

## Digestion of starch and glycaemic response to mixed meals in pigs

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**Abstract** — The digestion in the proximal intestine of mixed meals (5 160 kJ) containing either native (NS) or pregelatinized (PS) maize starches ( $\approx$  200 g), and the postprandial glycaemic responses they induced were compared in pigs. For both meals,  $\approx$  25 % of the ingested starch was assimilated above the duodenal cannula (positioned 75 cm beyond the pylorus). Larger amounts of starch were collected for NS than for PS during the first 30 min. The glycaemic responses, however, indicated a higher rate of glucose absorption for PS during the first 30 min, which could be explained by the higher susceptibility of PS to hydrolysis, as we observed *in vivo*. Indeed, malto-oligosaccharides (G1–G3) represented almost 80 % of the total  $\alpha$ -glucans collected at 150 min in the duodenum after the PS meal. At that time, after the NS meal, only 30 % of the  $\alpha$ -glucans were malto-oligosaccharides. Thus, even after a mixed meal, the starch digestion rate can alter the observed postprandial glycaemic response. © Inra/Elsevier, Paris.

**starch / bioavailability / glycaemic response / pigs**

**Résumé** — Digestion de l'amidon et réponse glycémique à des repas mixtes chez le porc. La digestion dans l'intestin proximal de repas mixtes (5 160 kJ) contenant de l'amidon de maïs ( $\approx$  200 g), natif (NS) ou pré-gélatinisé (PS), et les réponses métaboliques qu'ils induisent, ont été comparées chez le porc. Pour les deux repas,  $\approx$  25 % de la quantité d'amidon ingéré était assimilée en amont de la canule duodénale (placée 75 cm après le pylore). De plus grandes quantités d'amidon ont été recueillies pour NS que pour PS pendant les 30 min initiales de l'étude. Pourtant, la réponse glycémique indiquait une plus grande vitesse d'absorption pour PS pendant les 30 premières min, qui pourrait être expliquée par la plus grande sensibilité à l'hydrolyse de PS observée *in vivo*. En effet, les maltooligosaccharides (G1–G3) représentaient 80 % des  $\alpha$ -glucanes totaux collectés au niveau duodénal 150 min après le repas PS. À ce même moment, après le repas NS, seulement 30 % des  $\alpha$ -glucanes étaient des

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maltooligosaccharides. En conclusion, même après l'ingestion d'un repas complexe, la vitesse avec laquelle l'amidon est digéré peut modifier la réponse métabolique postprandiale observée. © Inra/Elsevier, Paris.

## **amidon / biodisponibilité / réponse glycémique / porcs**

### **1. INTRODUCTION**

Starch is a major component of a large variety of foodstuffs. Physical and chemical characteristics affect the rate of starch digestion. The absorption rate is often assessed by a postprandial increase in the peripheral blood glucose concentration. A slow absorption leads to a better control of postprandial hyperglycaemia [16, 33]. Moreover, it has been shown in rats that rapidly assimilated carbohydrates can be responsible, on a long-term basis, for insulin resistance [13] and increased glucose incorporation into adipose tissues [22]. The various effects of starchy foods on glucose absorption rates and subsequent metabolic responses are due to two principal parameters: the susceptibility of starch to enzymatic hydrolysis [3, 17] and the gastric emptying of the ingesta [25]. Although the role of the former has been emphasized in several works, less attention has been paid to it after the ingestion of a mixed meal. Coingestion of fat has been shown, however, to alter the concentration of blood glucose measured after the meal [6, 11]. Dietary proteins also stimulate pancreatic insulin secretion [30]. The main site involved in the assimilation process of starch is the upper part of the intestine [12]. Digestion is very efficient in the duodenum where pancreatic  $\alpha$ -amylase is secreted, and the high absorption capacities of the upper intestine have been shown in humans using intestinal perfusion techniques [24]. In pigs, it has been shown [20] that up to 70 % of an oral carbohydrate load could be assimilated in the duodenum.

The purpose of the present study was to examine how the digestive pattern of starch

in the proximal intestine (stomach and duodenum) of pigs could explain the peripheral metabolic responses to mixed meals.

