

Portal blood flow and heat production in the digestive tract of sheep

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1. A method is described for measurement of portal blood flow in the sheep by the principle of continuous thermal dilution produced by injection of cool saline into the portal circulation at 1 ml/s for 30 s.

2. In most animals phlebitis developed only around the catheter in the right ruminal vein. This affected their appetite and condition after surgery. When all catheters were introduced into the anterior mesenteric veins there was no phlebitis and appetite postoperatively was normal.

3. Portal blood flow in six out of nine sheep was 33–34 ml/kg body-weight per min in the morning before feeding. After a meal of dried grass it increased during the period about 2–6 h later.

4. Total heat production and oxygen consumption of the digestive tract were estimated from portal blood flow and arteriovenous differences in temperature and oxygen concentration. When the heat production of the digestive tract was increased by 1.77 kJ/min by the inclusion of a heating element in the rumen, estimated total heat production increased, on average, by 1.73 kJ/min.

5. During the period 2–6 h after a meal of dried grass, portal venous temperature rose, on average, by 0.7°, visceral O₂ consumption did not alter significantly, but total heat production rose by 1.19 kJ/min.

6. These initial results suggest that the heat of fermentation can be determined *in vivo*. In these experiments it was about 10 kJ per 100 kJ digestible energy consumed.

The factors which contribute to the large increase in heat production associated with food intake in ruminants have recently been reviewed (Webster, 1972). They include the energy cost of eating, the heat liberated during microbial fermentation in the rumen, the energy expended by the host animal in digestion and absorption, and the heat liberated during the metabolism of the end products of digestion, particularly the steam-volatile fatty acids (VFA). Only this last component is analogous to the specific dynamic effect as originally defined for man by Rubner (1902). The amount of heat liberated during the metabolism of infused VFA has been determined (Armstrong & Blaxter, 1957*a, b*; Armstrong, Blaxter & Graham, 1957; Blaxter, 1962) and the physiological changes associated with the energy expended during eating have been described (Christopherson & Webster, 1972). The contribution of the heat of fermentation and of the work of digestion have not been measured *in vivo* in ruminants.

Durotoye & Grayson (1971) estimated the heat production of the gastro-intestinal tract of the dog from the difference in temperature and oxygen content between arterial and portal venous blood and electromagnetic measurements of portal blood flow. Fegler & Hill (1958) and Bensadoun, Paladines & Reid (1962) have studied portal blood flow in sheep using single-injection thermal dilution techniques. We have adapted the continuous thermal-dilution method developed by Linzell (1966) for

measurement of blood flow in the mammary vein of the goat to measurement of blood flow in the portal vein of the sheep, and have attempted to apply the principle described by Durotoye & Grayson (1971) to estimate aerobic metabolism and total thermogenesis in the viscera drained by the portal system of the ruminant. A preliminary account of this work has been published (Webster & White, 1972).

EXPERIMENTAL

Animals

Catheters and thermocouples were implanted in five sheep in five experiments performed wholly under anaesthesia and in eighteen animals which were allowed to recover from anaesthesia. Of the eighteen sheep, nine were cross-bred wethers, two were Blackface wethers and seven were Cheviot ewes. The sheep were housed in individual metabolism cages and given chopped dried grass (900 g/d) before surgery and the same food *ad lib.* afterwards. Drinking-water was available at all times.

Measurement of blood flow

Principle of method. When physiological saline is injected into a blood vessel the temperature of blood flowing through that vessel is reduced by an amount related to blood flow and the volume and temperature of saline injected. This is the basis of the single-injection thermal dilution technique (Fegler & Hill, 1958). In the continuous thermal-dilution technique (Linzell, 1966) physiological saline is infused into a blood vessel at a constant rate sufficiently long enough to allow the temperature of mixed blood and saline to fall to a new steady state. At this steady state one of two extreme situations may apply (Linzell, 1966):

(1) The injected fluid may displace an equal volume of blood so that mixture flow equals normal blood flow. The blood flow (\dot{V}_{bl} , ml/min) is given by

$$\dot{V}_{bl} = \dot{V}_s (\Delta T_s / \Delta T_m), \quad (1)$$

where \dot{V}_s is rate of saline injection (ml/min), ΔT_s is the difference between blood temperature and saline temperature ($^{\circ}\text{C}$) and ΔT_m is the difference between blood temperature and mixture temperature ($^{\circ}\text{C}$).

(2) If the injected fluid does not displace any blood then equation (1), which measures the flow of the mixture, will overestimate normal blood flow. In this situation

$$\dot{V}_{bl} = \dot{V}_s \left(\frac{\Delta T_s}{\Delta T_m} - 1 \right). \quad (2)$$

The systematic error arising from the difference in specific heat between saline and blood (specific heat 0.89; Mendlowitz, 1948) is less than 0.1% at the rates of saline injection used in these experiments and can be neglected.

