

Partition of portal-drained visceral net flux in beef steers

2. Net flux of volatile fatty acids, D- β -hydroxybutyrate and L-lactate across stomach and post-stomach tissues*

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1. Net flux of volatile fatty acids (VFA), D- β -hydroxybutyrate (BOHB) and L-lactate across post-stomach (anterior mesenteric-drained viscera (MDV)), stomach and total hepatic portal-drained viscera (PDV) tissues was measured in two beef steers (mean live weight 390 kg).

2. Net flux was measured while steers were fed, in sequence, on (1) chopped lucerne (*Medicago sativa*) (twelve meals/d), (2) chopped lucerne (two meals/d) and (3) a pelleted concentrate diet containing 780 g ground maize/kg (two meals/d).

3. Five hourly net flux measurements were obtained on 2 d for each dietary regimen, beginning 0.5 h before a meal delivered at 08.00 hours. Net flux was calculated as venous–arterial concentration differences (VA) multiplied by blood flow (measured by downstream dilution of *p*-aminohippurate (PAH)).

4. Stomach tissues accounted for 85 to over 100% of net VFA and BOHB appearance across PDV. Net appearance across stomach tissues represented 74% of net PDV L-lactate appearance.

5. When lucerne was given, there was net utilization of arterial acetate and BOHB across MDV. This MDV utilization may reflect acetate and BOHB use as an energy source or their incorporation into mesenteric fat.

6. When concentrate was given, more *n*-butyrate and *n*-valerate and less L-lactate appeared across PDV and less 3-methylbutyrate appeared across stomach tissues than when lucerne was given. Postprandial increases in VFA, BOHB and L-lactate net flux across PDV followed meal-feeding of lucerne.

7. On a net basis, the relative contribution of MDV tissues to total PDV net appearance of VFA and BOHB was small (< 15%) in these steers.

In ruminants, much of the carbon oxidized to meet energy requirements and expired as carbon dioxide is initially assimilated from the diet as a component of volatile fatty acids (VFA). These VFA are the products of microbial fermentation of carbohydrates in the lumen of the gut. Calculations of Bergman & Wolff (1971) show that substantial quantities of acetate, propionate and butyrate produced in the rumen of sheep do not appear in the portal blood, presumably due to their metabolism by rumen epithelial tissues. The ketone bodies D- β -hydroxybutyrate (BOHB) and acetoacetate are products of the metabolism of butyrate and, to a lesser extent, acetate by tissues of the portal-drained viscera (PDV) (Stevens & Stettler, 1966) and L-lactate is a product of the metabolism of absorbed propionate by rumen epithelium (Giesecke & Stangassinger, 1980).

In the classic study of Barcroft *et al.* (1944), concentrations of VFA in blood draining sections of the gastrointestinal tract of anaesthetized sheep were compared with arterial VFA concentrations. The substantial venous–arterial concentration differences (VA) measured for the rumen, reticulum and, to a lesser extent, the omasum and caecum, led to the conclusion that significant amounts of VFA were absorbed from the gut into the portal blood. Since this pioneering research there have been few, if any, studies comparing relative amounts of VFA absorption across various sections of the ruminant PDV. We know of no studies in which measurements of net VFA flux have been obtained simultaneously from sections of the PDV of sheep or cattle.

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The anatomy of the PDV provides an opportunity for the venous return from the gastrointestinal tract to be separated into primarily stomach and post-stomach portions. The objective of our study was to compare net flux of VFA, BOHB and L-lactate across stomach and post-stomach tissues of beef steers fed on lucerne (*Medicago sativa*) or concentrate diets.

