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Original article

Effect of adding sugar beet fibre and wheat bran to a starch diet on the absorption kinetics of glucose, amino-nitrogen and volatile fatty acids in the pig

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Abstract – The purpose of this study with the pig was to analyse the influence of the type of dietary fibre on quantitative kinetics of the absorption of nutrients deriving from enzymatic digestion in the small intestine and that of volatile fatty acids (VFA) deriving from microbial digestion in the hindgut influenced by the length of adaptation to the diet. Two groups of four pigs were fitted with a device for measuring absorption by simultaneous analysis of the differences in the porto-arterial concentrations of nutrients and metabolites and of the portal blood flow rate. They received successively two diets containing fish- and heat-treated potato flour, balanced in vitamins and minerals, and only differing in the type of fibre added at the inclusion level of 10 %: wheat bran (S) or sugar beet fibre (P). Following an adaptation period of 30 d (C) or 5 d (A) to each of these diets, and after the last experimental meal of 800 g, the animals were subjected for 12 h to blood samplings every 30–60 min for the analysis of glucose, amino-nitrogen and volatile fatty acids (VFA) with a simultaneous recording of the portal blood flow-rate. The type of dietary fibre did not modify nutrient absorption (glucose and amino-nitrogen) but affected the amounts of VFA appearing in the portal blood. These amounts were higher ($P < 0.001$) after ingestion of the sugar beet fibre-rich diet (group PC+PA: 766 mmol/12 h) than after that of the wheat bran-rich diet (group SC+SA: 477 mmol/12 h). The proportion of acetic acid in the absorbed mixture rose (PC+PA 63.6 % versus SC+SA 58.5 %, $P < 0.01$) at the expense of propionic acid (PC+PA 27.4 % versus SC+SA 31.0 %, $P < 0.01$). Prolongation of the adaptation period from 5 to 30 d led to a decrease in the absorption of nutrients deriving from enzymatic digestion in the small intestine (glucose g/12 h : SA+PA 341.8 versus SC+PC 244.5, $P < 0.01$; amino-nitrogen g/12 h: SA+PA 29.4 versus SC+PC 21.0, $P < 0.001$) without any subsequent change in the absorption of the volatile fatty acids. © Inra/Elsevier, Paris

pig / type of fibre / wheat bran / sugar beet fibre / absorption / glucose / amino-nitrogen / volatile fatty acids

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Résumé – Influence de l'addition de pulpe de betterave ou de son de blé à un régime amylacé sur la cinétique d'absorption du glucose, de l'azote aminé et des acides gras volatiles chez le porc. L'étude réalisée visait à analyser chez le porc l'influence de la nature de la fibre alimentaire sur la cinétique quantitative de l'absorption des nutriments libérés par l'hydrolyse enzymatique dans l'intestin grêle et celle des acides gras volatils (AGV) produits dans le gros intestin et leurs variations en fonction de la durée d'accoutumance au régime. Dans ce but, deux groupes de quatre porcs munis chirurgicalement d'un dispositif permettant de mesurer l'absorption par analyse simultanée des différences de concentrations porto-artérielles des nutriments et métabolites et du débit sanguin dans la veine porte, ont reçu successivement deux régimes à base de farine de poisson et de farine de pomme de terre, bien équilibrés en vitamines et minéraux, ne différant que par la nature des fibres qui leur étaient ajoutées (à raison de 10 %) : son de blé (S) ou pulpe de betterave (P). Après une période d'accoutumance de 30 j (C) ou de 5 j (A) à chacun de ces régimes, se terminant par un repas expérimental de 800 g, les animaux étaient soumis pendant 12 h à des prises de sang espacées de 30 à 60 min en vue de l'analyse du glucose, de l'azote aminé et des AGV cependant qu'était enregistré le débit sanguin portal. Dans ces conditions, la nature de la fibre n'a pas modifié l'absorption des nutriments (glucose et azote aminé) mais a influé sur les quantités d'AGV apparaissant dans le sang portal. Celles-ci étaient plus élevées ($p < 0,001$) après ingestion des régimes riches en pulpe de betterave (groupe PC+PA : 766 mmol·12 h) qu'après celle des régimes riches en son de blé (groupe SC+SA : 477 mmol·12 h), la proportion d'acide acétique dans le mélange absorbé s'y élevant (PC+PA : 63,6 % vs SC+SA : 58,5 % ; $p < 0,01$) au détriment de l'acide propionique (PC+PA : 27,4 % vs SC+SA : 31,0 % ; $p < 0,01$). La prolongation de 5 à 30 j de la période d'accoutumance aux régimes s'est traduite par une diminution de l'absorption des nutriments provenant de la digestion enzymatique dans l'intestin grêle (glucose g/12 h : SC+PC 244,5 vs SA+PA 341,8 ; $p < 0,01$) (azote aminé g/12 h : SC+PC 21,0 vs SA+PA 29,4 ; $p < 0,001$) sans qu'il s'ensuive une modification de l'absorption des AGV. © Inra/Elsevier, Paris

