British Journal of Nutrition (2001), **85**, 343–350 DOI: 10.1079/BJN2000271

Changes in intragastric meal distribution are better predictors of gastric emptying rate in conscious pigs than are meal viscosity or dietary fibre concentration

S. Guerin[1], Y. Ramonet[1], J. LeCloarec[2], M. C. Meunier-Salaün[1], P. Bourguet[2] and C. H. Malbert[1]*

[1]*Station de Recherches Porcines, INRA, Saint-Gilles, France*

[2]*Laboratoire de Médecine Nucléaire, Centre Eugène Marquis, Rennes, France*

(Received 17 November 1999 – Revised 4 August 2000 – Accepted 25 September 2000)

The effect of dietary fibre on the gastric emptying rate of solids is controversial. Similarly, the mechanisms by which it modulates food intake are partially unknown. Gastric emptying and proximal *v.* distal stomach filling were evaluated in triplicate on four conscious pigs using scintigraphic imaging. Each animal received in an isoenergetic manner a concentrate low-fibre diet enriched in starch (S) and two high-fibre diets based on sugar beet pulp (BP) or wheat bran (WB). All meals had the same viscosity before ingestion (100·0–100·5 Pa·s). Viscosity of the gastric contents was measured in four additional animals fitted with a gastric cannula. The gastric emptying rate of BP diet was significantly slower than S and WB diets ($t_{1/2}$ 78·4 (SEM 5·68), 62·8 (SEM 10·01) and 111·6 (SEM 10·82) min for S, WB and BP diets respectively, $P<0·05$). For BP diet only, rate of distal stomach filling was steady during the first 120 min after the meal whereas that of S and WB diets decreased in an exponential manner. Numerous backflow episodes from the distal into the proximal stomach were observed for BP diet that generated the larger intragastric viscosity (0·26 (SEM 0·03), 0·3 (SEM 0·02) and 0·52 (SEM 0·002) Pa·s for S, WB and BP respectively). In conclusion, viscosity of the meal or the percentage total fibre, unlike viscosity of the gastric contents, are poor predictors for emptying. The reduced emptying rate observed with BP is associated with major changes in intragastric distribution of the meal absent with WB and S diets.

Gastric emptying: Dietary fibre: Viscosity

Dietary fibre is used increasingly in human and animal nutrition (Salminen *et al.* 1998). In man, it represents an alternative means for treating pathological conditions such as obesity, hypercholesterolaemia and diabetes (Miranda & Horwitz, 1978) since it reduces plasma glucose response to meal (Morgan *et al.* 1990) and slows down the return of hunger (Haber *et al.* 1977). In pregnant sows, dietary fibre minimises the stereotyped behaviour (Lawrence & Terlouw, 1993) associated with feed restriction used to limit excessive weight gain and fat deposition. These effects are supposed to be entirely or partially related to a decreased gastric emptying rate (Mcintyre *et al.* 1997) that in turn increases gastric distension and satiety (Phillips & Powley, 1996; Lepionka *et al.* 1997). Whereas the inhibitory effect of dietary fibre on liquids emptying is clearly demonstrated, its effect on the emptying of the solid phase of the meal is more controversial. Delayed (Brown *et al.* 1988; Di Lorenzo *et al.* 1988), normal (Rainbird & Low, 1986*a*,*b*) or accelerated gastric emptying (Meyer *et al.* 1986; Potkins & Lawrence, 1988) have all been reported.

The absence of consensus on the role of dietary fibre on gastric emptying of solids relates first to the difficulty of evaluating solid emptying of fibre-containing meals (Schade *et al.* 1991), and second to the inaccessible yet suspected difference between meal *v.* gastric chyme viscosity (Cherbut *et al.* 1990). The latter is supposed ultimately to be the main physical factor controlling emptying as hypothesised in the so-called ‘hydrodynamic’ theory (Meyer *et al.* 1986). Numerous methods have been evaluated to label fibrous contents of the meals but none can be claimed as ideal. Either they label unusual dietary components (Malagelada *et al.* 1980; Madsen & Jensen, 1989; Schade *et al.* 1991) or have some degree of inaccuracy due to a significant dissociation of the solid radioactive label into the liquid phase (Sagar *et al.* 1983; Houghton *et al.* 1989).

Abbreviations: BP, sugar beet pulp; S, starch; WB, wheat bran.

* **Corresponding author:** Dr C. H. Malbert, fax +33 02 23 48 50 80, email malbert@st-gilles.rennes.inra.fr

One expected effect of dietary fibre is reduced hunger sensation produced by early satiety. Since activation of vagal mechanoreceptors present in the proximal stomach is likely at the origin of this effect (Mei, 1986; Moran *et al.* 1999), it might be more interesting to evaluate the effect of satiety-inducing fibre on proximal gastric filling rather than total gastric emptying. Indeed, dissociation between these two variables has been demonstrated especially with meals containing ingredients of different physical properties (Collins *et al.* 1988; Edelbroek *et al.* 1994). Unfortunately, in animals none of the presently available methods was proved to differentiate proximal *v.* distal stomach filling. In human subjects, however, scintigraphic imaging of the stomach has such capabilities.

The aim of the present study was to evaluate non-invasively total gastric emptying and proximal *v.* distal stomach filling in conscious pigs after a meal containing dietary fibre classically incorporated in pig diets such as wheat bran (WB) and sugar beet pulp (BP) (Bourns *et al.* 1995; Ramonet *et al.* 1999). Emptying from and filling of the stomach was measured by scintigraphic imaging of the abdomen, the solid phase of the meal being labelled with ^{99m}Tc colloid. An additional aim was to correlate emptying rate and viscosity of the chyme present in the stomach by sampling the whole stomach contents from surgically prepared animals.

