Gut transit and carbohydrate uptake

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Classical assessments of nutritional adequacy rely on tables of supposed nutrient requirements for animals or for man on the one hand, and the ability of feedstuffs to provide them on the other. These are expressed in gross or overall digestibility terms and do not relate to differences in the rates of amounts of digestion occurring in different parts of the gut. Yet in the case of carbohydrates, these differences in the pattern of digestion are factors which have a considerable bearing on animal growth, or human metabolism, e.g. in the diabetic state. The aim of the present review is to consider the importance of interrelations between transit, digestion, fermentation and absorption of carbohydrates. Examples will be drawn from studies in man and related information from the pig which appears to digest, absorb and metabolize carbohydrates in a similar way to human beings.

From a nutritional and physiological point of view carbohydrates exhibit great diversity. In general, man and most animals are able to hydrolyse starch thoroughly and to absorb sugars rapidly in the small intestine. However, a substantial part of dietary carbohydrate can be in the form of non-starch polysaccharide (NSP; equivalent to dietary fibre): this is not hydrolysed by amylase, but is fermented by the gut microflora to a degree depending on its physical and chemical structure.

Transit through the gut

Much is said and written about transit through the gut but what exactly is transit? In many studies transit is regarded as the period of time taken for a certain percentage (often 5, 50 or 80%) of a marker introduced in a single meal to reach a specified point in the gut, or the period of time when a marker concentration is at its highest, or it may be the time taken for first arrival of a marker. In other cases the marker may be continuously administered to give an estimate of mean transit time (Cummings *et al.* 1976). Whatever the value obtained, or the method used, the physiological significance of transit time is somewhat elusive, because markers usually adhere only to certain dietary components, or to no specific component at all; most of these components are gradually hydrolysed during passage through the gut and eventually a marker may be completely free of the component it was marking and then may attach to an unrelated material. In the liquid milieu of the gut where major endogenous inputs occur, fluid and solid movements may take place at different rates. Under these conditions markers which are not phase-specific can move in a pattern which does not relate to any particular entity in the digesta.

Indirect measurements of transit include the appearance of Paracetamol in the blood (as an index of gastric emptying) and breath hydrogen (indicating the time of arrival of fermentable NSP in the caecum or colon after transit through the stomach and small intestine of fermentable NSP). Furthermore, it is clear that there is a high degree of individual variation in transit phenomena which is related to little-understood factors of genetic or psychological origin, rather than to the nature of the diet. In spite of all these uncertainties, the concept of measuring transit time has been particularly linked with the view that it is positively correlated with the amount of digestion, absorption and microbial fermentation occurring in specific regions, or in the whole gut. The subject has

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been reviewed in detail by Kotb & Luckey (1972), Cummings (1978), Van Soest *et al.* (1983) and Read (1986).

Secretion

The level and type of dietary NSP has a marked effect on secretion into the gut of pigs. For example, Zebrowska *et al.* (1983) found that 81% more pancreatic juice was secreted in pigs given a diet with 200 g NSP/kg than one with 50 g/kg; under similar nutritional conditions Sambrook (1981) found 47% more bile in pigs given the high-NSP diet, and P. D. Cranwell and A. G. Low (unpublished results) found that gastric secretion from isolated pouches of pigs receiving high-NSP diets was doubled. The NSP fraction of wheat was demonstrated by Zebrowska & Low (1987) to stimulate much greater pancreatic secretion than the starch fraction. These secretory responses are a component of the general observation that diets with a high content of NSP induce greater volumes of digesta. Whether this leads to acceleration of transit is not clear, because, although the flow-rate at any point in the gut is obviously increased, the velocity may not change because gut volume tends to increase when diets with a high NSP content are given to pigs (Kass *et al.* 1980).