porc / nature de la fibre / son de blé / pulpe de betterave / absorption / glucose / azote aminé / acides gras volatils

1. INTRODUCTION

The numerous effects of dietary fibres on the body have long been established in epidemiological, clinical and experimental studies. Hence, epidemiological studies have suggested that the dietary fibre-depleted diet consumed by Western populations is associated with a high incidence of colorectal cancers [5], constipation and colon diverticulosis [4, 6]. Clinical studies have shown that fibre-rich diets lead to a decrease in cholesterolaemia and an increase in glycaemia [1, 15, 16, 35]. Experimental studies have shown that dietary fibres play a role at each stage of nutrient digestion and absorption [38].

The present trend of offering fibre-enriched diets to the human consumer is therefore easy to understand. However, before using such diets, their effect on the physiology of digestion and metabolism should be evaluated by determining the physicochemical action of the fibres, and identifying their metabolic products as well as their influence on the overall metabolism. It is known that the fibres are degraded by the microflora in the large intestine and lead to production of volatile fatty acids (VFA) that provide energy and metabolic substrates for the host. In humans, only a few data are available because the production and absorption sites of VFA cannot be reached. Therefore, such studies require the use of an animal model such as the pig in which the

porto-arterial differences in the concentration of nutrients can be measured by means of surgical methods (chronical fistulations) [22, 26]. Moreover, the pig seems to be the best-adapted animal after the primate for studying the digestion of fibres and its consequences on metabolism since its diet, the retention time and the profile of VFA in the large intestine are quite similar to those found in humans [10].

The aim of this study was to compare the effects of two dietary fibres, i.e. sugar beet fibre and wheat bran fed to conscious pigs on the quantitative absorption kinetics of glucose and amino-nitrogen released in the small intestine as well as on the VFA production in the large intestine and their respective variations according to the length of the period of adaptation.

2. MATERIALS AND METHODS

Eight castrated male pigs of the Large White breed from the Inra experimental herd (National institute for agricultural research, La Minière, France) (mean initial weight: 64.1 ± 5.2 kg) were divided at random into two groups of four. They were placed in individual cages adaptable to the size of the animal. Two daily meals of 800 g each, i.e. 720 g dry matter (DM) were given at 0900 and 1700 hours. Water was available ad libitum. The animals of both groups were fed semi-synthetic diets based on heat-treated potato starch and fish meal and well-balanced in minerals and vitamins (*table I*). Only the type of dietary fibre that was included at a level of 10 %, was different in the two groups, i.e. diet P (for 'pulpe' in French) contained sugar beet fibre (dietary fibre content: 87.5 % of fresh matter FM) and diet S (for 'son' in French) contained wheat bran (dietary fibre content: 48.9 % of FM). These diets were successively given to both groups of animals according to different serial orders and length of feeding phases (*figure 1*). One of the groups received successively diet S for 30 d (phase 1, with adaptation), then diet P for 5 d (phase 2, without adaptation) and finally diet S for 5 d (phase 3, without adaptation). The other group received diet P first for 30 d (phase 1), diet S for 5 d (phase 2) and diet P for 5 d (phase 3). Between each experimental diet, a standard diet containing 10 % purified cellulose was given for 4 d (interphases A and B)

Table I. Diet composition (g/100g).