The starch contained in the two experimental meals was either rapidly digestible (pregelatinized form) or slowly digestible (native form). The meals also differed in their consistency: pregelatinized starch had a higher water binding ability than native starch. Peripheral glucose and insulin responses to the meals were followed in a first group of animals, and the principal factors responsible for the rate of glucose absorption (the rate of starch transit, rate of hydrolysis, osmolality of the digestive contents and enzymatic activity) were studied in the proximal intestine of a second group of animals.

### **2. MATERIALS AND METHODS**

#### **2.1. Animals and surgery**

Ten female 'Large White' pigs (purchased at Inra, Saint-Gilles, France), weighing 40–45 kg at the time of the operation, were used for the study.

Four animals were fistulated in the external jugular vein [28]. This surgical procedure allows chronic blood sampling at the peripheral venous level.

Six other animals were fitted with a simple 'Y' cannula [32] of 8 mm in inner diameter, positioned 75 cm beyond the pylorus (at the end of the duodenum). The cannula was exteriorized through the body wall in the region of the right flank. After each operation, pigs were allowed to recover for 7 days and the experiment did not begin until the animals had returned to their normal dietary intake. Animals, kept at room temperature in individual cages, were fed twice a day (9.00 a.m. and 4.00 p.m.) with 500 g food

(dry matter). The amount of water given was equal to three times the intake of dry matter. Animal treatment was always in accordance with French legislation. The surgeon was duly accredited by the *Assistance Publique des Hôpitaux de Paris*.

## 2.2. Diets

### 2.2.1. Starches

The two purified maize starches were supplied by Roquette Industries (Lestrem, France). Starch was either native ('standard') (NS) or pregelatinized ('Pregeflo M') (PS).

When pregelatinized, starch undergoes a rapid hydrothermic treatment that leads to the loss of crystallinity of the starch granules, and increased accessibility of enzymes to starch. The susceptibility of starch to hydrolysis was greater for PS than NS, as measured by the method of Bornet et al. [2]. After 30 and 180 min of incubation with  $\alpha$ -amylase, the proportion of starch converted to alcohol-soluble malto-oligosaccharides was  $65 \pm 1$  and  $71 \pm 3$  % for PS ( $n = 2$ ) and only  $8 \pm 1$  % and  $22 \pm 1$  % for NS ( $n = 2$ ), respectively.

### 2.2.2. Pre-experimental and experimental diets (table I)

The pigs received fibre-free meals during the 2 days preceding the experiment, and a starch-free meal the evening before the experiment.

The experimental diet contained either NS (187 g) or PS (178 g), given to supply similar amounts of digestible carbohydrates ( $\approx 200$  g glucose equivalent), as determined by the method of Champ et al. [5].

Polyethylene glycol (M.W.: 4 000) was added to the test meal (20 g per meal) to allow an estimation of the efficiency of the collection of the digestive contents.

## 2.3. Experimental design

### 2.3.1. Postprandial metabolic variables

The two meals were administered on a separate day to each of the four 17-h-fasted pigs fitted with a jugular catheter, and the postprandial glycaemia and insulinaemia were measured over a 180-min period following the meal. For one of the pigs, each experiment was repeated once.

**Table I.** Composition of pre-experimental and experimental meals.

	Amount (g)		
	Fibre-free meal	Starch-free meal	Experimental meal
Maize starch <sup>a</sup> (as digestible glucose equivalent)			200
Instant potato	450		
Sugar	10.5	40	
Meat flour (55 % w/w proteins)	25	100	225
Milk powder (lactose-free)		50	
Milk powder (lipid-free)	50		
Maize oil	6.2	15	37.5
Lard	56	56	
Mineral and vitaminic supplements	16.5	16.5	
Pea hulls			1.7
Total amount (g)	615	275	464
Energy (kJ)	8 820	8 820	5 560

<sup>a</sup> Maize starch was supplied by Hoquette Industries (Lestrem, France); starch was either native ('standard' or pregelatinized ('Pregeflo M')<sup>®</sup>).