Temperature measurements. Copper-constantan thermocouples enclosed in polyvinyl catheters were used for implantation into the dorsal aorta and portal vein. The

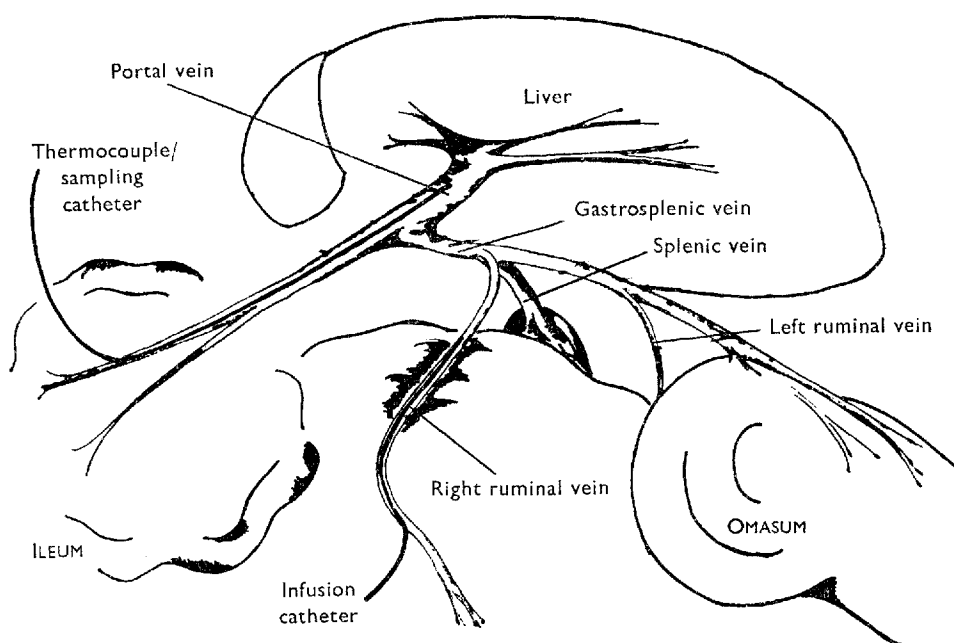


Fig. 1. The main vessels of the portal system in the sheep. The thermocouple in the portal trunk is introduced through a mesenteric vein, the catheter for injection of physiological saline is in the right ruminal vein.

temperature of these thermocouples *in situ* was measured by means of a constant-temperature reference junction maintained at 41.5° . The output of the two thermocouples was measured with two Rikadenki micro-voltmeters and recorded on a two-channel Rikadenki direct-writing potentiometer (T.E.M. Sales Ltd, Crawley, Sussex). The sensitivity of the micro-voltmeters was set at $200 \mu\text{V}$ full-scale deflection, and zero and span controls on the potentiometer were adjusted so that each thermocouple read from 37.50 to 41.50° over the 254 mm (10 in.) scale. No measurable departure from a linear response was observed over this range so that for each thermocouple a pen movement of 51 mm (2 in.) corresponded to a temperature change of 1.00° .

Anatomy of the portal circulation. The portal vein in sheep is formed by the convergence of two large venous trunks, the anterior mesenteric vein, which drains the small and large intestines and the caecum, and the gastrosplenic vein which receives principally the short, wide splenic vein, the left and right ruminal veins, and the omaso-abomasal vein. A drawing of the confluence of these veins, presented in Fig. 1, shows this arrangement, and also the position of a catheter inserted into the right ruminal vein for injection of saline and that of a thermocouple inserted through a branch of the anterior mesenteric vein and advanced into the portal vein.

Surgical procedure. Anaesthesia was induced with thiopentone sodium injected intravenously and was maintained, after endotracheal intubation, with Fluothane and oxygen. Aseptic procedures were followed throughout each operation.

The procedure for the first sixteen operations was as follows. The abdominal cavity

