Absorption and metabolism of fructose by rat jejunum

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The absorption and metabolism of fructose was investigated in the vascularly perfused jejunum of fructose-fed rats. With 10mM-glutamate and 10mM-fructose in the lumen, the viability of the tissue is maintained and fructose is absorbed and utilized at high rates. With 28mM-fructose in the lumen, glucose appears in the vascular bed. With 10mM- or 28mM-fructose in the presence of 10mM- or 28mM-glucose in the lumen, the fructose absorption is decreased. From 10mM- or 28mM-sucrose in the lumen, fructose uptake is also less than from the equivalent concentration of free fructose. The rate of appearance of fructose in the vascular bed is independent of the source of fructose from which it is derived. In the presence of glucose, either free or as sucrose, there is a marked decrease in the utilization of fructose, defined as the difference between that absorbed by the jejunum and that transported unchanged into the vascular bed. In all cases about half of the carbohydrate absorbed from the lumen is converted into lactate, most of which is secreted into the blood. The absorption of glucose and the rate of vascular appearance of glucose from glucose in the lumen are about 1.5 times greater than those of fructose from fructose in the lumen. It is concluded: firstly, that fructose uptake from the lumen of rat jejunum is determined by its concentration and by the demand for it as a fuel for the intestine, a demand that is severely decreased in the presence of glucose; secondly, that in the vascularly perfused jejunum there is no evident kinetic advantage for uptake of fructose or glucose from sucrose rather than from free monosaccharide in the lumen; thirdly, that some fructose can be converted into glucose.

In all species that have been studied, the absorption of fructose presents some unusual features. Thus it is absorbed at relatively high rates, although lower than those for glucose and galactose (Wilson, 1962); the process of uptake across the rat brush-border membrane appears to be independent of glucose and of Na⁺ and is not inhibited by phlorrhizin (Sigrist-Nelson & Hopfer, 1974; Crouzoulon, 1978). In many species the absorbed fructose is converted in the intestine in part into lactate and in some also into glucose, so that during absorption a mixture of fructose, glucose and lactate may be secreted into the blood (Gracey *et al.*, 1972; Herman *et al.*, 1972). Little work appears to have been done on the metabolism of fructose by the small intestine when present either with glucose or as sucrose, and we report here experiments on the transport and metabolism of fructose presented as monosaccharide or as sucrose to rat jejunum vascularly perfused *in vitro*.

Materials and methods

Animals

Male Sprague-Dawley rats (200–220 g) were supplied by OLAC, Bicester, Oxon., U.K., and fed on Oxoid Breeding Diet (Oxoid Ltd., Southwark Bridge Road, London SE1 8HF, U.K.) before experimentation. Early experiments with fructose prefeeding showed there to be a 2-fold increase in the rate of uptake of fructose from the lumen, with no effect on the rate of appearance of fructose on the vascular side (P. A. H. Holloway, unpublished work). Accordingly, 3 days before the experiment a high-fructose diet consisting of fructose plus ground normal diet (1:1, w/w) was given *ad libitum* to the rats, with free access to water.

Increased activities of various enzymes likely to be involved in the metabolism of fructose by rat jejunum have been reported by Stifel *et al.* (1968), Mavrias & Mayer (1973) and Crouzoulon &

Dandri-fosse (1975, 1979). Crouzoulon & Dandri-fosse (1979) described an increase in the synthesis of those enzymes, which reached a plateau after 3 days on a fructose-supplemented diet. Mavrias & Mayer (1973) demonstrated a 2-fold increase in the rate of transport of fructose after fructose had been given, although they found no increase in the rate of conversion of fructose into glucose or lactate in isolated mucosal epithelial cells.

Most rats gained weight, but those that failed to gain or actually lost weight during this feeding were not used. Experiments were performed between 11:00 and 14:00h.