Five millilitres of blood were drawn at -15 and 0 min, and at 15, 30, 45, 60, 75, 90, 105, 120, 150 and 180 min after the meal ingestion and placed in ice-chilled heparinized tubes. Between each sampling time, the catheter was filled with heparinized saline at 500 UI·mL<sup>-1</sup> (Léo S.A., Saint-Quentin-Yvelines, France). The blood samples were immediately centrifuged at 4 °C (9 000 g, 10 min) and the plasma was kept at -20 °C until glucose and insulin were analysed.

### 2.3.2. Collection of intestinal digesta

The six animals ate each of the meals twice (generally within 5–10 min), making a total of four studies per pig, except for two pigs for which a study had to be interrupted. The cannula was rinsed initially with water heated to body temperature. Before beginning the experiment, a Foley probe (rubber balloon) inflated with 20 mL air was placed through the cannula beyond the site of collection, to prevent the loss of any digestive content. The 17-h-fasted animals were fed the experimental diet at 9.00 a.m. Thirty minutes after the beginning of the meal, an infusion of isotonic solution (Viandox; LMA, Dijon, France), composed essentially of water, salt, protein extracts and sugar was started at a rate of 3 mL·min<sup>-1</sup> beyond the occlusive balloon and lasted until the end of the experiment. The solution, diluted with water to reach a physiological osmolality of 320 mOsmol·kg<sup>-1</sup>, was used to simulate the appearance of the digesta beyond the sampling cannula. At the same time, the digesta were continuously collected in a chilled receptacle at 0 °C for a 600-min period. Every 30 min, the samples were weighed and frozen at -70 °C; an aliquot was removed and stored at -20 °C until the analysis of osmolality and  $\alpha$ -amylase activity. The samples were freeze-dried (40 °C, 24 h) before analysis.

Each 30-min sample was analysed for the determination of starch (as total  $\alpha$ -glucans residues).

For each experiment, 5 % of the dried sample was aliquoted. Aliquots were pooled to constitute a 'total pool' that was analysed for its PEG content. The recovery of PEG was used as an indice of the efficiency of the collection of digestive contents over a 600-min period. Collection was arbitrarily assumed as efficient and complete when PEG recovery was over 80 % of the ingested amount, and only the experiments for which this value was reached were taken for analysis. Further qualitative analyses (such as the oligosaccharide content,  $\alpha$ -amylase activity and osmo-

lality of the samples) were performed on six experiments (three pigs  $\times$  two meals) that were selected on the basis of the best PEG recovery.

## 2.4. Measurements

The rates of hydrolysis of the two substrates were estimated by measuring the appearance of alcohol-soluble (80 % ethanol) oligosaccharides and dextrans produced during *in vitro*  $\alpha$ -amylolysis of starch in a buffered medium [2].

Plasma samples were analysed for glucose and for insulin using a Beckman autoanalyser II (Beckman Instruments, Fullerton, CA) and a radioimmunoassay (ORIS, Gif-sur-Yvette, France), respectively.

Polyethylene glycol was analysed in the samples by the turbidimetric method of Hyden [15]. Briefly, sulphate ions and proteins, which confound the measurement of PEG, were discarded by the addition of barium chloride, barium hydroxyde and zinc sulphate (Merck, Darmstadt, Germany). After centrifugation, trichloroacetic acid (30 % v/v; Merck, Darmstadt, Germany) was added to the supernatant. The resultant turbidity is proportional to the concentration of PEG in the samples and can be analysed at 650 nm by absorbance spectrophotometry.

Total starch (total recovered  $\alpha$ -glucans) was quantified in the digesta, using a near-infrared spectroscopy analytical method [26]. This rapid and non-destructive technique was used with the biochemical method of Faisant et al. [10] as a reference.

