the net hepatic production of glucose was not affected by

Table 7 Metabolism of nutrients by the liver and net flux across the splanchnic bed (mmol.h^{-1}; n = 4 per group; mean ± s.e.m.)

	HF	LF	s.e.m.	p
Net hepatic flux				
Acetate	21.00	–20.9	± 1.63	0.05
Propionate	–50.9	–53.4	± 4.41	NS
FFA	–5.83	–4.73	± 0.345	0.05
Glucose	31.5	37.59	± 1.95	NS
Hepatic utilization				
Acetate	25.1	38.7	± 1.98	0.05
Propionate	55.7	58.9	± 4.27	NS
FFA	6.54	5.69	±0.403	NS
Glucose	0.12	4.52	±0.532	0.05
Hepatic production				
Acetate	46.1	17.9	± 0.679	0.05
Propionate	4.09	5.6	±0.206	0.05
FFA	0.71	0.96	± 0.025	0.05
Glucose	31.7	41.1	± 2.23	0.05
Hepatic extraction ratio (%)				
Acetate	–3.5	3.96		
Propionate	54.2	46.4		
FFA	8.9	5.4		
Glucose	–3.5	–3.1		
Net splanchnic flux				
Acetate	157.7	103.7	± 12.13	0.05
Propionate	1.47	16.1	± 0.611	0.05
FFA	–6.39	–4.10	± 0.363	NS
Glucose	21.4	27.0	± 2.94	NS

s.e.m. = standard error of the mean; NS = not significant; A '–' sign indicates net utilization.

diet. However, acetate was taken up in net amounts by the livers of sheep fed the LF diet, while it was produced in similar quantities by the HF group. FFA were always produced by the liver in net amounts, although significantly more so in the case of the HF group.

Actual utilization of acetate and glucose by the liver was significantly higher on the LF compared to the HF diet. Glucose and propionate production rates were significantly higher on the LF diet compared to the HF diet. FFA utilization was similar for both diets while hepatic FFA production was higher for the LF compared to HF diet. Acetate production was lower under these circumstances.

The extraction ratio of propionate by the liver was 54% and 46% of the amount supplied in the HF and LF groups respectively. The results obtained in this study agree with those of Bergman and colleagues (Bergman & Wolff, 1971; Bergman *et al.*, 1966). The net amount of propionate removed by the liver represents 50% and 45% of the ruminal propionate production rates, while the net production of glucose represents 87% and 89% of the GIL rate for HF and LF diets, respectively. Despite the higher hepatic glucose utilization on the LF diet, net production was higher because of the much higher actual production rate.

Hepatic utilization of acetate is 11% and 18% of the ruminal acetate production rate. This is similar to other results (Pethick *et al.*, 1983) which show acetate utilization by the liver to range between 10 and 25% of entry rate. The hepatic metabolism of FFA differed significantly between diets. Net utilization by the liver was 56% and 77% of FFA entry rate, while hepatic production was 7% and 16% of the FFA entry rate for the HF and LF diets, respectively.

The net flux of FFA and glucose across the splanchnic bed is similar in both groups of sheep, i.e. a net production of acetate, propionate and glucose and a net utilization of FFA. More acetate was produced in the HF than the LF group, while more propionate was produced in the LF than the HF group.

Peripheral metabolism

The data describing peripheral metabolism of propionate and glucose and the contribution of propionate to glucose and CO_2 are given in Table 8. Apart from the percentage of CO_2 and glucose

Table 8 Peripheral metabolism of propionate and glucose and their interconversions in the liver of sheep fed the HF or LF diet. (n = 8 per group; mean ± s.e.m.)

Metabolism	HF	LF	s.e.m.	p
Corrected GILR ($mmol.h^{-1}$)	35.9	42.3	± 1.54	0.05
Peripheral use of propionate ($mmol.h^{-1}$)	2.5	11.4	± 0.293	0.05
Peripheral use of glucose ($mmol.h^{-1}$)	27.1	21.4	± 0.849	NS
% GILR from propionate	51	38	± 1.41	0.05
Glucose from propionate ($mmol.h^{-1}$)	18.6	16.1	±0.548	NS
Propionate to glucose ($mmol.h^{-1}$)	37.2	32.1	± 1.06	0.05
% Hepatic propionate uptake to GILR	69	55	± 2.15	NS
% Propionate absorbed to glucose	66	39	± 1.80	0.05
% Ruminal propionate to glucose	38	26	± 1.12	0.05
% CO_2 from propionate (whole body)	3.9	3.9	±0.125	NS

s.e.m. = standard error of the mean; NS = not significant.

derived from propionate, all aspects of propionate and glucose metabolism measured were significantly different between the diets.

