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Review

Energy metabolism in the digestive tract and liver of cattle: influence of physiological state and nutrition *

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Summary — Major functions of portal-drained viscera (PDV) and liver of cattle include absorption of digestion products and modification of the body's supply of intermediary metabolites. The disproportionately high metabolic rate of PDV and liver (7–13% of body tissues) is exemplified by their oxygen uptake (40–50 % of whole body). Extensive metabolism of glucose, volatile fatty acids and amino acids by PDV modulates nutrient supply from the diet such that most responses to diet or physiological state are a function of level of diet intake. Similarly, blood flow through PDV is highly correlated with energy intake across a range of body weight, physiological state or diet composition. Most common dietary responses in metabolite uptake by PDV are changes in uptake of ammonia and volatile fatty acids, which emphasize the strong energy: nitrogen interrelationship in the rumen and subsequently the rest of the body. The liver (tissue in series with PDV) removes glucose precursors and ammonia from its blood supply as part of its functions in gluconeogenesis, ammonia detoxification and urea synthesis. The liver also alters amounts and proportions of amino acids supplied by PDV. Accountable percentages of metabolizable energy from net PDV supply include: organic acids, 41–59 %; amino acids, 5–13 %; and heat energy (from oxygen uptake), 11–22 %.

cattle / gastrointestinal tract / liver / absorption / metabolism

Résumé — Métabolisme énergétique au niveau du tractus digestif et du foie chez les bovins : influence du stade physiologique et de l'état nutritionnel. *La digestion et le métabolisme des nutriments fournis à l'organisme comptent parmi les principales fonctions du tractus digestif (plus le pancréas, la rate et tissu adipeux mésentérique) et du foie. L'activité métabolique intense du tractus digestif et du foie (qui ne représentent que 7 à 13 % du poids corporel) se traduit par leur consommation élevée d'oxygène (40 à 50 % de celle de l'organisme entier). Le métabolisme intense du glucose, des acides gras volatils et des acides aminés dans le tractus digestif et le foie module l'apport de nutriments à tel point que la plupart des réponses aux modifications de la composition du régime et du stade physiologique de l'animal dépendent essentiellement du niveau d'alimentation. Le flux sanguin à travers le tractus digestif est également étroitement corrélé avec la consommation d'énergie pour une grande gamme de poids vifs, d'états physiologiques et de compositions des régimes. Les variations d'origine alimentaire des prélèvements de nutriments par le tractus digestif concernent généralement l'ammoniaque et les acides gras volatils, ce qui souligne les relations étroites azote–énergie dans le rumen et, par suite, dans l'ensemble de l'organisme. Le foie (organe placé en série après le tractus digestif) prélève les précurseurs du glucose et l'ammoniaque du sang porte pour la néoglucogenèse, la détoxication de l'ammoniaque et la synthèse d'urée. Le foie modifie également les quantités et les proportions d'acides aminés absorbés. L'ensemble des acides organiques absorbés représente de 41 à 59 % de l'énergie métabolisable, les acides aminés de 5 à 13 % et l'énergie dissipée sous forme de chaleur (déterminée à partir de la consommation d'oxygène du tractus digestif) de 11 à 22 %.*

bovin / tractus digestif / foie / absorption / métabolisme

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INTRODUCTION

Domesticated ruminants are perhaps the most versatile omnivores in the world, obtaining nutrition from forages, non-protein nitrogen (N) sources, cereal grains, legumes and feedstuffs of animal origin. Concomitantly, domesticated ruminants use their diets with a wide range of partial efficiencies. For example, use of metabolizable energy (ME) for growth can be as low as 0.21 for forages and as high as 0.65 for energetically dense diets [ARC (Agricultural Research Council, 1980)]. The ME not retained as tissue or released as milk is lost as heat energy (HE).

In most animals, including domesticated ruminants, the portal-drained viscera (PDV) is the interface between the diet and the organism. The liver, tissue in series with the PDV, is the central metabolic intersection between PDV and the rest of the body. Major functions of the splanchnic tissues (PDV and liver) are digestion and absorption of dietary nutrients, supply of a plethora of hormones and immune response. This review will focus on digestive and absorptive functions of cattle. The terms "gut" and "PDV" will be used synonymously, although PDV includes the pancreas, spleen and fat associated with the gut.