MATERIALS AND METHODS

Surgical procedures, dietary regimens and sampling protocol

Implantation of chronic catheters, dietary protocol and sampling procedures have been described (Reynolds & Huntington, 1988). Concisely, catheters were implanted using aseptic surgical techniques into the hepatic portal, anterior mesenteric, gastrosplenic and distal mesenteric veins and the caudal aorta of two Hereford beef steers (mean body weight, 390 kg). VA for VFA, BOHB and L-lactate were determined across the total PDV (tissues drained by the hepatic portal vein including the gastrointestinal tract, pancreas, spleen and mesenteric fat), the anterior mesenteric-drained viscera (MDV) or post-stomach tissues and the gastrosplenic-drained viscera or stomach tissues. Blood flow in the anterior mesenteric and hepatic portal veins was determined by measuring the downstream dilution of *p*-aminohippurate (PAH; 90 g/kg) infused continuously (1.2 ml/min) into a distal mesenteric vein. A priming dose (15 ml) of PAH was used to speed the equilibration of PAH concentration.

Steers were fed on chopped lucerne hay (maximum stem length 40 mm) before and following surgery using an automatic feeder which delivered 500 g hay every 2 h and 50 g trace mineralized salt (TMS) at 08.00 hours. Five measurements of net flux were obtained at hourly intervals 7 and 9 d after surgery (timed-fed lucerne).

Steers were then given 3.0 kg of the same chopped lucerne hay at 08.00 and 16.00 hours and 50 g TMS at 08.00 hours until measurements of net flux were obtained 21–24 d after surgery (meal-fed lucerne). After these measurements, steers were adapted over 12 d to a pelleted concentrate diet (Reynolds & Huntington, 1988), which was then given in equal meals (3.0 kg) at 08.00 and 16.00 hours. Measurements of net flux were obtained 28 and 30 d after the diet change began (meal-fed concentrate).

Sample analyses

Samples were kept on ice until analyses or treatment before freezing was completed, which was never longer than 3 h after sampling. Analyses of whole blood and plasma PAH and calculation of blood and plasma flow rates have been described (Reynolds & Huntington, 1988). Concentrations of L-lactate in fresh plasma were determined using a Yellow Springs Lactate Analyzer (Yellow Springs Instruments Co. Inc., Yellow Springs, OH). Portions of whole blood were deproteinized with 3.48 M-perchlorate, which was removed by precipitation with 6 M-potassium hydroxide, resulting in pH > 10. Following centrifugation at 9000 g, the resulting supernatant fraction was stored frozen until BOHB concentrations were determined using the enzymic procedures of Williamson & Mellanby (1974).

Portions of whole blood were stored frozen until analysed for VFA concentration using procedures of Reynolds *et al.* (1986). Briefly, the concentrations of acetate, propionate, *n*-butyrate, isobutyrate, 2-methylbutyrate, 3-methylbutyrate and *n*-valerate in this solution were determined by gas-liquid chromatography of blood samples deproteinized using procedures of Somogyi (1945) and passed through ion-exchange resins.

Statistical analyses

Calculations of net flux and statistical analyses performed on these values have been described (Reynolds & Huntington, 1988). Briefly, overall means were generated for each

steer and dietary regimen and used to test differences between timed- and meal-fed lucerne and concentrate feeding. Overall means for each sampling time (n 2) within each steer and diet were also produced and analysed to determine effects of time and surface responses within each dietary regimen. Orthogonal polynomials were used to test for linear, quadratic, cubic and quartic responses when time effects were significant ($P < 0.1$). Stomach net flux rates presented were calculated as PDV minus MDV net flux (Reynolds & Huntington, 1988).

RESULTS

VFA

With the exception of *n*-butyrate, arterial concentrations (Table 1) of C_4 and C_5 VFA were extremely small. Only arterial concentrations of 3-methylbutyrate were affected by dietary regimen, being higher ($P < 0.05$) when steers were fed on concentrate. Arterial concentrations of acetate increased linearly ($P < 0.01$) when lucerne was meal-fed (Table 2).

Comparison of net flux rates of VFA across MDV and PDV (Table 1) suggests the post-stomach tissues make a relatively minor contribution to net VFA absorption across the total PDV. Net flux rates (Table 1) for the VFA across stomach tissues were substantial and on a net basis accounted for nearly all the net absorption of VFA across PDV.