Malto-oligosaccharides (glucose, maltose, maltotriose) coming from starch degradation were extracted from the samples. Three hundred milligrams of dry samples were suspended in 10 mL boiling ethanol (80°GL at room temperature) and centrifuged (twice). After centrifugation, supernatants were collected, then evaporated. The final residue was solubilized in water before it was injected in a Cartridge HPLC column (244 mm  $\times$  4 mm, type RP18, Merck, Darmstadt, Germany) according to the method of Quemener and Mercier [27]. The solvent (water, 20 °C) was eluted at a rate of 0.8 mL·min<sup>-1</sup>.

The osmolality of the digesta was analysed using a Roebbling automatic osmometer (Roebbling, Berlin, Germany).

Amylase activity was measured using a Phadebas amylase test (Pharmacia, Uppsala, Sweden). Briefly, the principle of this method involves the hydrolysis by  $\alpha$ -amylases of a water-insoluble

cross-linked starch polymer, to form water-soluble blue fragments. These fragments are detected by absorbance spectrophotometry. One unit of  $\alpha$ -amylase activity is defined as the quantity of enzyme that catalyses the hydrolysis of 1  $\mu$ mol of the glycosidic bond per min at 37 °C. In the present study, amylase activity was expressed in  $\mu$ kat/30 min.

### 2.5. Statistical analysis

Each value was expressed as a mean  $\pm$  sem. Two-way variance analysis was used to test the effects of animals and test meals on metabolic variables. The effects of meals and animals were tested on the fresh weight, dry matter and starch recoveries in the duodenal effluents. The mean value was determined for the experiments performed in duplicate on the same pig. All the analyses were performed with the Statgraphics 3.0 plus program (STSC Inc., Rockville, Maryland, USA).

## 3. RESULTS

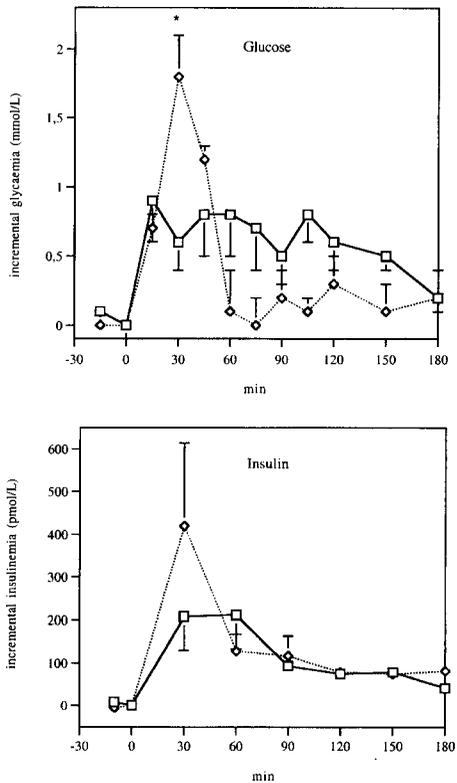
### 3.1. Plasma glucose and insulin responses to the meals

Plasma glucose concentrations after fasting were  $4.5 \pm 0.2$  mmol·L<sup>-1</sup> and  $4.4 \pm 0.2$  mmol·L<sup>-1</sup> for NS and PS, respectively. The maximal increment of glycaemia over the basal value was obtained at 15 min ( $0.9 \pm 0.3$  mmol·L<sup>-1</sup>) and 30 min ( $1.8 \pm 0.3$  mmol·L<sup>-1</sup>), respectively, for NS and PS ( $P < 0.05$ ) (figure 1). The postprandial area under the incremental glycaemia curve was not different for the two meals over a 180-min period, but was slightly higher for PS ( $P < 0.05$ ) during the first 30 min ( $38.0 \pm 4.3$  (mmol·L<sup>-1</sup>)  $\times$  min versus  $22.0 \pm 4.2$  (mmol·L<sup>-1</sup>)  $\times$  min). Plasma insulinaemia was  $67.1 \pm 24.1$  pmol·L<sup>-1</sup> and  $44.0 \pm 19.6$  pmol·L<sup>-1</sup> before the NS and PS meals, respectively (the values were not significantly different). Incremental insulin concentrations were maximal at 60 min for NS ( $211.3 \pm 78.2$  pmol·L<sup>-1</sup>) and 30 min for PS ( $419.5 \pm 194.6$  pmol·L<sup>-1</sup>). While an animal effect was found on the area under the incre-

mental insulinaemia curves ( $P < 0.05$ ), no statistical difference was found between the area under the curves or the peak insulin values for the two meals.