Methods

Imaging protocol

Imaging studies were carried out in four female Large White pigs (40 (SEM 3·2 kg)). All studies were performed in unsedated pigs trained to stand quietly in slings allowing approximately 40 cm movement in each direction. The slings were designed to allow the pig to stand for prolonged periods. Each animal was given three different test meals on separate days. For each meal the emptying experiments were performed in triplicate. The order of the studies was randomised with a minimum of 3 d between experiments. Meals were given after an overnight fast for solids only and were consumed spontaneously while the animal stood laterally to the head of a scintillation camera. Test meals were eaten spontaneously within 3 min after presentation. For 30 min before and during the imaging protocol, the animals had no access to drinking water.

The three test meals differed by the amount of total dietary fibre: 63·8, 207·1 and 340·5 g/kg DM for starch (S), WB and BP diets respectively (Table 1). To negate the influence of the energy density of meals on gastric emptying, the meals were given in isoenergetic quantities supplying 4·25 MJ: 242, 239 and 248 g DM for S, WB and BP respectively. Between experiments, the animals were fed once daily using a standard animal diet containing 63·8 g total dietary fibre/kg DM and they had free access to drinking water. Feeds were analysed for DM, ash and crude fibre according to the methods of the Association of Official Analytical Chemists (1990). Cell wall fractions, neutral-detergent fibre, acid-detergent fibre and acid-detergent lignan were determined according to Van Soest *et al.* (1991) with previous amylolytic treatment. Total soluble and insoluble fibre was analysed in accordance with the Association of Official Analytical Chemists' method described by Prosky *et al.* (1988).

Preparation of the labelled test meals

The dry components of the test meals were reduced into powder with a mean particle size of 1 mm necessary for uniform labelling with Tc and cancellation of the effect of particle size on gastric emptying rate. Afterwards, freshly-made ^{99m}Tc colloid (15 MBq, TCK 1; CISBio International, Fontenay au Roses, France) was diluted with 600 ml hot water (75°C). Diet powder was gently incorporated into this preparation and allowed to incubate for 5 min. The labelled meal was washed twice with an equal volume of cold tap water to remove ^{99m}Tc colloid in excess that was still in the liquid phase. Water in excess was removed by centrifugation (400 rpm, 5 min) of the mixture. The meal was allowed to cool to 20°C before consumption. At the time of eating, the consistency of the meals was identical to thick porridge. Immediately before ingestion the volumes of the meals were 598·4 (SEM 12·0), 638·4 (SEM 12·2) and 772·8 (SEM 13·7) ml for S, WB and BP diets respectively.

To evaluate the quality of the labelling and to confirm the adequate labelling of the solid phase only, 10 g labelled test meal were dissolved in 50 ml saline–HCl (2 M) and pepsin (three trials for each diet). The mixture was incubated for 60 min at 38°C. The assay tube was then centrifuged (4000 rpm, 5 min) and placed under the γ-camera for a static acquisition lasting 5 min. The amount of radioactivity was measured in two regions of interest delimiting the supernatant fraction and the sediment. The ratio between the counts obtained in the two regions was calculated afterwards. All values ranged from 92 to 95 % irrespective of the diet indicating that 8 to 5 % of the radioactivity was present in the liquid phase.

Physical characterisation of the meals

Four female Large White pigs (40 (SEM 3·6) kg) were surgically fitted with a gastric silicon cannula inserted in the mid corpus region according to a previously described

Table 1. Composition of the test meals containing increasing amount of total dietary fibre originating from starch (S diet), wheat bran (WB diet) and sugar beet pulp (BP diet). Test meals were given in an isoenergetic manner supplying 4·25 MJ to the animal

	S diet	WB diet	BP diet
DM (g/kg)	888·2	897·2	897·6
Gross energy (MJ/kg DM)	17·62	17·83	17·10
Minerals (g/kg DM)	49·2	75·6	79·3
Lipids (g/kg DM)	11	31·5	14·8
NDF (g/kg DM)	107·6	258·4	265·3
ADF (g/kg DM)	22·0	65·8	115·3
ADL (g/kg DM)	4·8	15	17
Crude protein (g/kg DM)	174·4	176·9	152·5
Crude fibre (g/kg DM)	25·1	60·9	94·9
Total dietary fibre (g/kg DM)	63·8	207·1	340·5
Starch (g/kg DM)	599	417	402

NDL, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignan.

procedure (Cuche & Malbert, 1998). Briefly, pigs were pre-anaesthetised with intramuscular ketamine. A surgical level of anaesthesia was obtained by halothane, air, and O_2 mixture supplied by a servo-ventilator. O_2 fraction and tidal volume were adjusted so that partial O_2 pressure measured by pulse oxymetry was $\geq$98 % and expired partial CO_2 pressure measured by infra-red capnometer <5 %. After a recovery period lasting at least 10 d, pigs were given in a random order unlabelled meals prepared as described earlier but without Tc. After the end of the meal (30 min), the cannula was opened and all the stomach contents collected for viscosity analysis. Viscosity of the meals before ingestion and of the gastric contents were measured at a constant temperature of 27°C (Viscotester VT02; Haake, Lausanne, Switzerland). Absolute viscosity (Pa·s) at shear rate of 45 s^{-1} is presented.

Scintigraphy acquisition and analysis

In each study, data were acquired for at least 120 min, commencing immediately before the ingestion of the meal. Data were collected in 120 s frames for the entire duration of the study using a computerised scintillation camera (Apex 900; Elscint, Israel) fitted with a high resolution–low energy collimator. The position of the camera head was right lateral relative to the animal. Since the long axis of the pig stomach was slightly tilted to the left, attenuation correction for tissue depth was necessary while acquiring a lateral image. Therefore, at the completion of the study, 1 litre glucose (100 g/l) labelled with 10 MBq ^{99m}Tc-diethylene triamine pentaacetate (TCK 6; Cis Bio International) was given orally to the pig and a dorso-ventral static image of the stomach was digitised over 60 s. Correction for tissue attenuation was performed off-line using this dorso-ventral image for calculation of the correction factors. Calculation of the total stomach counts was then achieved with the algorithm validated by Collins *et al.* (1983). Radionuclide data were also corrected for subject movement and radionuclide decay.