Transit, digestion and absorption in the small intestine

The effects of supplementary cellulose, bran and guar gum on gastroduodenal and jejunal motility and transit were investigated in dogs by Bueno *et al.* (1981); they found that although motility and transit were modified by the type of NSP used, there was no clear relation between changes in motility and transit. When pigs received bran-supplemented diets, transit was accelerated in the studies of Bardon & Fioramonti (1983); direct mechanical factors rather than the production of volatile fatty acids (VFA) from NSP in the caecum or colon were thought to be responsible. The effect of supplementary lactulose on transit through the stomach and small intestine of man was investigated by Read *et al.* (1982); lactulose accelerated transit time through the small intestine but not through the stomach. This is of interest because lactulose is used experimentally to indicate the transit time through the stomach and small intestine, by means of measurement of breath H_2, and shows that such measurements cannot provide information on the relative transit rates through the stomach and small intestine. Transit of carbohydrate through the stomach and small intestine and absorption in the jejunum have been shown to be delayed by ileal infusion of lipids in man, suggesting that the presence of lipid in the ileum may have a major influence on the digestion and absorption of a meal (the 'ileal brake') (Holgate & Read, 1985).

While the central role played by amylase in starch hydrolysis is well established, it is by no means clear why the amount secreted is theoretically capable of hydrolysing ten to fifty times the amount of starch that a pig can eat in 1 d; similar observations have also been made for man. However, the type of starch eaten can greatly modify metabolic responses to them; for example, O'Dea *et al.* (1981) found that four types of rice starch were digested in vitro from 17·6 to 71·8%, with corresponding differences in blood glucose and insulin measured in vivo in man. Similarly, Jenkins *et al.* (1983) found that legumes led to lower postprandial blood glucose concentrations than cereals in man, and this was directly related to the digestion rate of starch measured previously under in vitro conditions (Jenkins *et al.* 1982). Differences in the rate of digestion of starches in vivo were also seen by Rérat *et al.* (1979), who found that glucose derived from wheat starch reached the hepatic portal vein of pigs more rapidly than that from barley. Under normal conditions the supply of brush-border disaccharidases for completing starch digestion appears to be sufficient: even when a large amount of guar gum was present in pigs in studies by Rainbird *et al.* (1984) no reduction in the rate of maltose hydrolysis was seen.

Striking effects were seen in human studies when the amount of amylase activity was reduced by the presence of an amylase inhibitor (phaseolamin, from Great Northern white beans): (a) small intestinal amylase activity reduced by 95%, (b) increased flow of carbohydrate to the ileum, (c) increased breath H_2 excretion, (d) decreased water absorption and increased ileal digesta volume, (e) shortened small intestinal transit, (f) 85% reduction in postprandial blood glucose levels (Layer *et al.* 1986).

Although the potential benefits of NSP for man were discussed many years ago, the first detailed studies on its property of delaying or reducing the rate of absorption of glucose, and hence its value in the management of diabetes, began in the 1970s. Jenkins *et al.* (1978) showed that guar gum, pectin, gum tragacanth, methylcellulose and wheat bran all decreased peak peripheral blood glucose and insulin levels in man; although guar gum had the greatest effects, once hydrolysed it had no effect, thus implying that its viscous nature in solution was critical for its efficacy. All soluble NSP increased mouth–caecum transit time (as measured by breath H_2) except methylcellulose, while bran significantly decreased it. Following these observations several groups have investigated the mechanisms involved. While it is evident that guar gum can delay gastric emptying of a meal, for example in rats (Leeds *et al.* 1979), in man (Wilmshurst & Crawley, 1980) and pigs (Rainbird & Low, 1986*a*), it seems that the emptying of carbohydrates is not delayed but only that of water (Rainbird, 1986). Furthermore, other NSP sources had no effect on gastric emptying of carbohydrates in the studies of Rainbird & Low (1986*b*). These results emphasize the dangers of interpreting movements of digesta as an indication of movements of nutrients. Guar gum reduced the rate of absorption of glucose from the jejunum in vitro (Johnson & Gee, 1981) and in vivo (Rainbird *et al.* 1984); the reasons for this finding appear not to be a reduction in small intestinal contact area (Blackburn *et al.* 1984*a*), but seem to relate to reduced diffusion or convection of glucose to the epithelial cell surface (Blackburn *et al.* 1984*b*). The view that the locus of action is extra-epithelial is also supported in studies by Sigleo *et al.* (1984) who demonstrated that pectin and cellulose led to longer and wider villi and marked increases in unidirectional fluxes of 3-*O*-methylglucose. More recently Low *et al.* (1986) have shown that the rate of absorption of glucose in isolated loops of pig jejunum is delayed to differing degrees by different types of NSP: low-viscosity guar gum was less effective than high-viscosity guar gum: bran, cellulose, pectin and low-viscosity guar gum were equally effective. This indicates that differences in the physical and chemical nature of the NSP are of importance in determining their metabolic effects.