	S	P	Standard
Potato flour	36.8	44.6	46
Fish meal	23	23	23
Lard	10	10	10
Wheat bran	19.2	—	—
Sugar beet fibre	—	11.4	—
Purified cellulose	—	—	10
Sucrose	5	5	5
Maize oil	4	4	4
Mineral mixture[a]	1.5	1.5	1.5
Vitamin mixture[a]	0.5	0.5	0.5
Nutritional characteristics			
DM[b] %	90.7	91.0	91.9
N % of DM	3.40	3.08	2.79
Cellulose (AOAC)%DM	11.15	11.94	11.88
Gross energy (kcal/kg of DM)	5270	5140	5110

[a] According to Henry and Rérat [12]; [b]DM, dry matter.

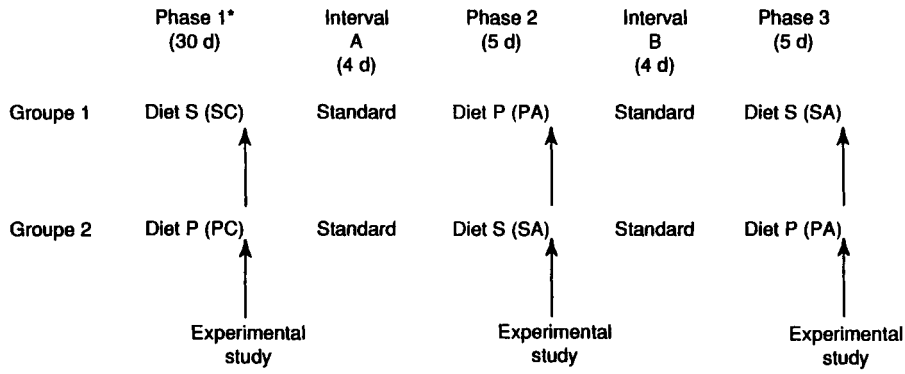

Figure 1. Experimental design. S, son (in French) = wheat bran; P, pulpe (in French) = sugar beet fibre; C, chronic (long adaptation); A, acute (short adaptation).

(*table I*). For studying the kinetics of the appearance of nutrients in the portal vein [26] an electromagnetic flowmeter probe around the portal vein and two catheters, one placed in the portal vein [2] and the other one in the carotid artery [28] were set up under general anaesthesia on day 21 of the first phase. After having progressively recovered a normal appetite (1600 g/d in two meals) the pigs were submitted to a series of blood samplings for 2 d after the experimental meals being offered following a fasting period longer than the digestion of the former meal in the small gut (more than 16 h; [23]). The blood samplings performed the first day aimed at evaluating the VFA concentration in the portal and arterial blood. The first sampling (10 mL) was performed after a 16-h fast and 10 min before the experimental meal (720 g dry matter DM) which was supplied at 0900 hours and before a series of samplings of the same volume carried out every hour during the 12-h postprandial period. After a 24-h fast, a second meal (720 g DM) was supplied at 0900 hours on the second day and blood samplings (5 mL each) for measuring the concentrations in glucose and amino-nitrogen were performed 10 min before the meal, during the meal and then every 30 min during the first 6 h of the postprandial period and every hour during the following 6 h. Haematocrit values were recorded every 2 h. Simultaneously, during these 2 d, the portal blood flow rate was measured continuously using an electromagnetic flowmeter probe CVI 3760 (Cardiovascular instrument Ltd, UK). The same samplings and the same flow measurements were carried out during the last 2 d of the short phases 2 and 3 based on experimental meals without any period of adaptation.