The amount of propionate metabolised by the peripheral tissues of sheep fed the LF diet (reflected in the percentage of ruminal propionate produced that was metabolised by the peripheral tissues, 2.5%) was about half that of the group on the HF diet (9.5%). The ratio of net propionate utilization by the liver and periphery (HF: 19.9, LF: 4.7) also clearly illustrates the shift in the site of metabolism from the liver to the peripheral tissues.

All the other variables of propionate and glucose metabolism were significantly lower in sheep fed the LF diet. Propionate contributed to 59% of hepatic glucose production on the HF diet, and only 39% of hepatic glucose on the LF diet. This was similar to the difference in contribution to the GIL rate. Hepatic propionate utilization for both diets was approximately 50% of ruminal propionate production (HF: 54%, LF: 49%).

The peripheral metabolism of acetate and FFA and the conversion of acetate to FFA and CO_2 are shown in Table 9. FFA oxidation contributed to approximately 16% of the CO_2 pool, irrespective of the diet There were, however, highly significant differences in the metabolism of these two metabolites between diets. In general, the net utilization of acetate and FFA, as well as the conversion and contribution of acetate to FFA, was significantly higher on the HF than on the LF diet.

Table 9 Peripheral metabolism of acetate and FFA and interconversions in the whole body of sheep fed the HF or LF diets (n = 8 per group; mean ± s.e.m.)

Metabolism	HF	LF	s.e.m.	p
Corrected FFA entry rate ($mmol.h^{-1}$)	10.3	5.19	± 1.32	0.05
Peripheral use of acetate ($mmol.h^{-1}$)	157.7	103.8	± 4.04	0.05
Peripheral use of FFA ($mmol.h^{-1}$)	6.4	4.1	± 0.190	0.05
% FFA entry rate from acetate	37.3	17.4	± 0.76	0.05
FFA from acetate ($mmol.h^{-1}$)	3.77	1.05	± 0.107	0.05
Acetate to FFA ($mmol.h^{-1}$)	60.4	16.8	± 1.68	0.05
% Acetate absorbed to FFA	28.9	9.8	± 0.669	0.05
% Peripheral acetate uptake to FFA	38.3	16.2	± 0.937	0.05
% Ruminal acetate to FFA	27.1	7.9	± 0.668	0.05
% CO_2 from acetate	15.9	16.6	± 0.453	NS

s.e.m. = standard error of the mean; NS = not significant.

The peripheral utilization of acetate in HF sheep was 71% of ruminal acetate production. This decreased to 48% in the LF sheep. Although peripheral use of FFA was quantitatively greater in the HF sheep, when expressed in terms of the FFA entry rate it was similar to that in the LF sheep (HF: 63%; LF: 68%).

Discussion

The tissues of the splanchnic bed form the protective barrier between an organism and its source of nutrition. These respond to endogenous and exogenous effectors and, *inter alia*, modulate the flux of nutrients. After absorption into the bloodstream, the incoming supply of intermediates are pro-

cessed by the liver and adjusted to accommodate the needs of the body.

The gastrointestinal tract comprises only 5% of the body mass (Ferrell *et al.,* 1986), and, relative to body mass, the visceral organs take a disproportionately large share of the whole body cardiac output (and therefore energy metabolism) at rest. Changes in blood flow occur as a result of changes in the level of nutrition, physiological state and phases of nutrient assimilation in sheep (Burrin *et al.,* 1989; Kelly *et al.,* 1993). The main causes of the increased blood flow associated with food presentation and ingestion are an increased heart rate and cardiac output, controlled by both the para- and sympathetic nervous systems (Vatner *et al.,* 1974). The presence of VFA in the rumen increases blood flow in the PDV (Sellers *et al.,* 1964). Tissue metabolic activity (Barnes *et al.,* 1983) is thought to play a role in this control, as well as O_2 consumption (Burrin *et al.,* 1989; Kelly *et al.,* 1993). The latter two authors concluded that blood flow to the liver is more sensitively regulated than PDV flow. This aspect may ensure that the rate of nutrient supply to the liver is not exceeded and will be chiefly determined by the mass of the liver. In the present experiment, the animals were fed continuously at isoenergetic concentrations. The data support the hypothesis that blood flow is dependent upon ME intake. Tissue energy use of the organs varied but did not affect blood flow. Since blood flow was similar in both groups, the changes that were found in transorgan metabolism were largely due to metabolic differences.