### 3.2. Recovery of digesta in the duodenal contents

Seven experiments were not considered in the calculations because the PEG recovery was under 80 % of the ingested quantity. The mean recoveries of PEG were then  $88.0 \pm 2.1$  % ( $n = 6$ ) after NS meals and  $89.0 \pm 2.0$  % ( $n = 4$ ) after PS meals. No difference was observed between the two meals for the total weight and dry matter weight of



**Figure 1.** Postprandial increment in plasma glucose and insulin concentrations after native starch ( $\square$ ) and pregelatinized starch ( $\diamond$ ) meals (means  $\pm$  sem,  $n = 5$ , four pigs; \*  $P < 0.05$ ).

digestive contents, but an animal effect was found ( $P < 0.05$ ). The mean recoveries of digesta over a 600-min period following the meals (on a fresh weight basis) were  $2\,768 \pm 316$  g ( $159 \pm 15$  % of the ingested amount) and  $3\,049 \pm 340$  g ( $171 \pm 18$  % of the ingested amount) after NS and PS meals, respectively. Dry matter recovery was  $358.1 \pm 26.6$  g ( $86.0 \pm 5.6$  % of the ingested amount) and  $378.2 \pm 22.9$  g ( $89.8 \pm 4.8$  % of the ingested amount) after NS and PS meals. The quantities of total digesta and dry matter recovered from the duodenal cannula were higher for NS than for PS during the first 30 min after the meal ( $P < 0.05$ ), then lower during the following hour (table II). The fraction of assimilated starch in the intestinal segment considered was  $26.8 \pm 4.3$  % for NS ( $n = 6$ ) and  $23.3 \pm 2.7$  % for PS ( $n = 4$ ). The total amount of assimilated starch over a 600-min period varied according to the animal studied ( $P < 0.05$ ). In the first 30 min, however, a higher amount of starch was collected for NS than for PS ( $P < 0.05$ ). More than 85 % of the masses

collected were recovered within the first 120 min and the collection of the digesta was nearly completed 300 min after the meal whatever the form of starch ingested (table II).

Qualitative analyses of the collected digesta were performed for the six experiments (three pigs  $\times$  two diets) that exhibited the best PEG recoveries ( $91.2 \pm 2.1$  and  $92.3 \pm 4.5$  % of the ingested amount for NS and PS, respectively). As shown in table III, the rates of starch hydrolysis, indicated by the appearance of malto-oligosaccharides (G1–G3) in the digesta, were close to those observed *in vitro*. The rate of hydrolysis seemed to be higher for PS; malto-oligosaccharides represented almost 80 % of the total  $\alpha$ -glucans collected at 150 min. At that time after the NS meal, only 30 % of the  $\alpha$ -glucans were malto-oligosaccharides. Malto-oligosaccharides (given as masses collected in the digesta) seemed to be present in larger amounts within the first 120 min after the PS meal (table III). A residual fraction of free glucose was present in the diges-

**Table II.** Amounts of digesta (g) collected by the jejunal cannula at different times after the two experimental meals (means  $\pm$  sem).