Experimental design

The procedure described by Hanson & Parsons (1976) for the vascular perfusion of the jejunum *in situ* was used, with a few minor modifications. The initial volume of vascular perfusate was 75ml (haematocrit 40%) and the flow rate 1.5ml/min; it was found that after careful washing of the erythrocytes it was not necessary to include a filter in the vascular circuit. Arterial pressure remained constant throughout at approx. 60mmHg. The lumen of the isolated segment was recirculated simultaneously with a Krebs-Ringer bicarbonate medium (40ml) at a flow rate of 2ml/min and a pressure of 17cmH₂O. The average time for the operative procedure was 22min, and at no time during this procedure was the mesenteric bed unperfused.

Experimental protocol

In all experiments the source of fuel for the perfused jejunum was present on the luminal side and no substrate was added to the vascular perfusate. Initial experiments with 10mM-fructose in the lumen showed that it was an inadequate fuel on its own: over a period of 60min the tissue deteriorated, manifested by poor venous recovery, elevated arterial pressure and sloughing of the mucosa. With 10mM-glutamate present in the lumen in addition to 10mM-fructose, the viability of the tissue was maintained and fructose was absorbed and utilized at high rates. Glutamate was added to the lumen because it is taken up from the vascular bed only at very low rates (Hanson & Parsons, 1977). When, in other experiments, glutamate was added to the lumen in the presence of glucose, no significant metabolic interactions between the fuels was found (see Table 1). Therefore, in the first series of experiments, 10mM-glutamate was present together with test substrates glucose, fructose, glucose plus fructose at equimolar concentrations, or sucrose, all at 10mM. In a second series of experiments, substrates were present in the luminal medium at concentrations of 28mM in the absence of glutamate. At this concentration, fructose alone is an adequate fuel

for the preparation. Samples (0.5ml) were taken from the vascular perfusate at 0, 20, 25, 30, 40, 50 and 60min, deproteinized in ice-cold 6% (v/v) HClO₄ and analysed for glucose, fructose and lactate. Samples (0.5ml) of luminal fluid were taken at the same times, and processed and analysed in the same way. To avoid hydrolysis of sucrose by HClO₄, luminal fluids containing sucrose were deproteinized in a Ba(OH)₂/ZnSO₄ medium.

Assays

Enzymic assays were performed for glucose (Slein, 1963), fructose (Bernt & Bergmeyer, 1974), lactate (Hohorst *et al.*, 1959) and sucrose (Bergmeyer & Bernt, 1974). HClO₄ extracts were centrifuged at 2000g for 15min at 4°C, and the supernatants were neutralized with 10% (w/v) KOH before analysis. Enzymes and coenzymes were supplied by Boehringer. Other chemicals were supplied by Fisons and were of analytical-grade quality.

Calculation and expression of results

The metabolism of the tissue is expressed with respect to the dry weight of the perfused segment. At the end of perfusion, the segment was removed, opened longitudinally and blotted dry before being dried in an air oven until there was no further decrease in weight. It was assumed that, when the uptake of substrate from the lumen increased linearly with time, the tissue was in a steady state of metabolism. If utilization is defined as metabolism to other products and sequestration of substrate within the tissue, the rate of uptake of substrate from the lumen minus the rate of appearance on the vascular side was taken as a measure of the rate of utilization of substrate by the tissue (Hanson & Parsons, 1976).

The slope of the line relating accumulated uptake of substrate or appearance of metabolite or substrate against time was calculated by using regression analysis to give rates of uptake or appearance (Hanson & Parsons, 1976). Results are expressed as means $\pm$ S.E.M., and statistical differences were determined by Student's *t* test.

Results

Low (10mM) sugar concentrations in the lumen

Effects of glutamate on glucose metabolism. In Table 1 the findings with glucose as substrate in the lumen in the presence and absence of glutamate are shown. The presence of glutamate had no significant effect on the glucose utilization, on the extent of conversion of glucose into lactate, or on the fate of the absorbed glucose expressed as percentage of the uptake from the lumen. These findings are in accord with those of Hanson &

Table 1. *Effect of luminal glutamate on the transport and metabolism of glucose*

For details see the text. Units are $\mu\text{mol/h}$ per g dry wt. ($\pm$ S.E.M.), except where values are given in percentages.