The effect of nutrition on basic metabolic rate is highly correlated to changes in the mass of visceral organs and their metabolic activity (Webster, 1989). The effect of nutrition is often reflected in the relationship between ME intake, blood flow and O_2 consumption of the splanchnic bed, and changes in this relationship may be partially responsible for changes in the whole body metabolic rate (Johnson *et al.,* 1990). It appears that tissue energy usage calculated from both O_2 uptake as well as CO_2 production is a more sensitive method of determining tissue metabolic efficiency. Furthermore, not only can the metabolic activity of an organ be accurately estimated, but the proportion lost as heat can be determined. In the present study approximately 40% of the energy usage was lost in heat. These results agree with Webster (1980), who calculated heat loss from the splanchnic bed to be approximately 20% of that from the whole body, but are higher than the 12% reported by Smith & Baldwin (1974), Webster & White, (1973). Tissue energy use of the PDV as well as its HE production was higher in sheep fed the LF rather than the HF diet. The energy use of the liver was not affect by the diet. However, tissue energy use and HE production of the total splanchnic bed reflected the differences between diets observed in the PDV. These results were surprising for a number of reasons. The splanchnic bed is the major consumer (*ca.* 50%) of the whole body oxygen consumption (Burrin *et al.,* 1989) and, as such, must substantially influence the whole-body data. However, despite the fact that the splanchnic bed in sheep fed the high-fibre diet appeared to be more efficient (lost 10% less heat), the animals as a whole were considerably less efficient (grew 30% slower) or conversely, digesting the LF diet was energetically less efficient despite showing an overall higher efficiency than the HF diet, thereby reflecting the importance of peripheral metabolism in nutrient utilization.

Reynolds *et al.* (1991b) fed HF and LF diets with ME and N content similar to those used in the present study to cattle. Their results differ from ours in that the energetic response of the bovine to changes in diet, specifically changes in the fibre fraction were determined largely by the PDV and the liver. Furthermore, they concluded that the splanchnic tissues dominate the partitioning of ME into heat energy and energy not lost as heat but conserved by the tissue. They suggested that this was due to the work of digestion, as well as the work of the splanchnic bed in absorbing and assimilating the components absorbed. If the VFA are responsible, it must be due to the visceral and hepatic metabolism of these nutrients. In order to explain this discrepancy, it is necessary to examine the metabolism of the splanchnic bed in more detail.

The energy use of the splanchnic bed accounted for 44 and 53% of the DE intake. These values fall nicely into the range reported by other authors, i.e. 45–60% of the whole body oxygen consumption (Burrin *et al.*, 1989; Reynolds *et al.*, 1991a). On the other hand, Caine & Mathison (1992a,b) found that lambs treated with cimaterol were more efficient in utilizing dietary energy than untreated lambs and that there was no difference in hepatic energy consumption. These authors suggested that, since protein metabolism is expensive, this might be responsible for the difference. Gill *et al.* (1989a,b,c) quantified the energetics of various organs and types of metabolism, and concluded that protein synthesis was responsible for 20% of energy expenditure. These findings supported the results of MacRae & Lobley (1986), who estimated this value to be 20–25%. Furthermore, the GIT and liver contributed 40–60% towards the energy expenditure. They could not account for 17% of energy expenditure. Thus, although the splanchnic bed is central to metabolism and does use a large proportion of whole body energy expenditure, it is probable that differences in energy utilization lie elsewhere.

The role of the ruminant liver in modifying the profile of absorbed nutrients before being presented to peripheral tissues is illustrated in Figures 1 and 2. These schematic diagrams show the flow of nutrients through the portal bed and liver and illustrate the concept of production (or absorption) and utilization as distinct from net flux. All values are in mmoles per hour for the whole body.

Arterial concentrations were affected by diet. A higher ruminal acetate concentration increased circulating concentrations as well as concentration differences across an organ. However, this apparently did not affect propionate concentrations. Glucose concentrations were increased with the LF diet but this did not affect the amount extracted by the PDV or liver. FFA are not metabolised greatly by the splanchnic bed and differences were small. The lower the fibre content of the diet though, the higher the circulating concentrations of FFA.