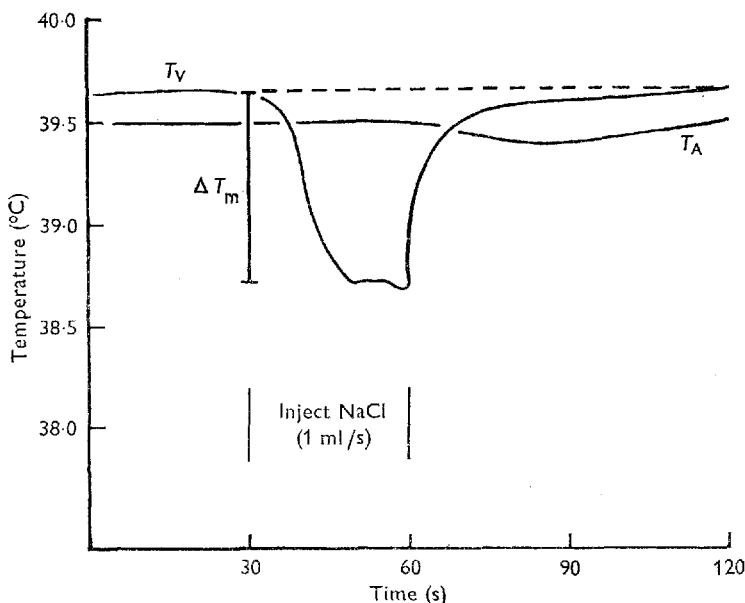


Fig. 2. A specimen record of changes produced in the temperature of the portal vein (T_V) and dorsal aorta (T_A) by injection of physiological saline at about 20° for 30 s at 1 ml/s. For further explanation see p. 283.

was exposed by an incision in the right flank. Part of the right side of the rumen was carefully drawn through the incision and the right ruminal artery and vein were located adjacent to the line of attachment of the omentum. A suitable branch was selected for catheterization. The artery and vein were separated, a loose ligature of umbilical tape was placed under the vein down-stream from the intended point of catheterization and a silk suture up-stream. A polyvinyl catheter (NT2, i.d. 0.9 mm, Shore scale 95, Portex Ltd, Hythe, Kent) was filled with heparinized saline (200 i.u./ml) and was enclosed within a larger bore catheter (NT4, i.d. 2.2 mm). The smaller bore catheter was inserted into the vein and advanced about 150 mm. The umbilical tape was then tied tightly above the catheter with silk, the outer catheter advanced to the tie-in point and there anchored firmly with the silk suture up-stream of the insertion. The free ends of both sutures were then sewn to the rumen wall. In this way the catheter was prevented from moving in or out of the vessel.

The rumen was allowed to regain its normal position and the small intestine was exposed. Catheterization of a branch of the anterior mesenteric vein was essentially similar to that described above. In the first seven operations the thermocouple was enclosed in a single, sealed polyvinyl catheter. Subsequently to permit sampling of portal venous blood a double-bore catheter (DV14; Dural Plastics Ltd, Dural, NSW, Australia) one bore containing the thermocouple, or two NT3 catheters cemented together were used.

The position of the thermocouple was checked by infusing cool saline at 1 ml/s for 30 s through the catheter in the right ruminal vein. One of three situations could occur. (a) If the thermocouple was in the anterior mesenteric vein thermal dilution

was not recorded; (b) correct positioning of the thermocouple in the portal vein produced a typical pattern of thermal dilution (Fig. 2); (c) if the thermocouple had entered the gastrosplenic trunk the extent of thermal dilution was markedly increased but disappeared when the catheter was advanced beyond the point of entry of the right ruminal vein. When the evidence of thermal dilution indicated that the thermocouple was in the portal vein its position was confirmed by radioscopy (Pl. 1).

The aortic catheter and thermocouple were inserted into the right carotid artery after exposure through a simple incision.

In two subsequent operations the catheter for the injection of saline was inserted, not into the right ruminal vein, but into a branch of the anterior mesenteric circulation as far away as possible from the point of insertion of the thermocouple. The arterial thermocouple was inserted through an anterior mesenteric artery.

All catheters were fitted with Intravenn two-way valves (Eschmann Bros & Walsh Ltd, Shoreham-by-Sea, Sussex) and were flushed with heparinized saline (200 i.u./ml) at least once daily.

After operation the animals received intramuscular injections of 5 ml Dipen (Bimeda Chemicals Ltd) for 3 d.

Physiological measurements on conscious animals. The temperature of aortic and portal venous blood was recorded continuously. Samples of blood from the aorta, portal vein and right ruminal vein were withdrawn for determination of oxygen content (C_{O_2} , ml/l) in a Van Slyke apparatus.

The routine procedure for measurement of blood flow was as follows. A modified Palmer syringe drive was used to inject saline containing heparin (10 i.u./ml) usually at a nominal rate of 60 ml/min for 30 s. Occasionally, to test the method, saline was injected at rates of 30–120 ml/min either 5–10 min before or after an injection at 60 ml/min.

Each volume of saline injected emerged from a reservoir placed in a water-bath that was kept usually at room temperature. In these circumstances, it was assumed that the temperature of the saline which entered the animal was the same as the temperature in the water-bath. In some experiments the temperature in the water-bath was increased up to 35° above room temperature but, as the saline cooled as it passed from the water-bath to the animal, T_s could not be measured precisely.