The total stomach region of interest was divided into proximal and distal regions with the proximal region corresponding to the fundus and proximal corpus and the distal region representing the distal corpus and antrum. Emptying curves (expressed as percentage retention of isotope *v.* time) were derived from total stomach, proximal stomach and distal stomach regions of interest. Emptying curves were fitted to a power exponential function (Elashoff *et al.* 1982) to calculate $t_{1/2}$ emptying time and the curve shape variable (β). Emptying curves with a loose fitting to the power exponential model indicated by a mean square error >0·005 were not taken into account in the final analyses.

Statistical analysis

Statistical significance between diets was tested using repeated measures fixed effect ANOVA (Prism, GraphPad Software; GraphPad Inc., San Diego, CA, USA). Matching was tested prior to ANOVA calculation and was found to be effective for all comparisons described. Bonferroni *post hoc* multiple comparison test was used to compare diets effect (Motulsky, 1999). Data are expressed as mean values with standard errors of the means. A P value <0·05 was considered significant in all analyses.

Results

Viscosity of the test meal

Before ingestion, the viscosity of the three test meals was not significantly different (Table 2). The viscosity of the gastric contents, however, was significantly greater for BP diet compared with S and WB diets.

Total stomach emptying

One emptying curve over a total of thirty-six experiments cannot be fitted adequately to a power exponential and this experiment was removed from subsequent analyses. Gastric emptying of WB diet was significantly faster than that of S and BP diets (Fig. 1). Similarly, BP diet was emptied significantly slower than S and WB diets. The same hierarchy was also observed for half-emptying times (Table 3). A lag phase cannot be identified and radioactivity can be found distal to the stomach immediately after the end of the meal ingestion. Surprisingly, the overall shape of the emptying curve, indicated by β value, was not significantly different for the three test meals. A clear mid-gastric band, e.g. a transverse band of reduced isotopic activity separating proximal and distal stomach, was observed for BP diet only (Fig. 2). This mid-gastric band was clearly shown during the first 60 min after meal ingestion.

Proximal stomach emptying

Proximal stomach retention of the test meals followed the same pattern as that found in the whole stomach, i.e. WB

Table 2. Viscosity of the test meals and of the gastric contents 30 min after the ingestion of the different test meals*
(Mean values with standard errors of the means for five measurements for each meal in four animals)

	S diet		WB diet		BP diet	
	Mean	SEM	Mean	SEM	Mean	SEM
Meal viscosity (Pa·s)	105·0	6·1^{a}	104·0	2·2^{a}	100·0	3·7^{a}
Gastric contents viscosity (Pa·s)	0·26	0·03^{b}	0·30	0·02^{b}	0·52	0·02^{c}

S, starch-enriched; WB, wheat bran-enriched; BP, sugar beet pulp-enriched.
^{a,b,c} Mean values within a row with unlike superscript letters were significantly different (P < 0·05).
* For details of the composition of the diets see Table 1.