	Luminal substrate	Glucose (n = 6)	Glucose + glutamate (n = 7)
Vascular glucose appearance		43.8 $\pm$ 6.5	51.4 $\pm$ 7.2
Luminal glucose uptake		364.2 $\pm$ 18.0	319.0 $\pm$ 24.8
Glucose utilization		320.4 $\pm$ 15.3	267.6 $\pm$ 22.9
Vascular lactate appearance		367.9 $\pm$ 18.9	312.8 $\pm$ 25.6
Luminal lactate appearance		105.0 $\pm$ 10.8	65.6 $\pm$ 8.3
(Lactate appearance $\times$ 0.5 $\times$ 100) (Glucose utilization)		74.2 $\pm$ 3.3	71.6 $\pm$ 3.1
Percentage of uptake appearing unchanged		11.9 $\pm$ 1.5	16.3 $\pm$ 2.3
Percentage of uptake appearing as lactate		63.6 $\pm$ 4.2	59.8 $\pm$ 2.8
Percentage of uptake oxidized or sequestered		22.8 $\pm$ 3.8	23.8 $\pm$ 2.7

Table 2. *Metabolism of fructose and glucose by rat jejunum at low concentrations of substrate*

Experiments were performed with fructose, glucose plus fructose, sucrose or glucose as luminal substrates; initial concentrations were 10mM, and all luminal fluids contained glutamate (10mM). Units are $\mu\text{mol/h}$ per g dry wt. In this and subsequent Tables, significance of comparisons between groups is indicated by: * $P < 0.02$; ** $P < 0.01$; *** $P < 0.001$.

Group	Luminal substrate	No. of expts.	Vascular glucose appearance	Luminal glucose uptake	Glucose utilization	Vascular fructose appearance	Luminal fructose uptake	Fructose utilization
A	Fructose	7	—	—	—	19.5 $\pm$ 2.8	226.2 $\pm$ 15.5	206.8 $\pm$ 20.3
B	Glucose + fructose	5	135.4 $\pm$ 34.4 *D	348.3 $\pm$ 26.5 **C	212.9 $\pm$ 10.8 ***C	18.0 $\pm$ 1.26	144.5 $\pm$ 17.0 *A	126.5 $\pm$ 16.2 *A
C	Sucrose	6	61.9 $\pm$ 8.2	205.9 $\pm$ 6.32	144.1 $\pm$ 9.2	14.0 $\pm$ 1.10	139.4 $\pm$ 10.4 **A	125.4 $\pm$ 11.1 **A
D	Glucose	7	51.4 $\pm$ 7.2	319.0 $\pm$ 24.8 **C	267.6 $\pm$ 22.9 ***C	—	—	—

Parsons (1977), who showed no effect of glutamine, which is readily converted in the tissue into glutamate, on the metabolism of glucose.

Intestinal metabolism of monosaccharide substrates plus glutamate. Table 2 shows the rates of vascular appearance, luminal uptake and utilization of glucose and of fructose with different luminal substrates. With 10mM-fructose alone in the lumen, no glucose was detected in the vascular effluent. When glucose was present as an equimolar mixture with fructose the appearance of glucose in the vascular effluent was significantly greater than with glucose alone in the lumen. The uptake of glucose from the lumen was similar when either glucose or glucose plus fructose were present, but, in both groups, uptake was significantly greater than from sucrose alone. The rates of glucose utilization from glucose alone and from glucose plus fructose were similar, although the glucose utilization was significantly less when sucrose was present in the lumen. The rate of appearance of fructose in the vascular fluid was similar in all three groups, but the uptake of fructose from the lumen was significantly higher from fructose alone

than from glucose plus fructose or from sucrose. The utilization of fructose is significantly greater when fructose alone is present in the lumen.