Metabolic function and therefore energy metabolism of splanchnic tissues responds to a variety of environmental stimuli, including heat (McGuire *et al,* 1989), cold (Sasaki and Weekes, 1986), fasting or level of feed intake (Lomax and Baird, 1983; Ferrell, 1988), diet composition and productive (physiological) state. The objective of this review is to describe effects of the latter two stimuli on function and energy metabolism of PDV and liver of beef and dairy cattle. Data used were derived mainly from use of one approach, *in vivo* fluxes across PDV and liver of multi-catheterized cattle (Huntington *et al,* 1989). Discussion of physiological state will center on growth or lactation.

PORTAL BLOOD FLOW AND ME INTAKE

There is a positive direct relationship between blood flow through PDV and ME intake in cattle and sheep. Linear (Huntington, 1984a; Weighart *et al,* 1986) or curvilinear (Webster *et al,* 1975; Lomax and Baird, 1983) regressions of portal blood flow on energy intake likely apply to liver blood flow as well, because liver blood flow derives predominantly from PDV. Figure 1 is a summary of 16 treatment means from studies with cattle from which estimates of average hourly portal blood flow are available, and treatments were intakes within diets. The characteristics of the cattle ranged from fasted beef steers (200 kg) to lactating dairy cows (650 kg) eating ME equal to 3 times their maintenance requirement. Diets ranged from forage to high concentrate diets. One can regress with high r^2 linear or curvilinear relationships among the data points (fig 1), with the bulk of the data between 40–100 MJ/d ME intake. Comparison of 11 portal blood flows from studies not used to generate these regressions (Huntington *et al,* 1981; Eisemann and Huntington, 1987; Harmon and Avery, 1987; Gross *et al,* 1988; Harmon *et al,* 1988; Huntington, 1989) showed good predictability. Mean ± SE of predicted divided by observed portal blood flow was 1.00 ± 0.04 for the exponential fit and 1.07 ± 0.04 for the linear fit (fig 1). The ME intakes in the studies used in the comparison ranged from 40–81 MJ/d.

Daily ME intake is highly correlated with other factors that may influence portal (or hepatic) blood flow, including breed, live

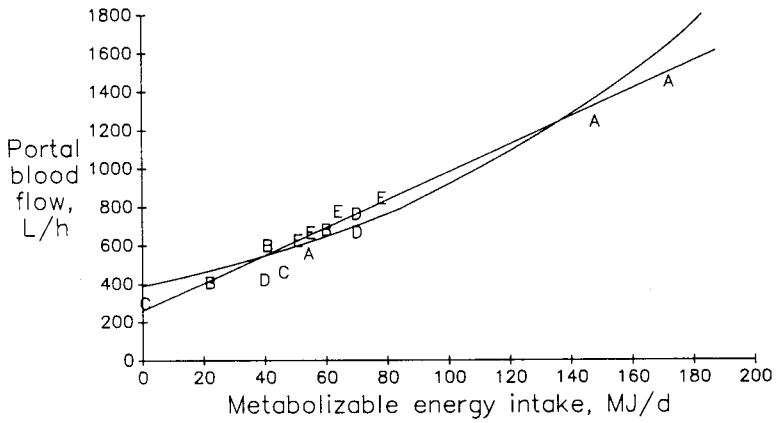

Fig 1. Linear and exponential relationships between metabolizable energy intake (x) and portal blood flow (y). The linear equation is $y = 259 + 7.24x$; $r = 0.98$. The exponential equation is $y = 391\ e^{0.0084x}$, $r = 0.94$. Observations (16) are treatment means from the following sources : A, Holstein cows (Huntington *et al,* 1983; Huntington, 1984b; Reynolds *et al,* 1988); B, Beef heifers (Huntington and Prior, 1983); C, Beef steers (Huntington *et al,* 1988); D, Beef heifers (Reynolds and Tyrrell, 1989). One value is hidden in the figure; E, Holstein steers (Huntington *et al,* 1988).

weight (or some exponent thereof) and energy density of the diet. However, direct (Huntington, 1984a) or implied (Weighart *et al,* 1986) evalution of these factors did not improve r^2. From a more physiological perspective, portal blood flow ranges from 25–52 $ml \cdot min^{-1} \cdot kg^{-1}$ body weight with a median value of ≈ 40 in cattle (Carr and Jacobson, 1968; Wangness and McGilliard, 1972; Harmon and Avery, 1987; Durand *et al,* 1988; Reynolds *et al,* 1988).