Fig. 2 shows the pattern of thermal dilution in the portal vein and the onset of thermal dilution in the aorta beginning, in this example, about 25 s after the start of injection. Repeated injections were given at intervals of not less than 5 min and as many as fifty determinations of blood flow were made over a period of 24 h. Oxygen consumption of the portal-drained viscera (\dot{V}_{O_2} , ml/min) was calculated by

$$\dot{V}_{O_2} = \dot{V}_{bl} (C_{aO_2} - C_{vO_2}) / 1000. \quad (3)$$

Total thermogenesis (H, J/min) in the portal drained viscera was estimated by

$$H = 4.18 \times 0.9 \dot{V}_{bl} (T_V - T_A), \quad (4)$$

where T_V and T_A are the temperatures of portal and aortic blood respectively. The specific heat of sheep blood was assumed to be 0.9. The factor 4.18 was used to

Table 1. *Postoperative histories of sixteen sheep with catheters chronically implanted in the portal circulation*

Sheep		Survival of preparation (d)	Reason for termination	Post-mortem findings
Breed	No.			
Cross-bred wethers	5987	14	Pulled out catheters	—
	5985	13	Disappearance of thermal dilution	Catheter penetrated wall of RRV; slight phlebitis
	5983	30	Blocked RRV catheter	—
	5409	36+	Christmas holidays	Slight phlebitis RRV
	4718	21	Sudden death	Ruptured aneurysm in pulmonary artery; severe phlebitis RRV
	3070	22	Anorexia	Severe phlebitis RRV
	4490	30	—	—
Blackface wethers	6813	1	Died	Pneumonia
	6814	22	Poor appetite	Moderate phlebitis RRV
Cheviot ewes	6648	8	Died	Torsion of small intestine
	2970	30	Deterioration of thermal dilution	Slight fibrosis RRV
	6649	30	Excessive thermal dilution throughout	Portal vein 30 mm long; thermocouple in gastrosplenic vein; slight fibrosis RRV
	5850	26		
	3010	2	No thermal dilution	Portal vein 30 mm long; thermocouple in anterior mesenteric vein
6651	3			
6639	2			

RRV, right ruminal vein.

convert calories (the units used to express H according to the definition of specific heat) into joules.

Equation 4 is based on the assumption that virtually all the heat produced within the viscera is convected out in the venous drainage. This assumption was tested in two acute preparations and in two sheep previously prepared with rumen fistulas by inserting into the rumen a heating cable, 1.5 m long, which had a heat output of 29.6 W (1.77 kJ/min). Heat production within the portal-drained viscera was estimated from equation 4 before, during and after the application of this additional heat load.

Eating trials

The extent and time-course of changes in blood flow, oxygen consumption and thermogenesis in the portal-drained viscera were studied in sheep that had recovered well from surgery and which were offered chopped, dried grass over a period of 2 h once a day. Measurements were made for 1 h before and 8 h after the meal. Ten trials with three sheep were carried out.

RESULTS

Postoperative history

The postoperative histories of the first sixteen sheep are summarized in Table 1.

The Cheviot ewes were not satisfactory subjects for this study. In five of the seven sheep the portal vein was very short (< 30 mm) and did not retain the thermocouple.

Table 2. Comparison between estimates of portal blood flow (\dot{V}_{bl}) made at three rates of infusion of saline (\dot{V}_s) and using two equations

Nominal saline infusion rates (ml/min)	60	30	60	120
No. of comparisons	18	18	12	12
Mean portal blood flow (ml/min)				
$\dot{V}_{bl} = \dot{V}_s(\Delta T_s/\Delta T_m)$	1954	2115 (+8.2%)	1974	2035 (+3.1%)
$\dot{V}_{bl} = \dot{V}_s(\Delta T_s/\Delta T_m - 1)$	1894	2085 (+10.0%)	1914	1915
Correlation coefficient (r)	0.70		0.74	

ΔT_s , difference between the temperature of blood and saline; ΔT_m , difference between blood and mixture temperatures; \dot{V}_s , rate of saline injection; \dot{V}_{bl} , blood flow.

In two sheep the thermocouple was found at *post mortem* to be in the gastrosplenic vein, as had been suspected since the extent of thermal dilution was abnormally large in these animals. In the other three the thermocouple was in the anterior mesenteric vein and thermal dilution was not observed after recovery from anaesthesia.

The cross-bred wethers all gave successful results for varying periods of time after surgery. One sheep died suddenly; the others were killed by intravenous injection of pentobarbitone sodium (Table 1). All sheep that survived the operation for more than 3 weeks were observed at *post mortem* to exhibit phlebitis in the right ruminal vein which contained the catheter for infusion of saline. Phlebitis was not observed around catheters inserted through the anterior mesenteric vein.