Monosaccharide metabolism and lactate production. The rate of uptake of monosaccharide from the lumen and that of lactate formation were greatest when glucose and fructose were present together in the lumen (Table 3). Monosaccharide utilization was greater from glucose and fructose than from sucrose. The rate of fructose utilization from fructose alone was the same as that of glucose from glucose alone, but a greater proportion of the glucose utilized appeared in the vascular effluent as lactate.

Although the sum of fructose uptake and glucose uptake from the lumen in groups with fructose alone and glucose alone approximates to the total luminal monosaccharide uptake in the group with fructose and glucose present as an equimolar mixture, the same is not true for the appearance of monosaccharide in the vascular bed.

Fate of the absorbed monosaccharide. The fate of monosaccharide absorbed by the intestinal mucosa, expressed as percentage of uptake appearing

Table 3. *Monosaccharide metabolism by rat jejunum at low concentrations of substrate*

Experiments were performed with fructose, glucose plus fructose, sucrose or glucose as luminal substrates; initial concentrations were 10mM, and all luminal fluids contained glutamate (10mM). Units are $\mu\text{mol/h per g dry wt.}$: * $P < 0.02$; ** $P < 0.01$; *** $P < 0.001$.

Group	Luminal substrate	No. of expts.	Monosaccharide vascular appearance	Monosaccharide luminal uptake	Monosaccharide utilization	Vascular lactate appearance	Total lactate appearance/2	Percentage of total lactate appearing in lumen
A	Fructose	7	19.5 ± 2.8 **B, ***C, **D	226.2 ± 15.5 ***B, **C, *D	206.8 ± 20.3 ***B	170.3 ± 26.0	129.1 ± 12.4 ***B, **C, **D	35.8 ± 4.3 **B, ***C, **D
B	Glucose + fructose	5	153.4 ± 35.4	478.8 ± 44.6 **C	339.4 ± 13.0	434.2 ± 11.7	254.7 ± 11.0 *C	14.5 ± 2.2
C	Sucrose	6	75.8 ± 8.20	345.3 ± 15.2	269.5 ± 15.5 **B	359.4 ± 20.0	205.7 ± 12.1	12.4 ± 2.2
D	Glucose	7	51.4 ± 7.15 **B, ***C	319.0 ± 24.8 **B, **C	267.6 ± 22.9	312.8 ± 25.6	189.2 ± 12.7 **B, **C	17.8 ± 2.3

Table 4. *Fate of monosaccharide uptake from the lumen of rat jejunum at low concentrations of substrate*

Initial concentrations were 10mM, and all luminal fluids contained glutamate (10mM). * $P < 0.02$; *** $P < 0.001$.

Group	Luminal substrate	No. of expts.	Percentage of uptake appearing unchanged or as monosaccharide on vascular side	Percentage of uptake appearing as lactate	Percentage of uptake oxidized or sequestered	Percentage of utilization converted into lactate
A	Fructose	7	8.79 ± 1.1 ***B, ***C, *D	57.8 ± 3.8	33.4 ± 4.2 *B	63.5 ± 4.4
B	Glucose + fructose	5	29.8 ± 4.4	53.0 ± 4.3	17.2 ± 2.3	75.3 ± 3.3
C	Sucrose	6	22.0 ± 2.4	55.4 ± 3.8	17.6 ± 4.9	77.4 ± 6.1
D	Glucose	7	16.3 ± 2.3	59.8 ± 2.8	23.8 ± 2.7	71.6 ± 3.1

either unchanged on the vascular side, or as lactate, or oxidized by the tissue or otherwise sequestered, is shown in Table 4. Compared with glucose and other mixtures, a significantly lower fraction of the absorbed fructose appeared unchanged on the vascular side. The percentage of monosaccharide absorbed that appeared as lactate was similar with all substrates, ranging from 53 to 60%. Compared with the mixture, from fructose alone in the lumen, a higher proportion was oxidized or sequestered by the tissue, reflecting the lower rate of uptake of this substrate and the greater subsequent demand for it as a fuel. The lactate production, expressed as a percentage of monosaccharide utilization, was high in all experiments (64–77%), and there was no significant difference between the experimental groups.