Measurements of VA and net flux of VFA across MDV were not affected ($P > 0.1$) by dietary regimen (Table 1). When lucerne was given, net flux of acetate across MDV was negative, indicating that use of arterial acetate was greater than acetate absorption from the gut lumen. Overall, net absorption of VFA across the MDV (excluding acetate) represented from 8 to 15% of net PDV absorption. Net *n*-butyrate absorption across MDV increased ($P < 0.01$) following meal-feeding of lucerne (Table 2).

Across the PDV, VA for isobutyrate and 3-methylbutyrate were lower ($P < 0.05$ and $P < 0.1$ respectively), while VA for *n*-butyrate were greater ($P < 0.05$) when concentrate was given than when lucerne was given. Ratios of net PDV absorption of acetate: propionate averaged 3.2:1, ranging from 2.5:1 when concentrate was given to 3.5:1 when lucerne was meal-fed (Table 1).

Across stomach tissues, VA were greater ($P < 0.05$) for *n*-butyrate when concentrate was given than when lucerne was given. Stomach tissue VA for 3-methylbutyrate were greater ($P < 0.1$) when lucerne was timed-fed than when lucerne was meal-fed. Net flux of 3-methylbutyrate across stomach tissue was lower ($P < 0.05$) when concentrate was given than when lucerne was given (Table 1).

There were some fluctuations ($P < 0.05$) in 2- and 3-methylbutyrate absorption across PDV and stomach tissues when lucerne was timed-fed (values not shown) and when concentrate was given (Table 3). Net absorption of *n*-butyrate across PDV and stomach tissue also increased slightly ($P < 0.05$) following meal-feeding of concentrate (Table 3). When lucerne was meal-fed there were significant postprandial increases in net absorption across PDV or stomach tissues, or both, for all the VFA measured except *n*-valerate (Table 2). These responses were generally linear or quadratic, or both ($P < 0.05$).

BOHB

When steers were meal-fed concentrate, arterial concentrations of BOHB (Table 1) were higher ($P < 0.01$) than when lucerne was given. However, dietary regimen had no effect ($P > 0.1$) on VA or net flux rates of BOHB across MDV, PDV or stomach tissues (Table 1). Across MDV, net flux of BOHB (Table 1) followed trends for acetate, being negative

Table 1. Arterial concentration and metabolism of blood volatile fatty acids, D- β -hydroxybutyrate (BOHB) and L-lactate across portal-drained viscera of two beef steers

Diet...	Time-fed lucerne (<i>Medicago sativa</i>)	Meal-fed lucerne	Meal-fed concentrate	Mean	SEM
Arterial concentration (mM)					
Acetate	1.352	1.435	1.073	1.287	0.167
Propionate	0.028	0.031	0.033	0.031	0.004
Isobutyrate	0.000	0.001	0.000	0.001	0.000
<i>n</i> -Butyrate	0.016	0.008	0.031	0.018	0.005
2-Methylbutyrate	0.000	0.001	0.000	0.000	0.000
3-Methylbutyrate	0.000	0.003	0.009*	0.004	0.001
<i>n</i> -Valerate	0.002	0.003	0.003	0.002	0.001
BOHB	0.424	0.456	0.838*	0.572	0.026
L-Lactate	0.363‡	0.526	0.371	0.420	0.027
Mesenteric-drained viscera flux (mmol/h)					
Acetate	-50	-26	3	-24	21
Propionate	9	10	24	15	4
Isobutyrate	1.5	1.7	1.6	1.6	0.3
<i>n</i> -Butyrate	-0.1	2.2	12.3	4.8	2.5
2-Methylbutyrate	0.4	0.6	1.2	0.7	0.2
3-Methylbutyrate	0.5	0.4	0.5	0.5	0.2
<i>n</i> -Valerate	1.0	1.8	3.6	2.1	0.6
BOHB	-3.5	-5.8	0.2	-3.0	1.1
L-Lactate	15.0	9.8	14.9	13.2	2.1
Portal-drained viscera flux (mmol/h)					
Acetate	586	610	448	548	77
Propionate	166	174	178	173	33
Isobutyrate	12.7	15.2	10.5	12.8	0.9
<i>n</i> -Butyrate	31.4	31.2	92.7*	51.8	10.2
2-Methylbutyrate	7.7	10.8	12.4	10.3	1.2
3-Methylbutyrate	7.9	6.5	2.0	5.5	1.2
<i>n</i> -Valerate	11.6	13.4	18.1*	14.4	0.9
BOHB	66.9	70.4	105.6	80.9	15.5
L-Lactate	53.9	55.7	43.1*	50.9	2.1
Stomach flux (mmol/h)					
Acetate	636	636	444	572	98
Propionate	156	164	154	158	36
Isobutyrate	11.2	13.5	8.9	11.2	1.2
<i>n</i> -Butyrate	31.5	29.0	80.4	47.0	12.2
2-Methylbutyrate	7.3	10.2	11.3	9.6	1.0
3-Methylbutyrate	7.4	6.1	1.5*	5.0	0.9
<i>n</i> -Valerate	10.6	11.6	14.6	12.3	1.4
BOHB	70.4	76.3	105.4	84.0	16.2
L-Lactate	38.9	45.9	28.2	37.7	4.1