Teleologically, portal and hepatic blood flow increase in response to increased ME intake to transport digested nutrients from the gut, through the liver, and on to the rest of the body. Heart rate and thereby cardiac output likewise increase with increased intake (Rumsey *et al,* 1980). Whether or not productive state or dietary composition directly alter the proportion of cardiac output flowing through splanchnic tissues remains to be determined. A preliminary report with beef steers (Huntington *et al,* 1988) indicates that these proportions are similar in fed and fasted steers, but change in acute response to a β-adrenergic agonist.

OXYGEN UPTAKE BY SPLANCHNIC TISSUES

In vivo measurements of oxygen uptake by PDV and liver of cattle provide estimates of HE attributable to those tissues (table I). Over a wide range of body weights and productive states the PDV accounts for 18–25 % and the liver 17–25 % of whole body oxygen uptake, or energy lost as HE. Similar or appreciably higher proportions of whole body oxygen uptake by splanchnic tissues have been reported for sheep (Thompson *et al,* 1978; Burrin *et al,* 1989). The PDV are 6.4–10 % of body tissues,

Table I. Portions of whole body oxygen uptake attributable to portal-drained viscera (PDV), liver and total splanchnic (TS) tissues of cattle. [a] Huntington *et al* (1988); [b] Huntington and Tyrrell (1985); [c] Reynolds *et al* (1986); [d] Huntington and Eisemann (unpublished); [e] Huntington *et al* (1989); [f] Reynolds and Tyrrell (1989).

	Dairy steers [a]	*Lactating cows* [b]	*Lactating cows* [c]	*Beef steers* [d]	*Beef steers* [e]	*Beef heifers* [f]
No animals	4	2	4	5	4	7
Live wt (kg)	334	491	660	221	198	318
Whole body (WB) oxygen uptake (mmol/h)	5 259	9 747	12 219	3 371	2 999	4 167
Oxygen uptake, % WB						
PDV	25	18	20	21	24	25
Liver	–	–	25	17	23	21
TS	–	–	45	38	46	46

and the liver 1–3 % (Smith and Baldwin, 1974; Doreau *et al,* 1985; Jones *et al,* 1985). Therefore, splanchnic tissues account for 35–50 % of HE which is a disproportionately high rate of oxidative metabolism relative to their contribution to body mass. Because these proportions or amounts are substantial, they are attractive targets for ways to improve overall energetic efficiency of cattle.

Absolute rates predictably increase with lactation (table I) or with increased intake (Webster *et al,* 1975; Ferrell, 1988; Reynolds *et al,* 1986 Huntington *et al,* 1988). Diet-related responses in amounts or proportions of oxygen uptake by PDV of steers fed legume or grass silage (Huntington *et al,* 1988) eluded statistical significance; however, increased intake of concentrate by beef heifers decreased oxygen uptake by PDV (Reynolds and Tyrrell, 1989).

NET NUTRIENT FLUX ACROSS PDV AND LIVER

Glucose

In the preponderance of reported studies encompassing a wide range of diets and intakes there is little if any net glucose absorption from dietary sources (see review by Huntington and Reynolds, 1987). This would be expected from consumption of forage diets, but also appears to be the case in cattle consuming substantial amounts of starch. For example, dairy cows consuming about 5 kg of starch as corn silage per day had net use of glucose (59 mmol/h) by PDV (Reynolds *et al,* 1988). Post-ruminal infusion of glucose or starch in a nonlactating cow, beef heifers and dairy steers (Huntington and Reynolds, 1986; Kreikemeier *et al,* 1987)

showed that about two-thirds of the glucose infused and one-third of the starch infused could be accounted for by increased net absorption of glucose. Ostensibly, the rest is used by PDV tissues or further metabolized in the lumen of the intestine. This is suggested by studies with dairy cows (Pehrson *et al,* 1981) and beef steers (Turgeon *et al,* 1983) which indicate the maximal capacity for starch disappearance from the intestine was not exceeded in the infusion studies cited.