Digestibility measurements at the end of the small intestine

It is widely accepted that starch, if suitably cooked, is fully digested and absorbed by the end of the small intestine. However, when starch was provided in uncooked form from potatoes (at up to 150 g/kg diet) then there was a significant decline in carbohydrate digestibility measured at the end of the small intestine in pigs (Just *et al.* 1983). When wheat bran or sugar-beet pulp were substituted (at 330 g/kg) for normally processed cereals in pigs, there was no depression in starch digestibility, but 11–37% of NSP disappeared before the end of the small intestine (Graham *et al.* 1986) indicating that substantial microbial action had occurred in the small intestine. Millard & Chesson (1984) also drew attention to the fact that NSP from swede was degraded in the small intestine of pigs, and found substantial amounts of cellulolytic and pectinolytic organisms in this region; on the other hand they found no cellulolytic organisms and much smaller numbers of pectinolytic organisms when bran-supplemented diets were given. Thus the nature of the NSP present appears to be critically important for determining its site of degradation and uptake, at least in pigs.

The fate of starch which is resistant to hydrolysis by amylase, probably as a result of excessive heat treatment during processing, has been studied by Englyst & Cummings (1985) in human ileostomists: the ileal effluent contained 0·6, 4 and 2·5% of ingested starch from oats, cornflakes and white bread respectively, and almost all was amylase-resistant. In addition, almost all the NSP eaten by the subjects was recovered in the effluent, indicating that little microbial degradation occurred in the small intestine under these conditions. Resistant starch can only be degraded in man by bacteria from the colon, according to the studies of Englyst & MacFarlane (1986). Chapman *et al.* (1985) increased (by loperamide) or decreased (by magnesium citrate) the transit time of a meal with wheat and potato starch given to human ileostomists and observed that the amount of unabsorbed starch was directly related to the amount eaten and also to the transit time. The amounts of starch which escaped amylase digestion in these studies were nevertheless small and did not exceed 7% of intake. Carbohydrate digestibility measured at the end of the small intestine in pigs is generally depressed by supplements of NSP, as shown, for example, by Keys & Debarthe (1974), Partridge (1978) and Dierick *et al.* (1983). However, it is not yet possible to relate the degree of depression to specific types of NSP; in most studies starch digestion was not measured and the reduction of carbohydrate digestion appears to be directly related to the decreased ratio of starch:NSP in the diet. Furthermore, there is little evidence that NSP directly reduces starch digestibility to any significant extent in pigs.

Significance of the large intestine in carbohydrate uptake

The uptake of carbohydrates in this region appears to occur entirely in the form of VFA, following microbial degradation of whatever carbohydrate residues are present; there is no evidence of significant levels of sugar absorption. Very large concentrations of principally anaerobic bacteria are responsible for a fermentation which typically lasts 24–48 h. The process is variable from individual to individual and is to some extent diet- or substrate-dependent: more or less soluble forms of NSP are completely degraded, while celluloses, for example, are only partially degraded, the extent depending on physical factors. Cummings (1984) has reviewed recent research on the microbial activity of the large intestine of man, and Ratcliffe (1985) has discussed microbial activity in the pig.

There is very little information on the nutritional significance of the large intestine in carbohydrate uptake in man because of the technical difficulty of measuring ileal and faecal output simultaneously. However, in pigs equipped with ileal cannulas, up to 18–33% of digestible energy digestion (Just *et al.* 1983) and up to 14–39% of organic matter digestion can occur in the large intestine (Metz *et al.* 1985). The VFA produced are rapidly absorbed and metabolized, as shown for acetic acid (Latymer & Low, 1984) and propionic acid (Latymer & Low, 1987). The eventual nutritional value of the VFA is not known accurately, but it is somewhat lower than that of an equivalent amount of glucose released by enzymic action in the small intestine, because the energy yield of the VFA supply is less than that of glucose, in terms of ATP. Just *et al.* (1983) showed that as the percentage of energy absorbed from the large intestine rose from 18 to 34, so the percentage of metabolizable energy which was used as net energy fell from 66 to 58. However, the eventual nutritional value of VFA may be considerable: Rérat *et al.* (1985) measured the amounts of VFA in the hepatic portal vein of pigs and found that their energy content amounted to about 30% of the energy eaten by the pigs (given a diet containing barley, maize, soya bean, lucerne (*Medicago sativa*) meal and cellulose).