Significantly different from time-fed or meal-fed lucerne: * $P < 0.05$.Significantly different from meal-fed lucerne: ‡ $P < 0.05$.

when lucerne was given and essentially zero when concentrate was given, indicating net stomach flux accounted for all net BOHB appearance across PDV tissues (Table 1). When lucerne was timed-fed (values not shown), slight fluctuations occurred in arterial BOHB concentrations (linear $P < 0.01$, quadratic $P < 0.05$, quartic $P < 0.01$). Following meal-feeding of lucerne, postprandial increases (Table 2) were measured for arterial concentration (linear $P < 0.05$), PDV production (linear $P < 0.05$) and stomach production

Table 2. Arterial concentration and metabolism of blood volatile fatty acids, D-β-hydroxybutyrate (BOHB) and L-lactate across portal-drained viscera (PDV) of two beef steers meal-fed lucerne (*Medicago sativa*)†

(Mean values for four determinations)

Sampling time (hours)...	07:30	08:30	09:30	10:30	11:30	SEM
Blood flow (l/h)						
MDV	196	322	285	282	242	26
PDV ^{a, b}	542	653	697	695	700	16
Arterial concentration (mm)						
Acetate ^a	0.778	1.270	1.595	1.748	1.784	0.155
Propionate	0.021	0.031	0.033	0.037	0.031	0.004
Isobutyrate	0.002	0.001	0.001	0.001	0.001	0.001
n-Butyrate	0.003	0.004	0.010	0.011	0.012	0.003
2-Methylbutyrate	0.001	0.001	0.001	0.001	0.001	0.001
3-Methylbutyrate	0.006	0.001	0.004	0.002	0.003	0.003
n-Valerate	0.002	0.002	0.005	0.003	0.003	0.002
BOHB ^{a, b}	0.323	0.414	0.491	0.511	0.539	0.021
L-Lactate ^{a, b}	0.379	0.499	0.618	0.569	0.566	0.024
MDV flux (mmol/h)						
Acetate	13	-23	-50	-18	-50	24
Propionate	6	18	11	10	7	5
Isobutyrate	1.3	2.6	1.8	2.2	0.7	0.5
n-Butyrate ^a	2.0	4.1	2.1	2.6	0.2	1.0
2-Methylbutyrate	0.6	1.4	0.6	0.6	0.1	0.3
3-Methylbutyrate	-0.3	1.6	0.1	0.7	-0.1	0.6
n-Valerate	0.9	4.342	1.0	1.7	1.1	1.4
BOHB	-1.4	-7.4	-7.4	-6.5	-6.5	1.7
L-Lactate	3.1	18.4	11.9	8.2	7.4	6.3
PDV flux (mmol/h)						
Acetate ^{a, b}	349	522	681	743	757	39
Propionate ^{a, b}	71	168	209	209	214	19
Isobutyrate ^{a, b}	10.4	17.2	17.2	16.4	14.9	1.1
n-Butyrate ^a	11.6	25.2	32.2	43.5	43.4	3.7
2-Methylbutyrate ^b	6.9	13.2	13.3	11.2	9.7	1.3
3-Methylbutyrate	0.9	7.9	8.9	8.5	6.2	2.8
n-Valerate	4.1	12.0	15.2	18.3	17.5	3.7
BOHB ^a	47.9	71.9	69.0	81.2	81.9	4.8
L-Lactate ^b	27.2	62.3	74.4	59.6	55.0	6.8
Stomach flux (mmol/h)						
Acetate ^{a, b}	336	545	731	761	807	48
Propionate ^{a, b}	65	150	197	199	207	21
Isobutyrate ^{a, b}	9.1	14.6	15.4	14.2	14.2	1.2
n-Butyrate ^a	9.6	21.1	30.3	40.9	43.2	4.3
2-Methylbutyrate ^b	6.3	11.8	12.7	10.6	9.6	1.2
3-Methylbutyrate ^{a, b}	1.1	6.3	8.8	7.8	6.4	2.4
n-Valerate	3.2	7.7	14.1	16.7	16.4	3.6
BOHB ^{a, b}	49.3	79.3	76.5	87.6	88.4	4.1
L-Lactate	24.1	43.9	62.5	51.4	47.6	8.4