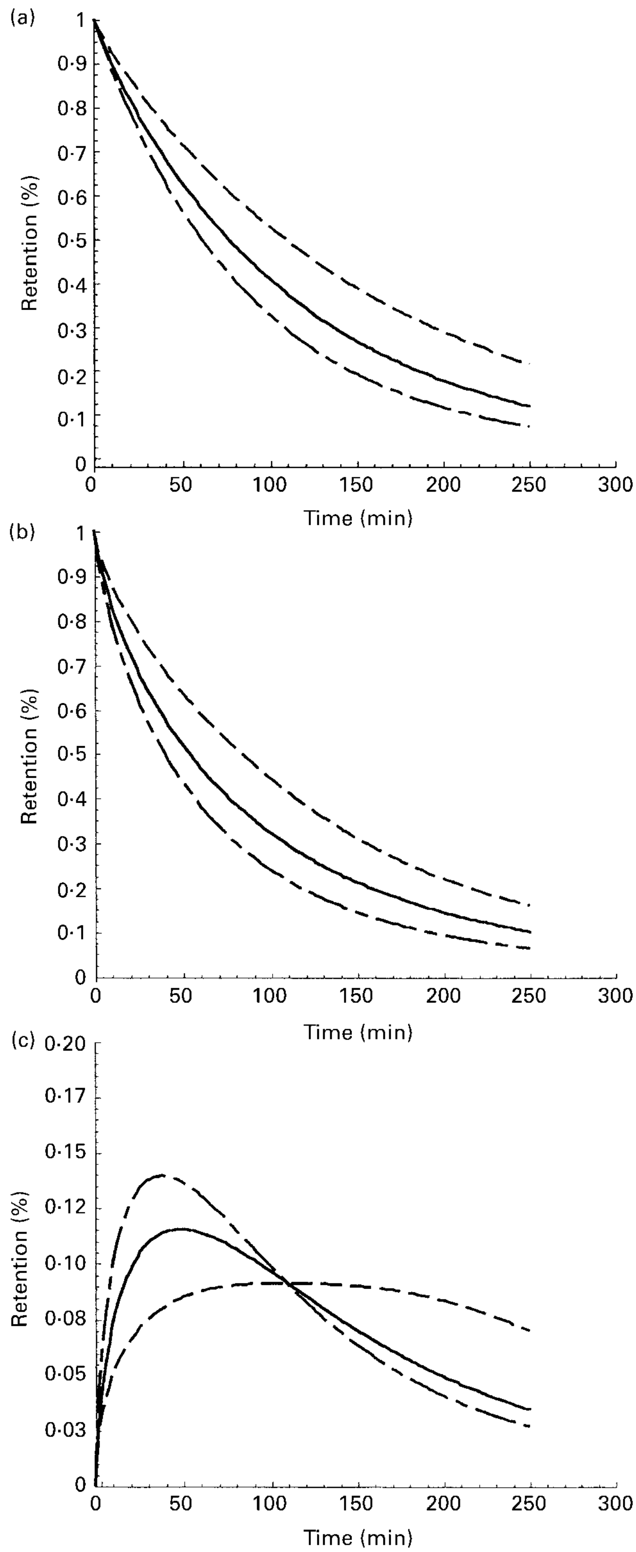

Fig. 1. Emptying rate from (a) the total, (b) proximal and (c) distal stomach after the ingestion of 4·25 MJ wheat bran- (- – -), sugar beet pulp- (—) and starch-enriched (– –) diets. For details of the diets and procedures see Table 1 and p. 244. Total and proximal stomach emptied in a power-exponential manner whereas a filling period followed by an emptying phase was observed at the distal stomach. No lag phase was noticed irrespective of the meal type. The wheat bran-enriched diet emptied faster than starch and sugar beet pulp-enriched diets despite a larger amount of dietary fibre present in the wheat bran- than starch-enriched diet.

Table 3. Half-emptying time of S, WB and BP diets in the total and proximal stomach*

(Mean values with standard errors of the means for three repeated measurements on four different animals)

	S diet		WB diet		BP diet	
	Mean	SEM	Mean	SEM	Mean	SEM
Total stomach						
$t_{1/2}$ (min)	78·4	5·68[a]	62·8	10·01[b]	111·6	10·82[c]
β	0·93	0·053	0·93	0·047	0·92	0·064
Proximal stomach						
$t_{1/2}$ (min)	53·6	5·55[a]	39·6	7·03[b]	81·6	5·23[c]
β	0·78	0·049	0·77	0·039	0·86	0·049

S, starch-enriched; WB, wheat bran-enriched; BP, sugar beet pulp-enriched.
[a,b,c] Mean values within a row with unlike superscript letters were significantly different ($P < 0·05$).
* For details of the composition of the diets see Table 1. Data for the distal stomach are not represented because the emptying curve cannot be fitted to a power exponential function for all diets.

diet emptied the fastest and BP diet emptied the slowest. Nevertheless, proximal stomach retention at half-emptying time was less for WB diet than for BP diet (63 % *v.* 73 %). This is in accordance with a significantly lower steepness of the emptying curve for BP compared with S and WB diets (Fig. 1). For S and WB diets, the emptying curve for the proximal stomach was approximately parallel to that of the proximal stomach.

Distal stomach emptying

The amount of the meal in the distal stomach followed a bi-exponential function for all diets. The amount of the meal in the distal stomach at 40 min was greater for WB diet compared with S and BP diets while the percentage remaining at 150 min was greater for BP and less for S diets. For BP diet only, the percentage radioactivity present in the distal stomach was almost constant from 58 (SEM 12·3) to 189 (SEM 15·0) min after the meal. Afterwards, the amount of radioactivity decreased rapidly so that half-emptying time of the distal stomach was 380 (SEM 25·4) min (compared with 144 (SEM 5·6) and 191 (SEM 6·0) min for WB and S diets respectively). In all studies involving BP diet, there was evidence of retrograde movement of radioactivity from the distal to the proximal stomach with a rise in proximal stomach counts associated with a fall in the distal stomach (Fig. 3). These events were observed between 40 and 90 min after the ingestion of the meal. Their number varied between animals but not within the same subject ranging from one to four backflow episodes for the duration of the imaging period.

Discussion

Using γ-scintigraphy imaging, the recognised gold standard for gastric emptying measurement, we have demonstrated that the amount of total dietary fibre in the diet, unlike the nature of the fibre, was not critical for emptying rate of the solids. S diet containing 63·8 g total dietary fibre/kg emptied slower than WB diet that contained 207·1 g total dietary fibre/kg. Furthermore, solid emptying rate was not related to meal viscosity since the medium-viscous meal (WB diet) emptied faster than low-viscous meal (S diet).