Little ruminal acetate is utilized by the PDV and liver during absorption. Approximately 75–90% of ruminal acetate appears in portal blood, with 10% being extracted by the liver. Acetate is utilized

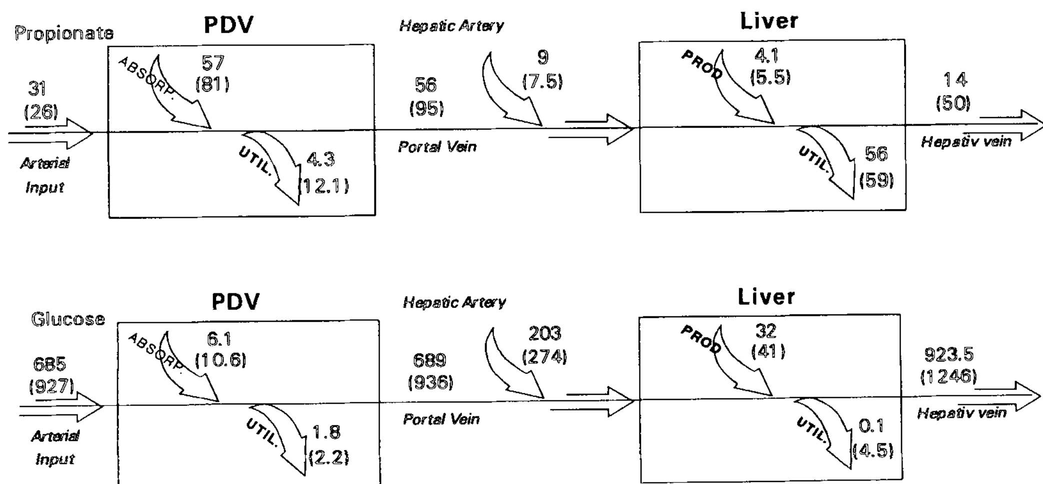

Figure 1 Scheme illustrating flow of propionate and glucose in the splanchnic bed. All values are in terms of mmoles per hour for whole body. The first number is the rate for the HF sheep, and the second number in brackets is the rate for the LF sheep. The rates are the mean values of four sheep.

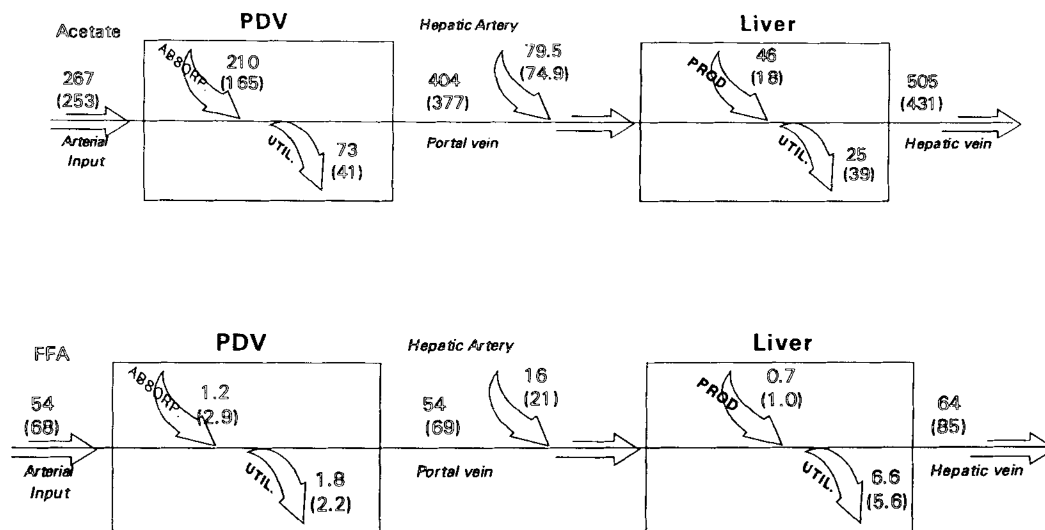

Figure 2 Scheme illustrating flow of acetate and FFA in the splanchnic bed. All values are in terms of mmoles per hour for whole body. The first number is the rate for the HF sheep, and the second number in brackets is the rate for the LF sheep. The rates are the mean values of four sheep. FFA metabolism by the PDV is low (Katz & Bergman, 1969b).

extensively by peripheral tissues as a major source of energy, especially for muscle and GIT, or used for FFA synthesis in adipose tissue (Pethick *et al.*, 1981). Although utilization by the splanchnic bed was responsible for only 30% of the ruminal production, acetate utilization by the PDV was moderately high, especially on the LF diet. This could possibly be responsible for the higher tissue energy usage of this organ on the LF diet.

About 35% and 42% of propionate produced in the rumen of sheep fed the HF and LF diets respectively, was metabolised before being absorbed into portal blood. Most of this is absorbed from the rumen, little from further down the tract (Reynolds & Huntington, 1988a). The high extraction ratio of propionate (52–56%) by the liver agrees with other published data (Reynolds & Huntington, 1988b).