High (28mM) sugar concentrations in the lumen

Intestinal metabolism of monosaccharide substrates at high concentration of sugars in the absence of glutamate. Table 5 shows that, with a high concentration of fructose in the lumen, the appearance of glucose in the vascular effluent was

detected. There was an approx. 3-fold increase in the rate of uptake from the lumen, appearance in the vascular bed and utilization of fructose when present alone at 28mM, compared with those values at 10mM. This 3-fold increase with an approx. 3-fold higher concentration in the lumen suggests that the transport mechanism is not saturated at these concentrations. As with the 10mM-fructose series, the rate of fructose appearance in the vascular effluent was similar in all the groups, and the rate of uptake of fructose from the lumen was significantly higher in the group with fructose by itself than in that with fructose plus glucose or with sucrose. Also, the fructose utilization was significantly greater from fructose alone than from the other two sugars. In contrast, there was a significantly faster rate of fructose utilization from 28mM-sucrose than from the equimolar mixture of glucose plus fructose.

Total monosaccharide metabolism and lactate production. Table 6 shows that with 28mM concentrations of substrates there was no statistical difference in the rates of monosaccharide utilization between the experimental groups. The

Table 5. *Metabolism of fructose and glucose by rat jejunum at high concentrations of substrate*

Experiments were performed with fructose, glucose plus fructose, sucrose or glucose as luminal substrates; initial concentrations were 28mM. Units are $\mu\text{mol/h}$ per g dry wt.: * $P < 0.02$; ** $P < 0.01$; *** $P < 0.001$.

Group	Luminal substrate	No. of expts.	Vascular glucose appearance	Luminal glucose uptake	Glucose utilization	Vascular fructose appearance	Luminal fructose uptake	Fructose utilization
A	Fructose	4	23.0 ± 6.7	—	—	68.9 ± 9.7	670.6 ± 67.8 ***B, **C	601.7 ± 62.4 ***B, **C
B	Glucose + fructose	5	313.1 ± 56.3	676.4 ± 29.9	363.3 ± 79.4	74.8 ± 4.1	254.8 ± 22.4	179.6 ± 24.2
C	Sucrose	5	314.7 ± 71.0	533.9 ± 81.9	219.2 ± 31.3	79.2 ± 15.5	370.8 ± 35.5	291.3 ± 22.7 *B
D	Glucose	4	341.2 ± 64.6	833.5 ± 192.9	492.4 ± 138.8	—	—	—

Table 6. *Monosaccharide metabolism by rat jejunum at high concentrations of substrate*

Experiments were performed with fructose, glucose plus fructose, sucrose or glucose as luminal substrates; initial concentrations were 28mM. Units are $\mu\text{mol/h}$ per g dry wt.: * $P < 0.02$; ** $P < 0.01$.

Group	Luminal substrate	No. of expts.	Monosaccharide vascular appearance	Monosaccharide luminal uptake	Monosaccharide utilization	Vascular lactate appearance	Total lactate appearance/2	Percentage of total lactate appearing in lumen
A	Fructose	4	91.9 ± 15.3 **B, *C, **D	670.6 ± 67.8 *B	578.7 ± 56.0	594.7 ± 43.9	365.4 ± 25.9	18.4 ± 4.0
B	Glucose + fructose	5	387.8 ± 56.1	931.2 ± 42.6	543.3 ± 88.3	769.0 ± 41.8	455.0 ± 30.2	14.9 ± 1.9
C	Sucrose	5	393.8 ± 85.0	904.3 ± 114.8	510.4 ± 39.7	772.4 ± 70.0	440.1 ± 35.7	12.4 ± 2.1
D	Glucose	4	341.2 ± 64.6	833.5 ± 192.9	492.4 ± 138.8	633.6 ± 46.8	363.0 ± 26.8	12.6 ± 1.8