MDV, mesenteric-drained viscera.

^{a, b} Linear and quadratic response respectively; $P < 0.05$.

† 3.0 kg chopped lucerne hay at 08.00 and 16.00 hours.

Table 3. Arterial concentration and metabolism of blood volatile fatty acids, *D*- β -hydroxybutyrate (BOHB) and *L*-lactate across portal-drained viscera (PDV) of two beef steers meal-fed concentrate†

(Mean values for four determinations)

Sampling time (hours)...	07.30	08.30	09.30	10.30	11.30	SEM
Blood flow (l/h)						
MDV	333	340	373	235	234	57
PDV	808	762	756	710	692	41
Arterial concentration (mm)						
Acetate	1.027	1.098	1.080	1.116	1.044	0.077
Propionate	0.032	0.033	0.033	0.036	0.032	0.004
Isobutyrate	0.002	0.001	0.001	0.001	0.001	0.001
<i>n</i> -Butyrate	0.028	0.038	0.026	0.036	0.034	0.007
2-Methylbutyrate	0.001	0.001	0.001	0.001	0.001	0.001
3-Methylbutyrate	0.004	0.015	0.014	0.004	0.009	0.004
<i>n</i> -Valerate	0.002	0.007	0.004	0.002	0.009	0.004
BOHB	0.788	0.821	0.811	0.898	0.872	0.032
<i>L</i> -Lactate	0.352	0.384	0.381	0.374	0.365	0.008
MDV flux (mmol/h)						
Acetate	14	7	-14	12	-4	11
Propionate	29	25	23	23	17	6
Isobutyrate	1.5	1.9	1.9	1.4	1.2	0.3
<i>n</i> -Butyrate	16.0	12.1	12.6	9.2	7.3	3.8
2-Methylbutyrate	1.0	1.8	1.2	0.9	0.7	0.3
3-Methylbutyrate	1.0	-0.8	0.4	3.2	-0.5	0.3
<i>n</i> -Valerate	4.1	3.4	3.6	2.5	2.8	1.6
BOHB	-3.6	-10.7	-6.2	-10.6	28.2	17.3
<i>L</i> -Lactate	15.4	18.1	15.4	10.6	46.1	12.5
PDV flux (mmol/h)						
Acetate	409	452	495	458	435	45
Propionate	185	190	180	173	157	7
Isobutyrate	10.0	12.3	11.4	9.8	8.8	1.2
<i>n</i> -Butyrate ^a	100.6	106.5	96.7	77.9	68.0	4.9
2-Methylbutyrate	13.5	15.5	9.8	12.4	10.5	2.1
3-Methylbutyrate	3.9	4.7	0.5	1.8	1.8	2.4
<i>n</i> -Valerate	20.1	17.2	20.4	15.6	14.1	4.2
BOHB	106.2	95.1	149.5	85.5	67.6	24.5
<i>L</i> -Lactate	42.5	46.0	42.1	42.9	43.2	2.8
Stomach flux (mmol/h)						
Acetate	396	445	510	446	440	38
Propionate	156	164	157	150	139	12
Isobutyrate	8.5	10.4	9.6	8.5	7.7	1.2
<i>n</i> -Butyrate ^{a, b}	84.6	94.3	84.1	68.7	60.7	2.9
2-Methylbutyrate	12.5	13.6	8.6	11.5	9.8	1.8
3-Methylbutyrate	2.9	5.5	0.1	-1.3	-1.3	2.2
<i>n</i> -Valerate	16.0	13.8	16.8	13.2	11.2	3.8
BOHB ^b	109.7	105.8	155.7	96.2	39.4	20.1
<i>L</i> -Lactate	27.1	27.9	26.7	31.3	-2.9	9.8