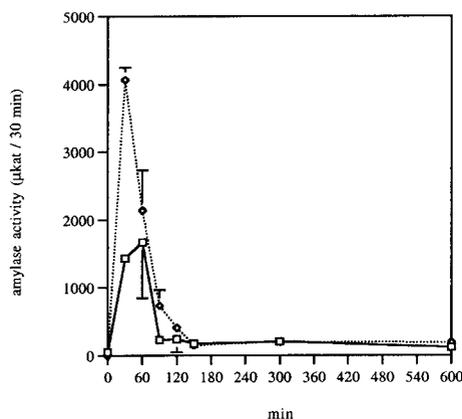
	Native starch meal			Pregelatinized starch meal		
	Total fresh weight	Dry matter	Starch	Total fresh weight	Dry matter	Starch
Ingested quantity (g)	1 734 $\pm$ 53	416 $\pm$ 13	179 $\pm$ 6	1 780 $\pm$ 38	421 $\pm$ 9	176 $\pm$ 4
Time (min)						
0	97 $\pm$ 34	4 $\pm$ 1	1 $\pm$ 0	111 $\pm$ 51	3 $\pm$ 2	0
30	1 244 $\pm$ 159 <sup>a</sup>	216 $\pm$ 39 <sup>a</sup>	87 $\pm$ 15 <sup>a</sup>	754 $\pm$ 89 <sup>b</sup>	121 $\pm$ 16 <sup>b</sup>	45 $\pm$ 6 <sup>b</sup>
60	464 $\pm$ 99 <sup>a</sup>	70 $\pm$ 19 <sup>a</sup>	28 $\pm$ 9 <sup>a</sup>	834 $\pm$ 99 <sup>b</sup>	143 $\pm$ 17 <sup>b</sup>	57 $\pm$ 7 <sup>b</sup>
90	154 $\pm$ 37 <sup>a</sup>	13 $\pm$ 4 <sup>a</sup>	4 $\pm$ 2 <sup>a</sup>	327 $\pm$ 41 <sup>b</sup>	43 $\pm$ 7 <sup>b</sup>	17 $\pm$ 3 <sup>b</sup>
120	109 $\pm$ 34	9 $\pm$ 3	2 $\pm$ 1	168 $\pm$ 26	15 $\pm$ 3	6 $\pm$ 1
150	79 $\pm$ 19	6 $\pm$ 2	2 $\pm$ 1	137 $\pm$ 44	10 $\pm$ 5	3 $\pm$ 2
180	130 $\pm$ 44	12 $\pm$ 6	3 $\pm$ 2	158 $\pm$ 51	9 $\pm$ 4	3 $\pm$ 2
210	86 $\pm$ 20	6 $\pm$ 3	1 $\pm$ 1	79 $\pm$ 36	5 $\pm$ 2	1 $\pm$ 1
240	52 $\pm$ 10	5 $\pm$ 3	1 $\pm$ 1	79 $\pm$ 20	6 $\pm$ 2	1 $\pm$ 1
270	74 $\pm$ 18	5 $\pm$ 2	1 $\pm$ 1	40 $\pm$ 15	2 $\pm$ 1	0
300	37 $\pm$ 11	2 $\pm$ 1	1 $\pm$ 0	32 $\pm$ 15	2 $\pm$ 1	0

Native starch,  $n = 6$ ; pregelatinized starch,  $n = 4$ . For a same parameter and for the same time, values with different superscripts denote significant differences between the two meals ( $P < 0.05$ ).

**Table III.** Oligosaccharides (G1–G3) collected in the jejunal digesta at different times after the two experimental meals (means  $\pm$  sem).

Time (min)	Oligosaccharides (g) (G1–G3)		Glucose (g)		% Oligosaccharides/total starch	
	NS	PS	NS	PS	NS	PS
0	0.1 $\pm$ 0.0	0	0.1 $\pm$ 0.0	0	0	0
30	6.8 $\pm$ 1.2	28.8 $\pm$ 5.3	1.0 $\pm$ 0.1	1.8 $\pm$ 0.2	7.2 $\pm$ 1.0	62.6 $\pm$ 2.3
60	2.9 $\pm$ 1.7	33.0 $\pm$ 5.5	0.6 $\pm$ 0.3	2.2 $\pm$ 0.4	9.6 $\pm$ 1.0	57.7 $\pm$ 3.3
90	0.4 $\pm$ 0.2	8.3 $\pm$ 1.8	0.2 $\pm$ 0.1	0.9 $\pm$ 0.2	11.3 $\pm$ 4.9	58.3 $\pm$ 3.0
120	0.6 $\pm$ 0.4	2.0 $\pm$ 0.8	0.3 $\pm$ 0.2	0.4 $\pm$ 0.1	15.5 $\pm$ 1.0	64.7 $\pm$ 6.0
150	0.5 $\pm$ 0.2	2.6 $\pm$ 2.3	0.3 $\pm$ 0.2	0.6 $\pm$ 0.5	32.4 $\pm$ 13.7	77.2 $\pm$ 13.4
300	0.1 $\pm$ 0.1	0.4 $\pm$ 0.3	0.1 $\pm$ 0.0	0.2 $\pm$ 0.2	45.6 $\pm$ 14.4	79.9 $\pm$ 4.9