Table 7. *Fate of monosaccharide uptake from the lumen of rat jejunum at high concentrations of substrate*
Initial concentrations were 28mM. * $P < 0.02$; *** $P < 0.001$.

Group	Luminal substrate	No. of expts.	Percentage of uptake appearing unchanged or as monosaccharide on vascular side	Percentage of uptake appearing as lactate	Percentage of uptake oxidized or sequestered	Percentage of utilization converted into lactate
A	Fructose	4	13.6 ± 1.5 *B, ***C, ***D	55.3 ± 4.2	31.1 ± 4.9	59.2 ± 5.1
B	Glucose + fructose	5	42.5 ± 6.9	48.9 ± 2.8	8.6 ± 7.9	83.7 ± 14.9
C	Sucrose	5	42.0 ± 3.8	51.3 ± 7.3	6.7 ± 7.3	86.2 ± 11.6
D	Glucose	4	42.2 ± 3.6	50.3 ± 10.4	7.7 ± 11.4	73.7 ± 18.7

appearance of monosaccharide in the group with fructose alone was significantly less than in the other groups. The fraction of absorbed carbohydrate that appeared as lactate in the lumen was similar in all groups.

Fate of absorbed monosaccharide. The fraction of monosaccharide taken up from the lumen that appeared either unchanged or as monosaccharide on the vascular side (Table 7) was similar in the groups with glucose plus fructose, sucrose, and glucose, and these values were approximately double those found in the 10mM-fructose series. As

in the first series, these values were significantly lower in the group perfused with fructose alone, suggesting a greater requirement of the tissues for the slower transported fructose as a fuel. The extent of conversion of monosaccharide into lactate was similar in all groups, and these values were similar to those in the 10mM-fructose series. Of the fructose taken up from the lumen, 31.1% was oxidized or sequestered within the tissues in the group with fructose alone, compared with 33.4% in the 10mM-fructose series and between 7 and 9% in the other experimental groups. The

fraction of absorbed carbohydrate that is converted into lactate was similar in all groups and to that found in the series with 10mM substrate concentrations.

Discussion

Many of the overall processes of absorption and metabolism in the small intestine are best studied by a procedure for vascular perfusion. Such a technique has the advantage over other methods *in vitro* in that the tissues are well oxygenated from the vascular side, the perfused vascular bed also allows immediate clearance of the transported substances, so that they do not accumulate to high concentrations in the intestinal wall, and the rates of transport into the vascular bed are readily measured.

Our findings are in accord with earlier work (Wilson, 1962) showing that fructose is absorbed rapidly from rat jejunum, under our conditions, at rates of 70% of those of glucose at an equivalent concentration. Although glucose in the lumen decreased fructose uptake, there was no effect of glucose on the rate of transfer of fructose into the vascular bed. At both 10mM and 28mM concentrations in the lumen, the rates of uptake of glucose and the vascular appearance and utilization were never greater from sucrose than from the equi-

molar mixture. The same is true for fructose at 10mM concentration. However, as shown in Table 5, a kinetic advantage for fructose uptake from fructose (see Macdonald & Turner, 1968) cannot be excluded at 28mM concentration. Our finding of an apparent absence of kinetic advantage for glucose uptake from sucrose in the rat contrasts with findings by Caspary (1977) for hamster intestine, but is in accord with the suggestion that disaccharide hydrolysis and the concomitant hexose transfer are separate and sequential events (Davidson & Leese, 1977).