MDV, mesenteric-drained viscera.

^{a, b} Linear and quadratic response respectively: $P < 0.05$.

† 3.0 kg concentrate at 08.00 and 16.00 hours.

of BOHB (linear $P < 0.05$, quadratic $P < 0.05$). A similar increase in stomach production of BOHB (quadratic $P < 0.05$) followed meal-feeding of concentrate (Table 3).

L-lactate

Greater ($P < 0.05$) arterial L-lactate concentrations (Table 1) were measured when lucerne was meal-fed than when lucerne was timed-fed. Dietary regimen also affected VA for L-lactate; VA were lower across PDV ($P < 0.05$) and stomach tissue ($P < 0.1$) when concentrate was given than when lucerne was given and were lower ($P < 0.05$) across MDV when lucerne was meal-fed than when lucerne was timed-fed. Net flux of L-lactate across PDV (Table 1) was lower ($P < 0.05$) when concentrate was given than when lucerne was given. This decrease in PDV L-lactate flux seems due to a decrease in appearance across stomach tissue, since MDV flux (Table 3) was not affected by diet ($P > 0.1$) and stomach L-lactate VA were lower ($P < 0.05$) when concentrate was given. Stomach flux of L-lactate (Table 1) was not affected ($P > 0.1$) by diet, although rates of absorption tended to be lower when concentrate was given and higher when lucerne was meal-fed. On average, MDV appearance of L-lactate accounted for 26% of PDV flux (Table 1).

Arterial L-lactate concentration increased 1.6-fold following meal-feeding of lucerne (linear $P < 0.01$, quadratic $P < 0.01$; Table 2). This substantial increase in arterial L-lactate concentration was associated with an increase in net PDV flux (quadratic $P < 0.05$; Table 2), yet VA across stomach tissue decreased slightly (linear $P < 0.01$) and increases in VA and net flux across MDV (Table 2) were not significant ($P > 0.1$). There were no significant effects of time ($P > 0.1$) when concentrate was given (Table 3).

DISCUSSION

VFA

Blood VFA concentrations in the present study were similar to those reported for dry Holstein cows determined using similar analytical techniques (Huntington & Reynolds, 1983). Net rates of absorption of VFA across PDV in the present study were also comparable to those reported by Huntington & Reynolds (1983) for dry Holstein cows consuming 5 kg dry matter/d and to rates reported for beef heifers on an identical concentrate diet at similar levels of intake (Huntington & Prior, 1983). Ratios of the net absorption of acetate:propionate were also similar to previous measurements from cattle (Huntington & Reynolds, 1983; Huntington & Prior, 1983) and sheep (Bergman & Wolff, 1971) fed on diets similar to those used in the present study.