The liver makes extensive use of fatty acids for catabolism or incorporation into glycerides and lipids.The ruminant synthesizes little of its own fatty acids from glucose, rather using acetate for this purpose. Smith *et al.*, (1992) showed that enzymes of the citrate cleavage pathway may increase in activity when maize-based concentrate diets are fed, suggesting that some glucose may well serve as a precursor for fatty acid synthesis. Little FFA was absorbed from the GIT, and the FFA that was taken up by the liver was most probably used for acetate production and lipoprotein synthesis. The fatty acid content of forages is low, and the main site of synthesis is in adipose tissue. It appears, therefore, that apart from utilization for essential requirements, fatty acid catabolism occurs mainly in peripheral tissues.

Evidence for glucose absorption from the small intestine is contradictory, owing to the technical difficulty of measuring the small arteriovenous differences found there. These difficulties are compounded by dilution of the mesenteric blood with blood from the ruminal vein, which contains little glucose (Janes *et al.,* 1985a). Furthermore, there is evidence that, as the amount of glucose available increases, the utilization of glucose increases (Agricultural and Food Research Council,

1987; Huntington *et al.*, 1980). Janes *et al.* (1985a) found that net absorption on grass- and maize-based diets was -2 and 19 $mM.h^{-1}$, respectively. Total absorption, however, was 1.5 and 23.33 $mM.h^{-1}$, which was 83% and 111% of glucose disappearing from the small intestine for the grass- and maize-based diets, respectively. Net appearance in this study was negative (i.e. translating to an uptake), while total appearance was 24.7 and 45.4 g per day, supporting the theory that utilization of glucose by the reticulo-rumen disguises glucose absorption. Total absorption accounted for 70% of the glucose disappearing from the small intestine.

The proportion of propionate oxidized in the PDV appears to be high. However, this CO_2 may originate from three pools, and does not necessarily reflect propionate oxidation by the PDV tissues *per se*. Firstly, there is a large flow of CO_2 between the rumen and blood, in that 55% of ruminal CO_2 may originate from blood, while 40% of blood CO_2 may be of ruminal origin (Veenhuizen *et al.*, 1988). Any CO_2 production from propionate in the rumen would increase blood concentrations. Secondly, any glucose oxidation would result in labelled CO_2 production. Finally, propionate oxidation itself would increase labelled CO_2 concentrations.

Veenhuizen *et al.* (1988) reported that, in order to optimize gluconeogenesis, the percentage of propionate converted to glucose should increase in proportion to the amount of propionate available. In the present study, the amount converted to glucose remained constant, although the percentage of glucose from propionate was higher in the group fed the high fibre diet. This is more in agreement with Judson *et al.* (1968), who found that the percentage of glucose from propionate decreased as propionate availability increased. However, the amount of glucose from propionate did not differ significantly between diets (15,5 $mM.h^{-1}$). These results suggest that the quantity of glucose synthesized is regulated according to both the need and the availability of precursors.

In general, splanchnic metabolism in the LF group tended to be greater for most nutrients, again reflecting the difference in TEU and HE production by this system when compared to the HF group. There appear to be major differences in the peripheral utilization of metabolites between diets (Tables 8 and 9). The peripheral use of propionate was higher on the LF than on the HF diet, possibly owing to increased availability. This is clearly shown in Table 8 where the peripheral use of propionate increased fourfold at the same time as its percentage contribution to the GILR declined by a third. This suggests that some glucose is either directly absorbed from the small intestine in sheep fed the LF diet (Janes *et al.*, 1985b) or is provided via gluconeogenesis from substrates other than propionate. It would, therefore, appear that the hepatic metabolism of propionate for gluconeogenesis is regulated by the glucogenic potential of the diet, and not the quantity of propionate available.

The peripheral usage of acetate was higher on the HF than the LF diet. This can be partially related to the higher circulating levels, but could also be related to the lower GIL rate. Black *et al.*, (1987) showed that acetate can be used to produce NADPH for anabolic reactions. However, they also showed that, as glucose increased, the percentage of acetate converted to FFA also increases.

The results of this study confirm that the splanchnic bed plays a central role in the partitioning of absorbed nutrients between various metabolic pathways. However, the differences observed in the utilization of metabolic energy between high- and low-fibre diets cannot be solely attributed to differences in splanchnic metabolism. Differences in energy flow in the splanchnic bed favour the high- rather than the low-fibre diet. It would thus appear that the difference in growth efficiency between sheep fed a high- or a low-fibre diet lies mainly in the ability of the peripheral tissues to metabolise acetate as well as propionate more efficiently.

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