Recent studies with steers (table II) help explain how substantial passage of glucose (or α-linked glucose polymers) from the rumen does not result in net glucose absorption. Partition of net glucose flux across stomach and post-stomach sites within PDV showed net use of glucose by both sites when the diet was alfalfa hay. When high-concentrate (corn) diet was fed, however, net use of glucose by stomach tissues increased, and net absorption of glucose by post-stomach tissues was measured, ostensibly in response to starch appearing in the small intestine (table II). Janes *et al* (1984) reported a similar response in post-stomach glucose absorption when the diet of sheep was changed from forage to high-concentrate. *In vitro* studies of rumen mucosa from cattle fed roughage or a high-concentrate diet confirm increased glucose uptake by mucosa in response to the high-concentrate diet with concomitant increases in oxidation of glucose to CO_2 and formation of lactate (Harmon, 1986).

Ruminants are eminently capable of gluconeogenesis to meet their metabolic needs (Young, 1977). Net hepatic glucose production (3.1 kg/d) of lactating cows previously cited as an example of net glucose use by PDV (Reynolds *et al,* 1988) was able to meet glucose required for their milk lactose synthesis, leaving 0.8 kg/d to meet other glucose requirements. Weighart *et al* (1986) made similar calculations for lactating cows. In fed cattle propionate is the major glucose precursor, followed by lactate and amino acids (table III). Studies of nonlactating and lactating cows (Baird *et al,* 1980) show how change in physiological state affects priority of uptake of glucose precursors by the liver to ensure an inverse relationship between glucose availability or propionate supply and use of endogenous precursors by the gut and liver. Fasting decreased gluconeogenesis and caused shifts in the sources of carbon from exogenous sources (propionate) to endogenous sources (lactate, amino acids and glycerol).

Table II. Net glucose flux (mmol/h) across stomach and post-stomach sites of portal-drained viscera (PDV) of steers fed alfalfa hay or a high concentrate diet. [a] Diet differ ($P < 0.05$).

Site	*Reynolds and Huntington (1988a)*		*Huntington (1989)*	
	Alfalfa	*High-concentrate*	*Alfalfa*	*High-concentrate*
PDV	− 35	− 1 [a]	− 53	− 4 [a]
Stomach	− 11	− 30	− 13	− 20
Post-stomach	− 24	+ 29 [a]	− 40	+ 16 [a]

Table III. Maximal contribution of glucose precursors to hepatic gluconeogenesis in cattle. [a] Huntington and Eiseman (1988); [b] Reynolds *et al* (1988); [c] Lomax and Baird (1983); data from lactating and nonlactating cows; [d] Alanine + serine + glycine; [e] Based on α-amino N uptake; [f] Alanine + glycine + serine + threonine.

	Beef steers [a]	*Lactating cows* [b]	*Dairy cows* [c]	
			Fed	*Fasted*
Net hepatic glucose production, mmol/h	180	713	324	74
% contribution to glucose				
propionate	72.8	55.4	46.0	0.8
L-lactate	13.1	17.5	16.0	74.4
amino acids	12.1 [d]	16.5 [e]	8.6	14.6 [f]
pyruvate			0.6	8.1
glycerol			0.8	19.5
Total	98.0	89.4	72.0	117.4

VOLATILE FATTY ACIDS, LACTATE AND KETONES

Volatile fatty acids (VFA) are the predominant source of energy absorbed from dietary sources. As do other tissues, the PDV use VFA as energy sources, which means the rates and pattern of VFA production in the rumen are not the same as their rates and pattern of absorption. Several studies with sheep and cattle (Bergman and Wolff, 1971; Pethick *et al*, 1981; Huntington *et al*, 1983; Seal *et al*, 1989) show that ≈ 33 % of the acetate and 50–80 % of the propionate produced in the rumen are metabolized by PDV. The liver further alters the dietary supply by removing propionate and 4- and 5-carbon VFA from portal blood, and adding acetate from endogenous production (Lomax and Baird, 1983; Huntington and Eisemann, 1988; Reynolds *et al*, 1988).