On a net basis, stomach tissues accounted for 85–100% of net PDV absorption of VFA. Barcroft *et al.* (1944) measured significant VA for VFA in blood draining the rumen and reticulum. For blood draining the omasum and caecum, VA of VFA were half those measured for the reticulo-rumen. Our measurements of stomach net flux include the reticulo-rumen and omasum. The caecum is a component of the MDV; however, net absorption of VFA from this section of the gut must be relatively small compared with the absorption across stomach tissues, since it receives a much lower portion of PDV blood flow than stomach tissues (Schaefer & Young, 1980).

There was net utilization of acetate across the MDV of steers given lucerne (Table 1), which agrees with the slightly negative VA for VFA across the small intestine of sheep reported by Barcroft *et al.* (1944). In sheep, about one-third of acetate in the arterial supply to the PDV is removed (Bergman & Wolff, 1971). Pethick *et al.* (1981) found that acetate used by PDV of sheep was primarily oxidized and not incorporated into mesenteric fat. Both Bergman & Wolff (1971) and Pethick *et al.* (1981) determined that PDV acetate use

represented about 25% of whole-body acetate turnover in sheep fed on lucerne. The relative contribution of stomach and post-stomach tissues to total PDV arterial acetate utilization is not known. Calculations of Bergman & Wolff (1971) and *in vitro* measurements of Stevens & Stettler (1966) show that 30–45% of the acetate absorbed from the rumen may be metabolized by rumen tissues, but no measurements of arterial acetate utilization by stomach tissues have been reported. These studies also found that 50–65% of propionate and 85–90% of butyrate absorbed from the rumen are metabolized by rumen epithelium and never appear in the portal vein. Our measurements of net PDV absorption of VFA underestimate actual absorption of VFA from the gut lumen to the extent of their metabolism by epithelial tissues before entering venous blood. For acetate, net PDV flux measurements also underestimate actual absorption to the extent of arterial acetate utilization by PDV tissues. Bergman & Wolff (1971) found net PDV flux measurements represented only 60–70% of actual acetate absorption.

Only arterial acetate concentrations fluctuated significantly during sampling. Masson & Phillipson (1951) reported that in sheep, arterial acetate, but not propionate and butyrate concentrations, relate to absorption across PDV. This is due to differences in the capacity of hepatic tissues for metabolism of individual VFA. Bergman & Wolff (1971) reported that 80–90% of the propionate and butyrate entering the liver were removed, while only 1–3% of acetate was removed from the hepatic circulation. The increase in arterial acetate concentration observed following meal-feeding of lucerne to steers in the present study was probably due to the concomitant postprandial increase in net PDV acetate absorption.

BOHB

In the fed ruminant, metabolism of absorbed butyrate to BOHB results in essentially all PDV ketone body production (Katz & Bergman, 1969). Therefore, our measurements of PDV production of BOHB directly reflect amounts of absorbed butyrate from the gut lumen metabolized to BOHB. Assuming all BOHB was produced from the metabolism of absorbed butyrate and that the metabolism of butyrate to other compounds was negligible, net PDV absorption of *n*-butyrate represents 30% of actual absorption (BOHB net production + *n*-butyrate net absorption) when lucerne was given. This is somewhat higher than the 10–15% value given by Bergman & Wolff (1971) for sheep fed on lucerne and may relate to conversion of *n*-butyrate to CO₂ and other metabolites. Stevens & Stettler (1966) reported that 75% of the butyrate metabolized by rumen epithelium *in vitro* was converted to BOHB.