NS, native starch; PS, pregelatinized starch;  $n = 3$ .



**Figure 2.** Amylase activity in the digestive contents after native starch meal ( $\square$ ) and pregelatinized starch meal ( $\diamond$ ) (means  $\pm$  sem,  $n = 3$ ).

tive contents after both meals. The amounts of free glucose collected were maximal at 30 min (1.0 g) and 60 min (2.2 g) for NS and PS meals, respectively.

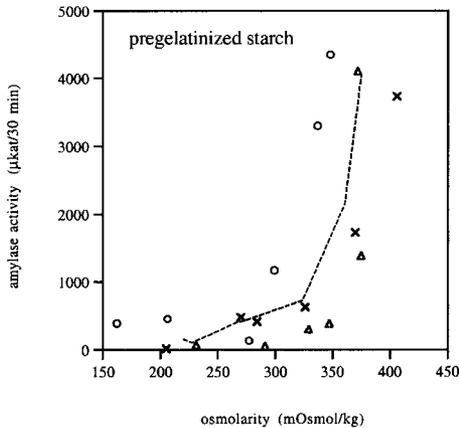
Mean osmolality ( $n = 3$ ) of the digesta over the study was  $258 \pm 11$  and  $274 \pm 12$  mOsmol $\cdot$ kg $^{-1}$  for NS and PS, respectively. Within the first 120 min, the mean osmolalities were  $332 \pm 20$  mOsmol $\cdot$ kg $^{-1}$  after the PS meal and  $223 \pm 46$  mOsmol $\cdot$ kg $^{-1}$  after the NS meal. For the PS load, the osmolality reached its maximal value of 375

$\pm 17$  mOsmol $\cdot$ kg $^{-1}$  after 30 min, while the osmolality of the digestive contents never exceeded  $320 \pm 18$  mOsmol $\cdot$ kg $^{-1}$  (after 180 min) for the NS meal.

The postprandial  $\alpha$ -amylase activities in the digestive contents (figure 2) increased after both experimental meals within the first 120 min, then returned to a basal level. For the PS meal, the amylase activity during the study was plotted against the osmolality of the digestive contents (figure 3). The higher enzymatic activities seemed to coincide with the higher osmolality levels of the digestive contents (350–400 mOsmol $\cdot$ kg $^{-1}$ ).

#### 4. DISCUSSION

Different plasma glucose responses were observed after the two experimental mixed meals, containing  $\approx 200$  g carbohydrate as either native or pregelatinized maize starch. The high increase in glycaemia during the first 30 min following the PS meal indicated an initial higher rate of glucose absorption. This can be explained by the difference in susceptibility to hydrolysis between the two starches chosen for the study. The area under the incremental glycaemia curve was not, however, different for the two meals over the postprandial 180-min period. The inges-



**Figure 3.** Amylase activity as a function of osmolality in the digestive contents of three pigs after the pregelatinized meal. The values for each pig are shown by symbols (×, ○, △). The mean curve is shown by a dotted line.

tion of starch in mixed meals probably attenuated the observed differences in the metabolic responses to the two meals. Flattened postprandial glucose curves have indeed been observed after coingestion of fat, although the nature of the lipids have been shown to influence postprandial plasma glucose rise [6, 11, 18]. Moreover, fat [6] and proteins [30] can enhance insulin secretion. Although maximal incremental insulinaemia seemed to be higher for PS than for NS, no statistical difference was calculated between the two meals owing to animal variability. However, maximal incremental insulinaemia was faster after the PS meal (30 min versus 60 min for NS).