There is net production of lactate by PDV; L-lactate predominates, but D-lactate is absorbed by cattle fed high grain diets (Huntington *et al*, 1981; Harmon *et al*, 1985). As discussed previously, L-lactate is used by the liver for gluconeogenesis (Huntington *et al*, 1981); D-lactate is oxidized (Harmon *et al*, 1983; Giesecke and Stangassinger, 1978, 1979).

The ketones β-hydroxybutyrate and to a lesser extent acetoacetate are produced by PDV. About 90 % of butyrate produced in the rumen is oxidized by PDV (Bergman and Wolff, 1971) and β-hydroxybutyrate is a major product of that metabolism. The liver also produces β-hydroxybutyrate (Heitmann *et al*, 1987; Reynolds *et al*, 1988). Net uptake of *n*-butyrate and nonesterified fatty acids by the liver of lactating cows accounts maximally for 76–83 % of β-hydroxybutyrate release (Lomax and Baird, 1983; Reynolds *et al*, 1988). Fasting causes the PDV to shift from production to

net use of ketones (Lomax and Baird, 1983).

AMINO ACIDS

Like glucose and VFA, the PDV uses amino acids from dietary and endogenous sources (Tagari and Bergman, 1978). For example, the PDV uses more glutamate and glutamine than is available from dietary sources (Harmon and Avery, 1987; Reynolds and Huntington, 1988a). Glutamate and glutamine are oxidized, and amino groups are transmitted to form alanine, serine and glycine (Bergman and Pell, 1985). In general, use of amino acids by PDV is related to the high rate of protein synthesis in PDV (Lobley *et al,* 1980). This use of amino acids by PDV explains at least in part why it has been difficult to show effects of diet on either rates or proportions of net absorption of amino acids or α-amino N (Prior *et al,* 1981; Huntington, 1987; Huntington *et al,* 1988).

The liver removes amino acids from portal supply in amounts that vary among individual acids, thereby further modulating the rates and proportions of amino acids available for the rest of the body (Baird *et al,* 1975; Bergman and Pell, 1985; Huntington and Eisemann, 1988). The liver is a major participant in N shuttles among various tissues that involve alanine, glycine, glutamate, glutamine, arginine, ornithine and citrulline (Bergman and Pell, 1985). The livers of lactating cows removed 43 % of net PDV supply of α-amino N (Reynolds *et al,* 1988) and the livers of growing beef steers removed 24 % (Huntington and Eisemann, 1988). Liver removal of α-amino N decreased in steers changed from hay to a high-grain diet, resulting in greater splanchnic release with constant PDV absorption (Huntington, 1989). Guerino *et al* (1988) increased PDV absorption of α-amino N abomasal infusion of casein into steers fed a high-grain diet, but liver removal increased correspondingly and splanchnic release of α-amino did not change.

AMMONIA AND UREA

Ammonia and urea are significant components in overall N metabolism of cattle (table IV). Over a variety of diets, N digestibility ranged from 61–72 % of N intake. Urine N and retained N varied with intake and productive state. Net PDV production of ammonia N ranged from 16–95 % of N intake and was directly related to N intake. Net removal of urea N by PDV (transfer from blood to the lumen of the gut) ranged from 15–37 % of N intake, and net production of α-amino N ranged from 18–36 % of N intake. With the exception of beef heifers fed the high-concentrate diet (table IV), net absorption of ammonia N was equal to or greater than net absorption of α-amino N. Net transfer of urea N and net absorption of α-amino are generally similar.