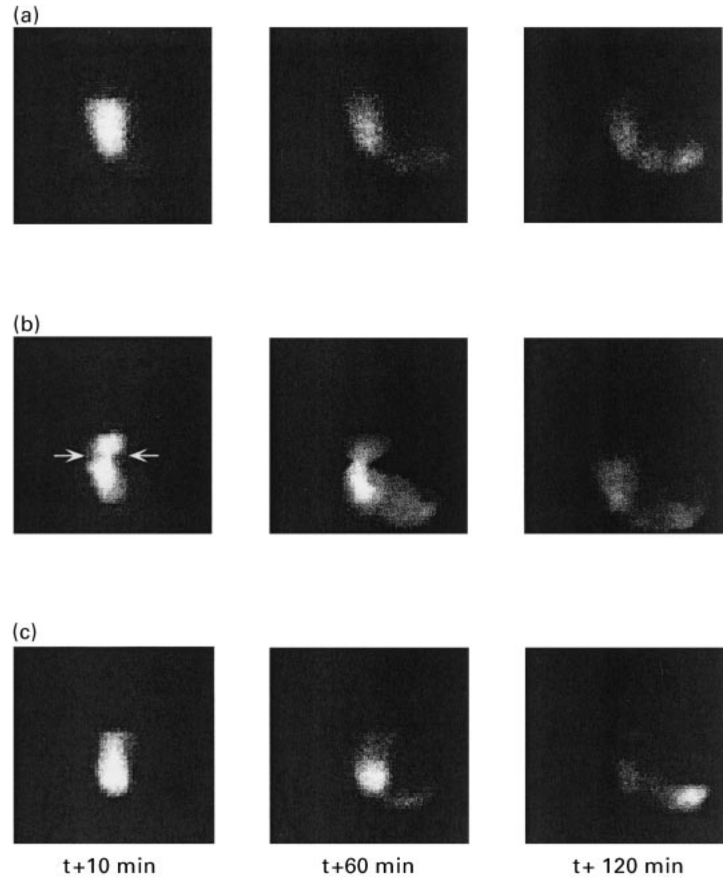

Fig. 2. Scintiphotographs showing the distribution of (a) wheat bran-, (b) sugar beet pulp- and (c) starch-enriched meals in one subject at 10, 60 and 120 min after meal ingestion. For details of the diets and procedures see Table 1 and p. 344. At 10 and 60 min, there was evidence of a mid-gastric band for sugar beet pulp-enriched diet only (→←). Note that the whole stomach is outlined for an extended period of time (up to 60 min) for sugar beet pulp-enriched diet.

Soluble sources of dietary fibre have been shown to delay absorption of glucose, an effect thought to be mediated through a reduced gastric emptying rate of liquids and a diminished intestinal glucose absorption. However, the effect of soluble dietary fibre on solid emptying was ambiguous (Rainbird & Low, 1986*b*; Cherbut *et al.* 1990; Johansen *et al.* 1996) mainly because of the difficulties in evaluating non-invasively gastric emptying of the solid phase in conscious animals (Malbert *et al.* 1997). Our present work demonstrates that a significant increase in gastric contents viscosity (BP diet) resulted in a marked decrease in overall gastric emptying of solids. As a first approximation, transpyloric flow relates to the Poiseuille law describing the relationship between pressure gradient across the pylorus, pyloric diameter and the flow of viscous contents (Meyer *et al.* 1986; Malbert & Ruckebusch, 1991). Assuming that the pressure gradient and the pyloric diameter remained unchanged, the doubling in viscosity between S and BP diets (0·52 *v.* 0·26 Pa·s) will theoretically result in a doubling in half-emptying time, a feature confirmed by experimental data (111 *v.* 78 min). Nevertheless, as already suggested (Johansen *et al.* 1996), the viscosity relevant to gastric emptying was that of the gastric contents and not that of the meal itself. Indeed, the viscosity of BP, WB and S diets before ingestion do not differ significantly, a situation that was modified within the stomach probably in relation to salivary and gastric secretions.

Meal volume is known as a major factor controlling gastric emptying (Hunt & Stubbs, 1975; Moran *et al.* 1999). However, the differences in gastric half-emptying time between S, WB and BP meals were unlikely to be related to different meals volumes. Indeed, the largest volume meal (BP) had the slowest emptying rate. In addition, S meal, which has the smallest volume, exhibited an intermediate half-emptying time compared with BP and WB. Whereas meal volume was probably not involved in the differences in emptying, lipid concentration might be important. Indeed, S, WB and BP meals differed in their lipids concentration and this variable is critical for gastric emptying time (Heddle *et al.* 1989; Latge *et al.* 1994; Maes *et al.* 1996). Nevertheless, the difference in lipid concentrations is unlikely to be involved in the differences between the rates of S, WB and BP diets emptying since WB diet, which supplied the largest amount of lipid, was also the fastest to empty.

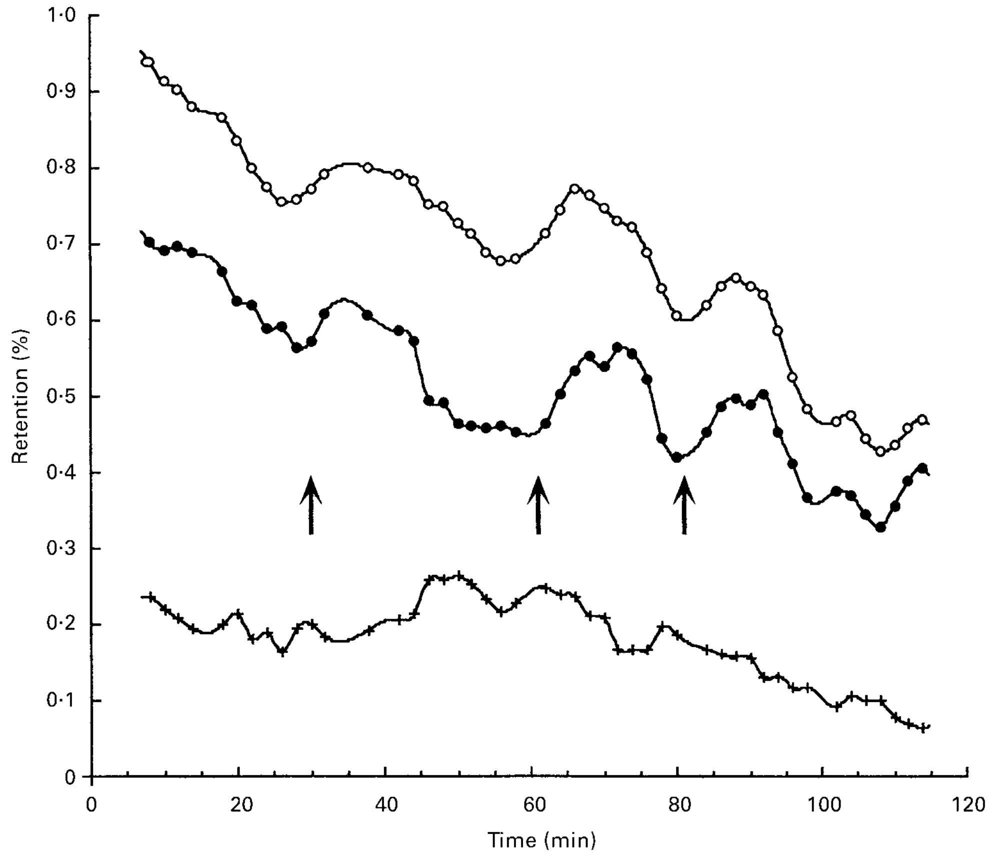

Fig. 3. Raw percentage retention of wheat bran-enriched diet in one subject. For details of the diets and procedures see Table 1 and p. 344. ○, Total stomach; ●, proximal stomach; +, distal stomach. Retrograde movements of the meal from distal to proximal stomach are demonstrated by the increase in proximal radioactivity. ↑, decrease in distal radioactivity.