In the present study essentially all net PDV production of BOHB was attributable to stomach tissues. In rats, Windmueller & Spaeth (1978) found that arterial BOHB was a primary source of the carbon in CO₂ produced across the jejunum. Our findings suggest that some utilization of arterial BOHB by PDV tissues also occurs in the bovine. Like acetate, BOHB removed across MDV tissues may be oxidized or incorporated into mesenteric fat. Katz & Bergman (1969) reported net utilization of BOHB across the total PDV in fasted, twin-pregnant sheep. Net absorption of *n*-butyrate across MDV in our steers was relatively small, yet on average net *n*-butyrate absorption was greater than the net use of BOHB. In the caecum and large intestine of rabbits, *n*-butyrate is largely metabolized to CO₂ rather than ketone bodies and represents an important energy substrate for hind-gut tissues (Marty & Vernay, 1984). Pennington (1951) found that the conversion of *n*-butyrate to BOHB *in vitro* by caecal tissue from sheep was much lower than that for rumen tissue. One explanation for the absence of BOHB production across MDV in these steers is that *n*-butyrate absorbed from the hind-gut and metabolized is oxidized to CO₂ rather than ketone bodies as in the rumen epithelium. Another explanation would be that BOHB production occurred across MDV, yet was slightly less than MDV

use of arterial BOHB such that small negative net flux rates were measured. Regardless, on a net basis PDV production of BOHB appears to be attributable totally to the stomach tissues in beef steers.

Increases in arterial concentration of BOHB when concentrate *v.* lucerne was given (Table 1) were not associated with significant increases in PDV production (Table 3). While not measured in the present study, increased hepatic ketogenesis or decreased utilization or both, may have caused the increase in arterial concentration of BOHB with concentrate feeding. If butyrate uptake by hepatic tissues increased in response to increased PDV absorption of *n*-butyrate when concentrate was given (Table 1), then additional precursors for hepatic BOHB production would be available.

Increased absorption of *n*-butyrate with concentrate feeding could be due to changes in rumen VFA production (Thorlacius & Lodge, 1973) or to increased *n*-butyrate absorption across the rumen epithelium due to lower rumen pH. Decreased lumen pH increases *n*-butyrate absorption across the rumen epithelium *in vitro*, without increasing ketone body production (Stevens & Stettler, 1966). In the present study, concentrate feeding increased net absorption of *n*-butyrate without affecting net BOHB production (Table 3). Increases in net absorption of *n*-butyrate were due to increases in VA across stomach tissues.

L-lactate

Arterial concentrations of L-lactate were similar to values measured in steers fed on identical diets by Huntington *et al.* (1981), though net flux rates for PDV were somewhat higher in the present study. Our net L-lactate flux rates across PDV were lower than rates for heifers fed on the same concentrate diet at similar intakes (Huntington & Prior, 1983). While Huntington *et al.* (1981) observed no change in PDV L-lactate appearance in steers switched from lucerne hay to concentrate, we observed a decrease in PDV appearance (Table 3). Janes *et al.* (1985) found net MDV L-lactate VA in sheep to be variable and often negative. In contrast, VA for L-lactate across MDV in the present study were positive for all but two of sixty observations and averaged 60.0% of VA for PDV. Portions of PDV L-lactate production attributable to known sources (dietary lactate absorption and tissue metabolism of glucose and propionate) are not known. Studies by Weigand *et al.* (1972) and Weekes & Webster (1975) suggest that the conversion of propionate to L-lactate in rumen epithelium is relatively small compared with the conversion of glucose to L-lactate. Findings of Janes *et al.* (1985) indicate that 42.5% of the L-lactate appearing across MDV of sheep results from glucose metabolism, which suggests that substantial glycolytic activity occurs in tissues of MDV. *In vitro* studies have shown that epithelial tissue from the entire length of the small intestine of sheep has a large capacity for the conversion of glucose to L-lactate (Wahle *et al.* 1972).

In conclusion, MDV tissues contribute relatively minor amounts to the net flux of VFA and BOHB across the total PDV of beef steers fed on lucerne or concentrate. Net utilization of acetate and BOHB was measured across MDV when lucerne was given to these steers. Feeding concentrate *v.* lucerne increased net PDV absorption of *n*-butyrate and *n*-valerate, decreased net PDV appearance of L-lactate and decreased net stomach absorption of 3-methylbutyrate but had no effect on the relative contribution of MDV to total PDV flux.

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