Diet composition affected site of urea N flux across PDV of steers (table V). In steers fed hay, urea was transferred predominantly to the post-stomach. When the same steers were fed a high-concentrate diet, urea flux shifted to the stomach (rumen). Earlier work with ^{15}N similarly showed transfer of urea N was predominantly to the lower gut of sheep fed forage (Nolan and Leng, 1972). Bunting *et al* (1989) used radioisotopes to show increased protein intake of calves increased production of ammonia in the rumen, increased urea synthesis, and doubled the percentage of total gastrointestinal urea degradation occurring in the rumen. Net production of ammonia N in steers fed twice daily was 2.7: 1 stomach: post-stomach for the hay diet and about 1:1 for

Table IV. Nitrogen metabolism in cattle. [a] DN, digested N; UN, urine N; TN, tissue N; MN, milk N; NH_3N, net portal absorption of ammonia, AAN, net portal absorption of α-amino N or amino acids; [b] Net transfer of urea N across portal-drained viscera to the lumen of the gut; does not include salivary urea; [c] Huntington (1984b); [d] Reynolds *et al* (1988); [e] Huntington et al (1988); [f] Reynolds and Tyrrell (1989); [g] Huntington and Prior (1983; 1985).

Animal	*Diet*	*N intake (g/d)*	*Percentage of N intake* [a]						
			DN	*UN*	*TN*	*MN*	*NH_3N*	*Urea*[b]	*AAN*
Lactating cow [d]	60:40 Silage: supplement	387	69	38	2	30	38	24	35
Lactating cow [d]	60:40 Silage: supplement	388	69	45	−14	38	47	37	36
Holstein steer [e]	Alfalfa silage	233	71	58	13		64	15	18
	Grass silage	178	61	48	12		55	20	24
Beef heifer [f]	75:25 Hay: concentrate	161	69	61	7		34	33	32
	25:75 Hay: concentrate	132	72	58	13		51	35	36
Beef heifer [g]	10:90 Hay: concentrate	34	70	88	−20		35	20	28
		64	66	60	4		20	22	30
		93	62	36	25		16	19	33

Table V. Net flux [a] (mmol/h) of ammonia N and urea N across stomach and post-stomach sites of portal-drained viscera (PDV) of steers fed alfalfa hay or a high concentrate diet. [a] Positive numbers indicate absorption, negative numbers indicate transfer from blood to the lumen of the gut; [b] Fluxes measured at meal time in steers fed twice daily; [c] Fluxes measured in steers fed 12 equal meals daily; [d] Within studies, diet means differ ($P < 0.05$).

Site	*Reynolds and Huntington (1988a)*		*Huntington (1989)*	
	Alfalfa	*High-concentrate*	*Alfalfa*	*High-concentrate*
Ammonia N				
PDV	348	154 [d]	291	128 [d]
Stomach	253	74	195	85
Post-stomach	95	80	96	43
Urea N				
PDV	−96	−101	−79	−76
Stomach	9	−68	−24	−71
Post-stomach	−106	−32 [d]	−55	−5 [d]

the high-concentrate diet (measurements made at meal time). In steers fed 12 meals/d net production of ammonia N was about 2:1 stomach: post-stomach on both diets (table V), suggesting that about 2/3 of absorbed ammonia N emanated from ruminal fermentation and tissue metabolism, and one-third from metabolism of N sources in the lower gut.

The liver receives directly the ammonia N produced by PDV and essentially removes all of it from blood (Huntington and Eisemann, 1988; Reynolds *et al*, 1988; Huntington, 1989). Net liver removal can account maximally for 70 to 80 % of urea N released (Huntington and Eisemann, 1988; Reynolds *et al*, 1988; Huntington, 1989). The capacity of a healthy liver to remove ammonia is not exceeded with normal diets (Symonds *et al*, 1981; Orzechowski *et al*, 1987), even when PDV production is substantial.

ENERGETIC SUMMATION OF PDV AND LIVER METABOLISM

Baird *et al* (1975) first published a comprehensive summation of energy flux by PDV of a lactating cow. Energy absorbed as VFA, lactate and ketones, and amino acids summed to 135 MJ/d, which was 84 % of calculated ME intake. Further studies with steers and dairy cows include HE from oxygen uptake by PDV (table VI). In the steers, energy from net absorption plus HE accounted for 75–91 % of measured ME intake of legume or grass silage. Not all energy sources were measured in all studies with dairy cows, but in lactating cows nutrient absorption plus HE accounted for 85% of ME intake. In both steers and cows the largest single source of energy was acetate followed by propionate, except for first lactation cows in which the order was reversed. The third largest source (again

Table VI. Energetic summation of net absorption and oxygen uptake by portal-drained viscera of cattle. [a] Huntington *et al* (1988); [b] Huntington *et al* (1983); [c] Huntington and Tyrrell (1985); Reynolds and Huntington (1988b); [d] Reynolds *et al* (1988).