Early glucose absorption was found to be more rapid for PS, but the glucose peak was obtained faster for the NS than for the PS meal (15 min versus 30 min). This must be the consequence of a shorter oro-duodenal transit time for NS. The masses of digesta (either total weight or dry matter weight) were, indeed, much higher for NS during the first 30 min following the meal. Moreover, 50 % of the ingested amount of NS was recovered in the intestinal effluents

during the first 30 min following the meal. The ingestion of starch in a mixed meal did not modify the results observed by Cuber and Laplace [8], who showed that a semi-purified native maize starch was emptied from the stomach rapidly at first, then more slowly. On the contrary, we found that only 25 % of the ingested PS was recovered in the digesta 30 min after the meal. The slower transit rate for PS probably resulted from the meal. Because of the high water binding capacity of PS [7], mixing the ingredients of the meal with water resulted in the formation of a gel. It has been shown that gastric emptying is delayed by increased consistency of the ingesta [14].

More than 80 % of the starch collected over the study period was recovered within the first 120 min, and recovery was nearly completed 300 min after both meals. About 25 % of the ingested starch was assimilated by the intestinal segment studied. This proportion is in accordance with the values found in previous studies for pigs weighing 50 kg [20, 21, 29]. Moreover, it shows that the major role of the proximal small intestine is in the assimilation process, especially when we consider that the studied segment only represented about 5 % of the small intestine. Although glucose absorption seemed to be faster after the PS meal, the proportion of assimilated starch was, however, the same after both meals. The similar values for starch assimilation may be explained by changes in the transit rates for the two meals. The transit rate for NS was high in the first 30 min, then slowly decreased. On the contrary, the initial rate of transit was low for the PS meal; after the first 30 min, gastric emptying may have been highly accelerated by the hydrolysis of starch to soluble malto-oligosaccharides. As glucose absorption is altered by the rate of nutrient transit [31], absorption in the studied segment may have decreased for PS and increased for NS after the first 30 min.

Whereas little total starch was recovered as malto-oligosaccharides (G1–G3) after

the NS meal, large amounts of malto-oligosaccharides were found within the first 60 min following the PS meal. The presence of glucose in the digesta may indicate that part of the glucose produced by the brush border oligosaccharidases was liberated in the duodenal lumen, and collected before it was absorbed; glucose from bacterial hydrolysis may have been used by micro-organisms for their own metabolism. The large content of glucose in the digesta after the PS meal may be due to saturation of the rate of absorption or hydrolysis of the malto-oligosaccharides. Indeed, it has been shown that hydrolysis by brush border oligosaccharidases may be the rate-limiting step in the assimilation process [19].

Within the first 120 min following the PS meal, the appearance of hydrolysis products in the digestive contents was paralleled by an increase in osmolality; osmolality has been shown to decrease the rate of gastric emptying [23], and to increase the rate of glucose absorption [4]. In the present study, we tried to relate the observed changes in duodenal osmolality after the PS meal to amylase activity. In the three pigs we studied, there seemed to be a critical area of osmolar levels (300–350 mOsmol·kg<sup>-1</sup>) above which amylase secretions were increased. Pancreatic secretions are controlled by a humoral system [1]. However, Dooley and Valenzuela [9] have shown that increasing the osmolality of the duodenal content from 300 to 370 or 520 mOsmol·kg<sup>-1</sup> can enhance pancreatic secretion via a cholinergic mechanism in humans. Specific humoral and neurally mediated processes that regulate absorption and pancreatic secretions may be associated with the fast appearance of starch hydrolysis products in the proximal intestine.

In the present study, in which starch was ingested in a mixed meal, the rate of starch digestion was found to have a predominant influence (greater than the rate of gastric emptying) on the early digestive mechanisms, and subsequent metabolic responses. The oro-duodenal transit rate was higher for

the native starch than for the pregelatinized starch. However, the native starch elicited a lower glycaemic response during the first 30 min of the study, indicating that the susceptibility to hydrolysis of starch is critical for the control of blood glucose rise after a meal.

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