This is, to our knowledge, the first study evaluating gastric emptying rate and gastric distribution of a solid energy-containing meal in conscious pigs using γ-scintigraphic imaging. The anatomical location of the porcine stomach, lying from left to right flank, makes depth correction an absolute requirement while using lateral imaging of the stomach. Alternatively, lateral imaging of the stomach is superior compared to dorso-ventral projection since minute motion of the partially restrained pig relative to the γ-camera head is far less. Nevertheless, attenuation errors are likely to occur with a single-head camera imaging. It is impossible to evaluate the magnitude of the error induced by our method since all available methods capable of monitoring emptying of a solid meal in conscious pigs have not, by far, the temporal resolution of γ-scintigraphy. Nevertheless, based on studies of human subjects (Collins *et al.* 1983), the correction method applied, while not affecting the temporal resolution of the imaging, suppressed day-to-day variations in gastric emptying within individual subjects while preserving inter-individual and inter-treatments variations. Furthermore, the overall gastric emptying can be adequately fitted to a power exponential function, unlike other studies performed in pigs (Gregory *et al.* 1990; Johansen *et al.* 1996) but in accordance with most of the studies performed earlier in almost all mammals (Heading *et al.* 1976; Hinder & Kelly, 1977; Theodorakis, 1980; Dubois, 1982; Elashoff *et al.* 1982; Hornof *et al.* 1989). The possibility of an incorrect binding between ^{99m}Tc and the meal was an important issue since previous studies have reported dissociation up to 50 % of the radioactive label into the liquid phase of the gastric contents using ^{99m}Tc alone (Sagar *et al.* 1983; Houghton *et al.* 1989). This poor result has made the ‘Mayo clinic method’ using ^{131}I an interesting but complex labelling method for cellulose fibres (Malagelade *et al.* 1980). Labelling fibrous test meals using ^{99m}Tc colloid was proven to be a fast and efficient method. Indeed, *in vitro* ^{99m}Tc release from the meal into the liquid phase was only 5 %. Nevertheless, it is probable that the labelling performed with our present method is not limited to the fibre component of the meal but involved also the other components of the meal, mainly the protein fraction.

The faster emptying rate of WB compared with S diet is a surprising result since the viscosity of WB is slightly greater, yet not significantly so, than S gastric contents. It is impossible, based on our results, to understand the origin of such discrepancy since the intragastric distribution for both diets is almost identical. However, the possibility that the thermal processing of WB meal required for ^{99m}Tc to bind with the diet may have modified the physical characteristics of the fibre cannot be excluded. Nevertheless, this was unlikely since the temperature required to break starch–H bonds is greater than 50°C, i.e. a temperature greater than that used during our labelling process (Champ & Colona, 1993).

Scintigraphic imaging of the stomach allows identification of the proximal and distal parts of the stomach and measurements of proximal *v.* distal stomach filling. Three differences relevant to intragastric distribution of the meal can be identified during the process of emptying of BP diet compared with S and WB diets. First, there was a well-defined mid-gastric band that has been suggested to contribute to retention of the meal in the proximal stomach (Moore *et al.* 1986; Edelbroek *et al.* 1992). Second, there were retrograde movements of BP diet from the distal into the proximal stomach. The time of occurrence of such intragastric reflux episodes is consistent with that already mentioned for slow-emptying meals such as those containing oil (Houghton *et al.* 1990; Horowitz *et al.* 1993). The increased pyloric resistance observed while the viscosity of the digesta was increased (Keinke *et al.* 1987) might be one of the causative factors for such backflow. Third, for BP diet only, the amount of radioactivity in the distal stomach remained almost constant during most of the emptying phase. This indicates that the amount of digesta leaving and entering the distal stomach is identical. Whereas the underlying viscoelastic mechanisms responsible for this constant antral filling were complex is beyond doubt, nonetheless a reduced antral motor activity already described with high viscous meals (Ehrlein *et al.* 1987; Keinke *et al.* 1987) might be one important factor. Furthermore, a similar accumulation of fibre meal in the distal part of the stomach has been already observed in human subjects (Mcintyre *et al.* 1997).

The greater retention in the proximal stomach of BP diet compared with S and WB diets must also be considered outside the scope of gastric emptying *per se* and also in relation to vagal mechanoreceptors activation controlling short-term food intake. Several lines of evidence have suggested, in various mammalian species, a short-term control of food intake related to the arrival and storage of the meal in the proximal part of the stomach (Wirth & McHugh, 1983; Phillips & Powley, 1996). Recently, our group has demonstrated a reduction in voluntary food intake in conscious pigs during mild isobaric distension of the proximal stomach while receptive relaxation was artificially suppressed (Lepionka *et al.* 1997). Since BP diet stayed longer in the proximal stomach, it is likely that the amount of nervous afferent information relevant to satiety was greater in this situation compared with WB or S diets. This is probably one of the mechanisms explaining the drastic reduction of food intake in adult sows fed with BP (Bourns *et al.* 1995).