Measurements of the transit time of the liquid and solid phases of digesta through the small intestine, caecum, colon and overall were made in pigs with three cannulas by Latymer *et al.* (1985). Supplements of bran, lactulose and pectin had few effects when added to a cereal-based diet: the transit time of pectin and lactulose was longer than that of bran (solid phase); in the liquid phase transit time was decreased least by pectin, and most by bran. Few significant differences in transit time occurred in the large intestine. When pigs were given cereal-based diets without or with supplements of oat husk or lucerne, Den Hartog *et al.* (1985) observed that the high-NSP diet moved more slowly through the stomach and small intestine but faster through the large intestine; the high-NSP diet significantly depressed organic matter digestibility, but as intakes were higher the total amounts of organic matter absorbed were similar.

Measurements of overall transit times in pigs have shown marked reductions when semi-purified diets were supplemented with lucerne-leaf meal (Kuan *et al.* 1983), or coarse and fine bran, lucerne and cellulose (Ehle *et al.* 1982). Bran addition to milk-substitute or milk diets greatly reduced transit time (Canguilhem & Labie, 1977; Fioramonti & Bueno, 1980; Bardon & Fioramonti, 1983). This emphasizes that the effects of NSP supplements may be large when added to diets without NSP, but small when the amount present is already substantial.

Considerable variation in faecal output among individuals has already been noted; Cummings *et al.* (1978) found that the transit time through man varied inversely with the faecal weight. At the same time faecal weight also increased, after supplements of 20 g/d were given, by (%) 127 (bran), 69 (cabbage), 59 (carrot), 40 (apple) and 20 (guar gum) (Cummings *et al.* 1978). However, the fate of different sources of NSP differed: cabbage fibre was degraded and led to an increased bacterial (and thus water) output in faeces, while wheat bran was largely undegraded and retained water in the gut lumen instead.

A further complication in the interpretation of transit-time findings is that of feeding level in relation to NSP intake, as shown in pigs by Roth & Kirchgessner (1985). Feeding at 2·5 times maintenance rather than 1·0 times maintenance significantly reduced transit time from 68 to 39 h (52 g crude fibre/kg) and from 47 to 32 h (96 g crude fibre/kg); digestibilities of energy were lower for the latter diet, and were reduced with the higher levels of intake for both diets.

A comprehensive study by Kass *et al.* (1980) in pigs given 0, 200, 400 or 600 g lucerne/kg diet demonstrated inverse relations between NSP content and digestibility of energy and NSP components. The weight of the water content of digesta and rate of passage increased as dietary NSP content rose; Kass *et al.* (1980) concluded that the negative effects of the lucerne were due to increased passage rate which limited time for microbial degradation of the NSP. Drochner (1984) and Van Soest (1985) have shown that the fermentation rate of NSP varies inversely with the associated lignin content; this provides an explanation for the depressive effects of NSP on digestibility seen by Kass *et al.* (1980) because lucerne has a high content of lignin (approximately 70 g lignin/kg) and a low fermentation rate. It is possible that physical features of highly lignified feeds also stimulate motility by purely mechanical means.

Conclusion

In general starches are fully digested by the enzymes of the small intestine of man and the pig, although the rates differ for different starch types. Starches which are inaccessible to amylase and NSP are degraded by the microflora to an extent depending in part on the degree of lignification, as well as other physicochemical properties of the diet. Many types of NSP increase secretion into the gut and the amount of digesta present. Transit rates vary greatly and appear to be the result of many factors, including the nature of the diet, the amounts of secretions into the gut and hydration of digesta components; decreased transit times correlate with increases in lignin content. As yet accurate prediction of the fate of NSP in the diet of pigs and of man is not possible and cannot be achieved purely by classical methods of assessment of the nutritive value of feedstuffs.

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