Recovery of most of the sheep immediately following surgery was good. Blood flow in the portal vein was often increased on the 2nd and 3rd days after operation but in all sheep it stabilized within 5 d. Six sheep developed inappetence and pyrexia about 8–10 d after surgery. They were treated daily with 5 ml Trivetrin (Wellcome Ltd, London) administered in 10 ml NaCl solution (90 g/l) through the catheter. Three sheep failed to respond to treatment. At *post mortem* these animals exhibited the most marked phlebitis in the right ruminal vein. The other sheep regained their appetite reasonably well but were undoubtedly eating less than before surgery. In the two most recent preparations, the right ruminal vein was not cannulated and the injection catheter was placed in a mesenteric vein. These animals have been in good health for over four months after surgery. Their appetite has been excellent throughout.

Tests of method

Effect of injection rate. Estimates of portal venous flow made in conscious sheep by injecting saline for 30 s at nominal rates of 30, 60 and 120 ml/min are given in Table 2. Blood flow was estimated from both equations (1) and (2). Estimates of blood flow were consistently higher at injection rates of 30 ml/min than at 60 or 120 ml/min. Equation (1), which assumed that the injected saline displaces an equal volume of blood, gave higher estimates for blood flow at an injection rate of 120 ml/min than at 60 ml/min. Equation (2), which assumes that blood flow is unaffected by saline injection, gave excellent agreement between estimates made at injection rates of

Table 3. *Effect of intraruminal heating on blood flow and estimated thermogenesis in the portal-drained viscera in anaesthetized and conscious sheep*

Sheep no.	Before heating			Intraruminal heating (1.77 kJ/min)				Recovery of heat increment (%)
	\dot{V}_{bl} (ml/min)	$T_V - T_A$ (°C)	H (kJ/min)	Time to equilibrium (min)	\dot{V}_{bl} (ml/min)	$T_V - T_A$ (°C)	H (kJ/min)	
Anaesthetized sheep								
4241	1560	0.140	0.91	220	1250	0.360	1.69	46*
2750	2080	0.090	0.70	360	2540	0.235	2.25	88
Conscious sheep								
6814	1380	0.120	0.63	90	2210	0.270	2.24	91
4490	2343	0.165	1.45	90	2106	0.400	3.16	97
4490	2445	0.170	1.63	100	2750	0.355	3.67	115

\dot{V}_{bl} , blood flow; T_V , portal temperature; T_A , arterial temperature; H, heat production.

* Animal not in thermal equilibrium.

60 and 120 ml/min. At an injection rate of 30 ml/min a significant proportion of the injected coolant may have been conducted out of the gastrosplenic vessels rather than convected to the down-stream thermocouple. This would overestimate blood flow. Estimates of blood flow are consistent at injection rates between 60 and 120 ml/min if the appropriate equation is used. A standard procedure in which rate of infusion of saline was nominally 60 ml/min was therefore adopted for all subsequent determinations of portal blood flow and the assumption was made that blood flow was unaffected by injection of saline (equation (2)). This assumption is the same as that made by Linzell (1966).

Estimates of thermogenesis in the portal-drained viscera. Table 3 indicates the effect of intraruminal heating on blood flow and visceral thermogenesis estimated from equation (4) in anaesthetized and conscious sheep. Equation (4), in fact, measures convection of heat away from the viscera in the portal blood. In anaesthetized sheep this increased very slowly after the intraruminal heaters were switched on. The first experiment with sheep 4241 had to be terminated before thermal equilibrium was achieved. In the other acute preparation this took 6 h, by which time estimated visceral thermogenesis had increased by 1.55 kJ/min, 88% of the intraruminal heat load.

In the three experiments with conscious sheep thermal equilibrium was established within 100 min of switching on the intraruminal heat source. The recoveries of the applied heat increment were 91, 97 and 115%. The agreement is about as precise as one could hope for from this method, although the way in which this increase was achieved by altering \dot{V}_{bl} and $(T_V - T_A)$ varied markedly between trials.

Portal blood flow in the conscious sheep

Effects of saline injections. In most experiments, repeated injections of cool saline at intervals of 5–30 min did not induce changes in portal blood flow. It was noticed, however, that on several occasions the sheep shivered for about 20–30 min and blood

Table 4. Mean and extreme values for portal blood flow in sheep not less than 18 h after their previous meal

Sheep no.	Body-wt (kg)	Portal blood flow (ml/min)		Mean portal blood flow (ml/min per kg body-wt)
		Mean	Range	
5987	47	1965	1328-2570	42
5985	57	1955	1686-2361	34
5983	55	1834	1466-2470	33
5409	84	2396	1809-2846	29
4718	66	2926	2776-3103	44
3070	60	2074	1885-2292	34
2970	66	2283	1982-2761	34
6814	43	1477	1263-1619	34
4490	73	2379	2052-2750	33

temperatures rose sharply after three to six injections. This response was most marked when saline temperature was below 15° but did not occur if saline was at 39°. Shivering and the increase in body temperature of the sheep may have been due to the effect of cold *per se* and not to pyrogens present in the autoclaved saline. It is our custom now, however, to ensure that the temperature of the saline for injection is about 20°.