In conclusion, meal viscosity alone is not the only factor controlling gastric emptying rate of solids. Furthermore, gastric emptying is not only directly related to gastric digesta viscosity but depends also on dietary fibre type. The unique capability of γ-scintigraphy to evaluate non-invasively proximal gastric filling might be essential to estimate the satiety-related effects of dietary fibre.

Acknowledgements

The authors wish to acknowledge the contribution of A. Chauvin and G. Reuzeau for the animal care before and during the experimental sessions.

References

Association of Official Analytical Chemists (1990) *Official Methods of Analysis*. 15th ed. Arlington, VA: AOAC.

Bourns F, Edwards SA & English PR (1995) Influence of fibrous feed ingredients on voluntary intake of dry sows. *Animal Feed Science and Technology* **54**, 303–313.

Brown NJ, Worlding J, Rumsey RD & Read NW (1988) The effect of guar gum on the distribution of a radiolabelled meal in the gastrointestinal tract of the rat. *British Journal of Nutrition* **59**, 223–231.

Champ M & Colona P (1993) Importance de l'endommagement de l'amidon dans les aliments pour animaux (Impact of starch in animal feed). *INRA Productions Animales* **6**, 185–198.

Cherbut C, Albina E, Champ M, Doublier JL & Lecannu G (1990) Action of guar gums on the viscosity of digestive contents and on the gastrointestinal motor function in pigs. *Digestion* **46**, 205–213.

Collins PJ, Horowitz M & Chatterton BE (1988) Proximal, distal and total stomach emptying of a digestible solid meal in normal subjects. *British Journal of Radiology* **61**, 12–18.

Collins PJ, Horowitz M, Cook DJ, Harding PE & Shearman DJC (1983) Gastric emptying in normal subjects. A reproducible technique using a single scintillation camera and computer system. *Gut* **24**, 1117–1125.

Cuche G & Malbert CH (1998) Relationships between cecoileal reflux and ileal motor patterns in conscious pigs. *American Journal of Physiology* **37**, G35–G41.

Di Lorenzo C, Williams CM, Hajnal F & Valenzuela JE (1988) Pectin delays gastric emptying and increases satiety in obese subjects. *Gastroenterology* **95**, 1211–1215.

Dubois A (1982) Methods for studying propulsion and retropulsion of the alimentary tract contents with special reference to man. In *Techniques in the Life Sciences*, vol. P202, pp. 1–18 [D-A Titchen, editor]. Sydney: Elsevier Medical.

Edelbroek M, Horowitz M, Dent J, Sun WM & Malbert CH (1994) Effects of duodenal distention on fasting and postprandial antropyloroduodenal motility in humans. *Gastroenterology* **106**, 583–592.

Edelbroek M, Horowitz M, Maddox A & Bellen J (1992) Gastric emptying and intragastric distribution of oil in the presence of a liquid or a solid meal. *Journal of Nuclear Medicine* **33**, 1283–1290.

Ehrlein HJ, Thoma G, Keinke O, Tsiamitas C & Schumpelick V (1987) Effects of nutrients on gastrointestinal motility and gastric emptying after distal gastrectomy with Roux-Y gastrojejunostomy in dogs. *Digestive Diseases and Sciences* **32**, 538–546.

Elashoff JD, Reedy TJ & Meyer JH (1982) Analysis of gastric emptying data. *Gastroenterology* **83**, 1306–1312.

Gregory P, Mcfadyen M & Rayner DV (1990) Pattern of gastric emptying in the pig-relation to feeding. *British Journal of Nutrition* **64**, 45–58.

Haber GB, Heaton KW, Murphy D & Burroughs LF (1977) Depletion and disruption of dietary fibre. Effects on satiety, plasma-glucose, and serum-insulin. *Lancet* **2**, 679–682.

Heading RC, Tothill P, McLoughlin GP & Shearman DJC (1976) Gastric emptying rate measurement in man: A double isotope scanning technique for simultaneous study of liquid and solid components of a meal. *Gastroenterology* **71**, 45–50.

Heddle R, Collins PJ, Dent J, Horowitz M, Read NW, Chatterton B & Houghton LA (1989) Motor mechanisms associated with slowing of the gastric emptying of a solid meal by an intraduodenal lipid infusion. *Journal of Gastroenterology and Hepatology* **4**, 437–447.

Hinder RA & Kelly KA (1977) Canine gastric emptying of solids and liquids. *American Journal of Physiology* **233**, E335–E340.

Hornof WJ, Koblik PD, Strombeck DR, Morgan JP & Hansen G (1989) Scintigraphic evaluation of solid-phase gastric emptying in the dog. *Veterinary Radiology* **30**, 242–248.

Horowitz M, Jones K, Edelbroek MAL, Smout AJPM & Read NW (1993) The effect of posture on gastric emptying and intragastric distribution of oil and aqueous meal components and appetite. *Gastroenterology* **105**, 382–390.

Houghton AD, Lazarus C, Liepins P, Mason R & Clarke S (1989) Technetium-labelled bran to measure solid gastric emptying (letter). *Nuclear Medicine Communications* **10**, 486.

Houghton L, Mangnall Y & Read NW (1990) Effect of incorporating fat into a liquid test meal on the relation between intragastric distribution and gastric emptying in human volunteers. *Gut* **31**, 1226–1229.

Hunt JN & Stubbs DF (1975) The volume and energy content of meals as determinants of gastric emptying. *Journal of Physiology (London)* **245**, 209–225.

Johansen HN, Knudsen KEB, Sandstrom B & Skjoth F (1996) Effects of varying content of soluble dietary fibre from wheat flour and oat milling fractions on gastric emptying in pigs. *British Journal of Nutrition* **75**, 339–351.

Keinke O, Ehrlein HJ & Wulschke W (1987) Mechanical factors regulating gastric emptying examined by the effects of exogenous cholecystokinin and secretin on canine gastroduodenal motility. *Canadian Journal of Physiology and Pharmacology* **5**, 287–292.