When fructose is the sole carbohydrate in the lumen, significantly more fructose is utilized than when glucose is present. Thus fructose can act as a fuel for the jejunum, and glucose can 'spare' fructose from utilization. Although from 10mM-fructose alone in the lumen there is no secretion of glucose into the vascular bed, with 28mM-fructose glucose consistently appeared. The finding that with 10mM-fructose in the lumen no glucose appears in the vascular bed demonstrates that any glucose released from glycogen or glucose stores in the intestinal wall must be lost during the first 15 min of perfusion, because during that period the venous effluent is not recirculated to the reservoir.

There are three possible routes for conversion of fructose to glucose by the intestine (Scheme 1): (a) fructose phosphorylated directly either by hexo-

Scheme 1. Possible routes for intestinal conversion of fructose into glucose

kinase to fructose 6-phosphate and thence to glucose via glucose 6-phosphate, or (b) by fructokinase or a phosphoenolpyruvate-dependent monosaccharide phosphotransferase to fructose 1-phosphate and thence to glyceraldehyde 3-phosphate, or (c) via sorbitol. As for pathway (c), the thermodynamic properties appear to favour the formation of sorbitol and fructose from glucose while the aldose reductase activity of the intestinal mucosa is low and not increased by fructose feeding (Stifel *et al.*, 1968). It might be possible for glucose production to occur with high (e.g. more than 50 mM) intracellular concentrations of fructose. Indeed there may be differences in the apparent metabolism of fructose by the gut depending on the nature of the preparation used: with vascular perfusion the fructose concentration in the extraluminal fluid is kept low. For route (a) hexokinase has a 5–10-fold greater affinity for glucose than for fructose (Sols, 1956), so that phosphorylation of fructose via this route would be inhibited if glucose were also present. It seems likely that conversion into glucose in the small intestine of the rat is via fructose 1-phosphate. The enzymes involved in this pathway have been shown to increase after fructose feeding (see Scheme 1, and Crouzoulon & Dandriofosse, 1979). Despite this increased enzyme activity, net conversion of fructose into glucose was detected in our experiments only when 28 mM-fructose was present in the lumen. The estimated maximum rate of utilization of fructose from these experiments (15.0 nmol/min per mg of whole wall protein) is less than, but of the same order of magnitude as, the maximum activity of fructokinase that has been reported in fructose-fed rats (36.8 nmol/min per mg of mucosal protein; Crouzoulon & Dandriofosse, 1975).

A striking feature of the fructose metabolism at 10 mM concentrations is that the lactate formation is substantially less than when glucose is present, and a larger fraction appears in the lumen. The high rate of aerobic lactate formation from monosaccharides present in the lumen in these preparations, despite a high degree of tissue oxygenation and good perfusion, supports the previous findings by Hanson & Parsons (1976) that a significant proportion (up to 50%) of absorbed monosaccharides appears as lactate and not as unmetabolized transport products. It is tempting to suggest that during carbohydrate absorption lactate may be a better precursor of hepatic glycogen, so that aerobic lactate formation by the intestine is of physiological significance.

Comparing the findings with high and low concentrations of sugars, the main differences found were that only at high concentrations could there be demonstrated net conversion of fructose

into glucose by this tissue. In this group approx. 10% of the fructose uptake from the lumen appeared as fructose in the vascular bed and approx. 3% as glucose. It was assumed that any glucose formed in the tissue from fructose at the lower luminal concentrations was rapidly utilized as a fuel in the absence of other adequate fuel supplies, thus preventing net glucose appearance in the vascular effluent. Other aspects of fructose metabolism appeared similar at the two concentrations.

In conclusion, fructose uptake from the lumen by rat jejunum appears to be determined by two factors: the fructose concentration in the lumen and the ability of the intestine to metabolize fructose, an ability that is severely decreased in the presence of glucose. The cellular mechanisms whereby glucose decreases the fructose metabolism and becomes the preferred fuel have yet to be elucidated.

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