Blood flow in relation to feeding. Mean and extreme values for portal blood flow obtained between 08.30 and 10.30 hours, 18-24 h after a previous meal are given in Table 4. The range of blood flows observed in these circumstances in any one animal and between animals was considerable, for example 1477 ml/min in a 43 kg sheep and 2396 ml/min in an 84 kg sheep. When mean values for portal blood flow were expressed per kg body-weight the agreement between those from different sheep was remarkable, six out of nine animals having mean flows of 33-34 ml/min per kg body-weight.

Portal blood flow usually increased in a biphasic fashion during a 2 h period of eating (Fig. 3). After eating there was usually a temporary decline in blood flow followed by a marked secondary rise which persisted from about the 2nd to the 6th hour after feeding. Similar observations were made by Bensadoun *et al.* (1962). The mean consumption of dried grass in all trials was 490 g and blood flow in the period 2-6 h after receiving food increased, on average, by about 400 ml/min (Table 5).

Visceral thermogenesis in relation to feeding

The results of the experiments in which satisfactory amounts of food were consumed are summarized in Table 5. The amounts of food consumed varied considerably and various technical problems prevented the collection of complete results on all occasions. However, certain consistent observations emerged. Portal venous temperature consistently rose during and after the meal (Fig. 3 and Table 5), the average increase being 0.7°. The oxygen consumption of the portal-drained viscera estimated from equation 3 did not appear, from the limited results available, to change as a consequence of eating. Total thermogenesis in the portal-drained viscera, estimated from equation 4, was on average 1.18 kJ/min higher in the period 2-6 h after eating than in the hour preceding the meal.

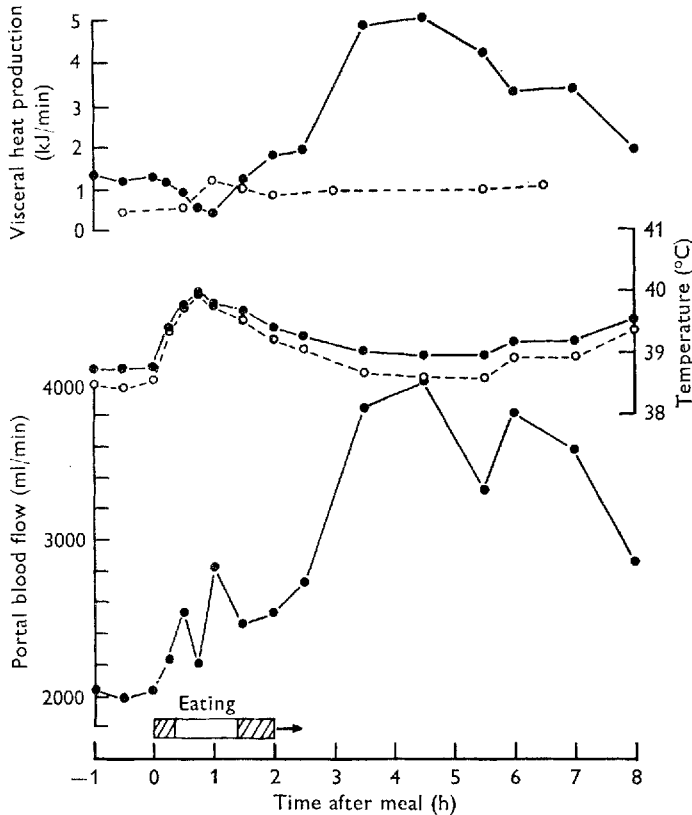


Fig. 3. Portal blood flow, portal (●) and arterial (○) blood temperatures, total heat production (●) and 'aerobic' heat production (○) in the portal-drained viscera of a sheep that ate 810 g dried grass in a single meal.

The results in the last two columns in Table 5 were obtained by integrating the rise in visceral thermogenesis above the prefeeding value over a period of 8 h after the animal began to eat. In the five trials shown, visceral heat production had returned to the prefeeding level within 8 h. In these circumstances this integral was considered to represent the total increase in thermogenesis in the portal-drained viscera resulting from the consumption of the meal. In trials, 5, 8 and 10 visceral heat production had not returned to the prefeeding value after 8 h and this integration could not be attempted. These results indicate that the amount of heat produced in the portal-drained viscera of sheep as a direct consequence of eating was about 1.0 kJ/g dried grass consumed.