	Holstein steers [a]				*Holstein cows* 60:40 Corn silage: supplement		
	Alfalfa silage		*Orchardgrass silage*		*dry* [b]	*1st lact* [c]	*2+ lact* [d]
Live weight (kg)	320	335	334	345	493	496	645
Dry matter intake (kg/d)	5.0	7.2	5.0	6.4	5.0	14.0	15.6
Metabolizable energy intake (MJ/d)	60	84	56	70	59	171	178
Net absorption (MJ/d)							
Acetate	12.5	22.8	16.5	21.2	12.1	27.0	39.2
Proprionate	9.2	14.6	8.0	11.0	6.1	27.2	30.1
Other VFA	4.7	7.2	3.7	4.6	4.3	11.0	15.9
L-lactate	3.0	3.9	2.4	3.3	2.0	4.9	7.0
β-Hydroxybutyrate	–	–	–	–	–	–	12.1
amino-acid	3.0	7.1	5.4	7.2	–	18.9	27.1
Oxygen uptake (MJ/d)	12.6	16.3	12.6	16.7	–	18.9	27.1

except for first lactation cows) was HE from oxygen uptake and fourth was energy from amino acids. Other VFA, L-lactate and β-hydroxybutyrate supplied lesser amounts of energy. L-lactate plus VFA accounted for 41–57 % of ME intake (table VI). A similar percentage of ME intake was attributable to L-lactate and VFA in beef heifers fed a high-concentrate diet (46%; Huntington and Prior, 1983). Sources of ME not accounted for in table VI include heat of fermentation, absorption of long-chain fatty acids, and absorption of other nitrogenous compounds such as nucleic acids and peptides (Webb, 1986).

Dietary effects on sources of energy absorbed or HE by PDV were slight in the steers. Steers fed alfalfa silage absorbed more energy as branched-chain VFA and *n*-valerate than steers fed grass silage (table VI). Comparison of differences between intake within silages suggests some dietary effects; compared to the grass silage, the alfalfa silage caused a greater increment as acetate (40 *vs* 30% of the increment) and a lesser increment as HE (15 *vs* 26 % of the increment) (Huntington *et al,* 1988). This may explain in part some of the metabolism behind greater efficiency of energy use by ruminants fed legumes compared to grasses (Rattray and Joyce, 1970; Tyrrell *et al,* 1982; Thompson *et al,* 1985; Varga *et al,* 1987).

Nonlactating and lactating cows were fed the same diet, but at different intakes to support production (table VI). Compared to non-lactating cows, lactating cows absorbed a greater percentage of ME intake as propionate (16 *vs* 10%). The percentage of ME absorbed as acetate was less by cows in first lactation (16%) than dry cows (20%) or older lactating cows (22%).

CONCLUSIONS

Five major points can be derived from information in this review. First, blood flow throught PDV of cattle is highly and positively correlated with their ME intake, which provides a transport for increased absorption of nutrients. Second, the PDV and liver are metabolically active at rates disproportionately greater than their contribution to body tissue mass; together, they can account for one-half of HE. Third, altough cattle derive little if any glucose directly from dietary sources, they are metabolically designed and tuned to synthesize glucose, which provides a use for propionate and lactate absorbed by PDV. Fourth, nonprotein N sources are significant participants in overall N metabolism which is orchestrated by the liver. Fifth, dietary or physiological effects on nutrient absorption and liver metabolism are most evident for VFA, ammonia and urea, which emphasizes the close and perhaps obligate interrelation between energy and N metabolism in cattle.

These points show the central role gut and liver tissues play in energy metabolism, both by regulating and modulating dietary energy sources and by virtue of their high energy expenditures. It follows then that a small change in mode or efficiency of splanchnic metabolism could have a major effect on the whole animal's response to physiological state or nutrition.

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