Latge C, Thouvenot P & Kedzierewicz F (1994) The influence of a lipid loading on gastric emptying and glycemia. *American Journal of Clinical Nutrition* **59**, (Suppl. 3), S782.

Lawrence AB & Terlouw EM (1993) A review of behavioral factors involved in the development and continued performance of stereotypic behaviors in pigs. *Journal of Animal Science* **71**, 2815–2825.

Lepionka L, Malbert CH & Laplace JP (1997) Proximal gastric distension modifies ingestion rate in pigs. *Reproduction, Nutrition and Development* **34**, 449–457.

Mcintyre A, Vincent RM, Perkins AC & Spiller RC (1997) Effect of bran, ispaghula, and inert plastic particles on gastric emptying and small bowel transit in humans: the role of physical factors. *Gut* **40**, 223–227.

Madsen JL & Jensen M (1989) Gastrointestinal transit of technetium-99m-labeled cellulose fiber and indium-111-labeled plastic particles. *Journal of Nuclear Medicine* **30**, 402–406.

Maes BD, Ghoos YF, Geypens BJ, Hiele MI & Rutgeerts PJ (1996) Relation between gastric emptying rate and rate of intraluminal lipolysis. *Gut* **38**, 23–27.

Malagelada JR, Carter SE, Brown ML & Carlson GL (1980) Radiolabeled fiber: a physiologic marker for gastric emptying and intestinal transit of solids. *Digestive Diseases & Sciences* **25**, 81–87.

Malbert CH, Mathis C, Bobillier E, Laplace JP & Horowitz M (1997) Measurement of gastric emptying by intragastric gamma scintigraphy. *Neurogastroenterology and Motility* **9**, 157–165.

Malbert CH & Ruckebusch Y (1991) Relationships between pressure and flow across the gastroduodenal junction in dogs. *American Journal of Physiology* **260**, G653–G657.

Mei N (1986) Rôle du système nerveux autonome dans la régulation du transit, de l'absorption et du stockage des nutriments (Role of the autonomic nervous system in transit, absorption and food storage regulation). *Reproduction Nutrition and Development* **26**, 1151–1162.

Meyer JH, Gu Y, Elashoff J, Reedy T, Dressman J & Amidon G (1986) Effects of viscosity and fluid outflow on postcibal gastric emptying of solids. *American Journal of Physiology* **250**, G161–G164.

Miranda PM & Horwitz DL (1978) High-fiber diets in the treatment of diabetes mellitus. *Annals of Internal Medicine* **88**, 482–486.

Moore JG, Dubois A, Christian PE, Elgin D & Alazraki N (1986) Evidence for a midgastric transverse band in humans. *Gastroenterology* **91**, 540–545.

Moran TH, Wirth JB, Schwartz GJ & McHugh PR (1999) Interactions between gastric volume and duodenal nutrients in the control of liquid gastric emptying. *American Journal of Physiology* **45**, R997–R1002.

Morgan L, Tredger J, Wright J & Marks V (1990) The effect of soluble-fibre and insoluble-fibre supplementation on post-prandial glucose tolerance, insulin and gastric inhibitory polypeptide secretion in healthy subjects. *British Journal of Nutrition* **64**, 103–110.

Motulsky HJ (1999) *Analyzing data with GraphPad Prism*. San Diego, CA: GraphPad Software Inc.

Phillips RJ & Powley TL (1996) Gastric volume rather than nutrient content inhibits food intake. *American Journal of Physiology* **40**, R766–R779.

Potkins ZV & Lawrence TLJ (1988) Studies on the effects of composition and physical form of the diet on gastric abnormalities and nutrient utilization in the growing pig. *Animal Production* **38**, 534.

Prosky L, Asp NG, Furda I, Schweizer T & De Vries JW (1988) Determination of insoluble, soluble and total dietary fiber in foods and food products. *Association of Official Analytical Chemists' Journal* **71**, 1017–1023.

Rainbird AL & Low AG (1986*a*) Effect of guar gum on gastric emptying in growing pigs. *British Journal of Nutrition* **55**, 87–98.

Rainbird AL & Low AG (1986*b*) Effect of various types of dietary fibre on gastric emptying in growing pigs. *British Journal of Nutrition* **55**, 111–121.

Ramonet Y, Meunier-Salaün MC & Dourmad JY (1999) High fibre diets in pregnant sows: digestive utilization and effects on the behavior of the animals. *Journal of Animal Science* **77**, 591–599.

Sagar S, Grime JS, Little W, Patten M, Gulliford P, Critchley M, Bennett R & Shields R (1983) Technetium-99m labelled bran: a new agent for measuring gastric emptying. *Clinical Radiology* **34**, 275–278.

Salminen S, Bouley C, Boutronruault MC, Cummings JH, Franck A, Gibson GR, Isolauri E, Moreau MC, Roberfroid M & Rowland I (1998) Functional food science and gastrointestinal physiology and function. *British Journal of Nutrition* (Suppl. 1), **80**, S147–S171.

Schade JH, Hoving J, Brouwers JR, Riedstra-van Gent, Zijlstra J & Dijkstra JP (1991) Technetium-99m carboxymethylcellulose: a newly developed fibre marker for gastric emptying studies. *European Journal of Nuclear Medicine* **18**, 380–384.

Theodorakis MC (1980) External scintigraphy in measuring rate of emptying in beagles. *American Journal of Physiology* **239**, G39–G43.

Van Soest PJ, Robertson JB & Lewis BA (1991) Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583–3597.

Wirth JP & McHugh PR (1983) Gastric distension and short-term satiety in the rhesus monkey. *American Journal of Physiology* **245**, R174–R180.