DISCUSSION

When the surgical implantation of thermocouples and catheters was successful and recovery from anaesthesia uneventful, we were usually able to obtain satisfactory measurements of portal venous flow for about 4 weeks. However, the appetite of the sheep during this time, and particularly in the period 7–12 d after surgery, was undoubtedly impaired. It is reasonable to attribute this to the phlebitis that developed

Table 5. Portal blood flow and temperature, visceral oxygen consumption and total thermogenesis in sheep before and after eating a meal of chopped, dried grass

Sheep no.	Trial	Food consumed (g)	Portal blood flow (ml/min)		Portal venous temperature (°C)		Visceral \dot{V}_{O_2} (ml/min)		Visceral thermogenesis (kJ/min)		Increased thermogenesis† due to eating (kJ)	
			Before	After*	Before	After*	Before	After*	Before (H ₀)	After (H)*	(kJ)	(kJ/g food)
5983	1	250	2109	2607	40.84	41.09	—	—	0.94	1.99	179	0.72
	2	250	2020	2697	39.81	40.44	—	—	0.98	1.64	167	0.67
	3	450	2063	2235	40.14	40.64	54.3	42.4	—	—	—	—
2970	4	650	2150	2215	39.66	40.81	44.1	50.9	—	—	—	—
	5	420	2310	2784	40.17	39.65	—	—	1.73	2.24	—	—
	6	810	2105	3289	38.72	39.55	—	—	1.42	4.02	978	1.21
5409	7	500	2065	2542	39.42	40.50	80.3	89.0	1.72	2.95	819	1.64
	8	270	2336	2483	39.54	40.26	—	—	0.93	1.40	—	—
	9	500	2420	2774	39.10	40.22	51.7	61.7	1.00	2.97	410	0.82
Means	10	800	2547	2584	39.16	40.30	—	—	0.88	1.89	—	—
		490	2212	2621	39.65	40.34	57.6	61.1	1.20	2.39	510	1.01

* Mean of values obtained 2-6 h after beginning of meal.
 $\dagger \int_{t_0}^{t_0+t} (H-H_0)$ (for further explanation see p. 288).

Table 6. *Published estimates of portal venous flow in the ruminant*

Animal	Method	Status of animals	Average blood flow		Increased flow after feeding (%)	Source of values
			ml/min	ml/min per kg body-wt		
Sheep	Dye dilution	Anaesthetized	1850	37	—	Schambye (1955)
Sheep	Thermal dilution (single injection)	Anaesthetized	700-1100	12-20	—	Fegler & Hill (1958)
Sheep	Thermal dilution (single injection)	Conscious	1300	—	26	Bensadoun <i>et al.</i> (1962)
Sheep	<i>p</i> -Aminohippuric acid clearance	Conscious	—	31	39	Katz & Bergman (1969)
Sheep	Döppler shift	Conscious	—	39 (± 3.4)	—	Hume (1971)
Sheep	Continuous thermal dilution	Conscious	2143	34 (29-44)	18 (2-56)	Present study
Calf	Dye dilution	Conscious	—	17-61	—	McGilliard, Thorp & Thorp (1971)

around the polyvinyl catheter in the right ruminal vein. Phlebitis around other catheters did not occur.

Bensadoun *et al.* (1962) implanted both the injection catheter and the portal thermocouple through the mesenteric veins. The disadvantage of this method is that it is not always possible to confirm that the thermocouple is in the portal vein. In two sheep prepared in this way we observed that the change in temperature at the portal thermocouple during continuous injection of cool saline was erratic, not always showing the typical plateau (Fig. 2) observed when saline was injected through the ruminal vein. This suggests that poorer mixing may occur when saline is injected through an anterior mesenteric vein. However, these sheep have been in excellent health and appetite for over 4 months after surgery. We may have to reconsider our priorities concerning quality of signal in relation to the health and normal performance of the animals. Moodie, Walker & Hutton (1963) reported that their sheep tolerated nylon catheters better than polyvinyl ones. They did, however, observe some phlebitis around mesenteric vessels which we have not seen.

The continuous thermal-dilution method for estimating blood flow was compared by Reynolds, Linzell & Rasmussen (1968) with the N₂O diffusion and antipyrine absorption techniques against a tested electromagnetic method. These authors concluded that the thermal-dilution method was the most reliable of the three methods they tested. The continuous thermal-dilution method is undoubtedly more precise than the single-injection technique; the magnitude and duration of the signal are longer and disturbances of the signal are immediately identifiable. For the same reason, thermal dilution is more attractive than dye dilution since the extent of the dilution can be recorded instantaneously, continuously and *in situ*. For consistent measurement of portal venous flows in the region of 2000 ml/min we concluded that saline at about 20° should be injected at a rate of not less than 60 ml/min.

Our estimates of portal venous flow in the conscious sheep are compared in Table 6 with other published estimates of portal flow in anaesthetized and conscious ruminants.

These findings indicate that portal blood flow in sheep and calves is about 30–40 ml/min per kg body-weight 24 h after food and increases by 20–40% after eating. Our observations in Table 6 represent the average increase in the period 2–6 h after eating; those of Bensadoun *et al.* (1962) and Katz & Bergman (1969) are probably peak values.

The normal variation in portal blood flow in the individual animal would appear from Table 4 to be greater than the between animal variation in average portal flow (ml/min per kg body-weight). Clearly, the normal variation is such that any attempt at quantifying the extent of visceral absorption or tissue metabolism from arterio-venous differences in heat content or the concentration of a particular metabolite must include reliable simultaneous measurement of blood flow.

Measurement of visceral thermogenesis using equation (4) assumes that all the heat produced in the digestive tract is convected from the area in the portal circulation. This is obviously an oversimplified assumption, but our results (Table 3) suggest that it is not seriously in error. The temperature difference between aortic and portal blood ranged from about 0.15° before eating to about 0.35° about 4 h later. Counter-current exchange of heat from the mesenteric veins to arteries would in these circumstances be very small relative to the convective transfer into the venous drainage. Transfer of heat through the lymphatic drainage would also appear from our results to be insubstantial.

The sensitivity of equation 4 as a predictor of visceral heat production is limited by the precision of measurement of blood temperature. In normal circumstances an error of 0.01° in the measurement of ($T_V - T_A$) would give an error of about 5% in estimated heat production. Thus the technique is not capable of resolution to better than $\pm 5\%$. The variation observed in recovery of heat added to the rumen (Table 3) is probably due largely to this inherent limitation. Nevertheless, systematic error would appear to be absent and repeated experiments should achieve reasonable precision of measurement of total thermogenesis in the portal-drained viscera.

Some idea of aerobic thermogenesis in the portal-drained viscera may be gained by applying a thermal conversion factor of 20.4 kJ/l O₂ (McLean, 1972) to visceral O₂ consumption. Such an estimate must however be regarded with caution since it is unknown whether all oxidations begun in the portal-drained viscera proceed to completion before the venous drainage enters the liver.

Our preliminary studies on the effect of eating on visceral thermogenesis prompt certain tentative conclusions. There would not appear to be a significant increase in the heat production of the portal-drained viscera during eating. Thus the marked rise in the total heat production of a sheep that accompanies eating (Christopherson & Webster, 1972) cannot be attributed to increased metabolism in the rumen or in the tissues of the digestive tract. The oxygen consumption of the digestive tract would appear to vary little as a consequence of eating, of fermentation or of subsequent digestion. Thus the aerobic 'work of digestion' would appear to be too small to be measured by equation (3). This confirms the early observations of Rubner (1902).

Applying, with the reservations already stated, the value of 20.4 kJ/l O₂ consumed, the aerobic metabolic rate of the digestive tract before eating (Table 5) becomes 1.18 kJ/min which is almost exactly the same as the total visceral thermogenesis

estimated from equation (4). The rise of visceral thermogenesis after eating was not accompanied by an increase in O_2 consumption and may be considered to be due to anaerobic metabolism, principally the heat of fermentation in the rumen. The heat of fermentation then, in our experiments, must have been very small indeed before the single meal of the day, and almost all the increased heat produced during fermentation occurred during the first 8 h after the meal (Fig. 3). The average increase in thermogenesis in the digestive tract was 1.0 kJ/g food (Table 5). Digestibility trials were not performed on the chopped, dried grass but an estimate of 10.0 kJ digestible energy per g fresh weight would be reasonable. In these experiments, therefore, the heat of fermentation was about 10% of the digestible-energy intake. Marston (1948) showed that 6% of the combustible energy of cellulose was dissipated as heat during fermentation *in vitro*. Blaxter (1962) has calculated on a stoichiometric basis that 4–12% of digestible energy may be lost as heat during fermentation. Our preliminary attempts to measure directly the fermentation heat *in vivo* confirm these observations without adding precision; this should emerge from subsequent experiments.

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EXPLANATION OF PLATE

Radiograph showing a thermocouple (thin white line) in the portal vein of a sheep, and the infusion catheter, filled with Urografin (Schering, Germany) (thick white line) in the right ruminal vein. Scale about life size.