The blood samples were analysed for amino-nitrogen [19], glucose (glucoseoxidase; [13]) and VFA [9]. The method for VFA analysis (adapted from Pethick et al. [20]) consisted of extracting them via cold sublimation under vacuum and then concentrating the sublimate. The blood sample (5 mL) was immediately centrifuged (5 000 G) at 0 °C for 5 min and the plasma rapidly frozen at –80 °C which made it possible to keep it over long periods without modifying the VFA concentrations. After rapid thawing at 40 °C in a boiling water bath, a fraction of plasma (2 mL) was placed in a 10-mL flask with 0.25 mL isobutyric acid as internal standard and 1 mL 1.5 % perchloric acid to release VFA. This mixture was frozen in liquid nitrogen for 5 min under continuous stirring to let a thin layer of the mixture deposit on the wall. The flask was then connected to a collecting tube containing 1 mL NaOH via a U-shaped system equipped with a tap to obtain the vacuum. The vacuum was obtained in the

whole system at 10 mbar and the collecting tube was placed in liquid nitrogen for obtaining full sublimation of the plasma within 2 h via pressure difference. The VFA collected as salts were immediately thawed and concentrated by evaporation at 40 °C for 1 h using an evaporator. They were assayed by gas chromatography with a Delsi 330 device (Delsi-Nermag, Argenteuil, France) equipped with a glass column 2.10 m long and 10 mm in diameter containing a phase (chromosorb W. AW) impregnated with SP 1200 (Supelec France, St-Germain-en-Laye, France). The temperature of the oven was 120 °C, that of the injector 160 °C and that of the detector 170 °C. Before being injected into the column the salt residues were mixed with 0.2 mL orthophosphoric acid 5N (pH = 3) for VFA release. The chromatograph was associated with a Delsi Enica 10 integrator.

Amounts of microbial metabolites and nutrients appearing in the portal blood were measured by determining the variation in the porto-arterial differences (Cp – Ca) of their concentration at any time after the intake of the meal and by multiplying these differences by the corresponding blood flow rate (D) and by the length of the observation period according to the following formulas

$$q = (\mathrm{Cp} - \mathrm{Ca})\, D\, \mathrm{d}t$$

and

$$Q = \sum_{t_{n-1}}^{t_{n-2}} q$$

where q is the amount absorbed during the short time dt (5 min) during which each factor can be considered as constant, Cp the portal concentration, Ca the arterial concentration, D the blood flow rate in the portal vein and Q the quantity absorbed during the postprandial period between time t_{n-2} and t_{n-1}. This measurement only concerns the net intake of nutrients in the portal blood and not the total absorption because a fraction of nutrients originating from the intestinal lumen or from the mesenteric arterial blood can be metabolized in the gut wall. For a given ingested nutrient, the values measured correspond to the absorption minus the metabolism of the intestinal tissue.

The coefficients defined by Hodgman [14] were used to calculate the metabolizable energy related to the absorption of VFA. The coefficients of Schiemann et al. [36] were used to calculate the energy produced by the other nutrients.

Statistical analyses [37] included the comparison of two sets of data using the Student's-t test, matched paired Student's-t test and blocked one way ANOVA.

3. RESULTS

During the experiment, four animals received the diet based on bran (batch SC) for 30 d in the first phase; the other four animals received the diet based on sugar beet fibre (batch PC) during this first phase. All the animals received the bran diet for 5 d, either in the second phase for four of them (first phase PC) or in the third phase for the other four (first phase SC) and their blood parameters were gathered in batch SA. Similarly, the eight animals received the sugar beet fibre diet for 5 d, either in the second phase (first phase SC) or in the third phase (first phase PC) and the corresponding blood parameters were gathered in batch PA.

3.1. Portal blood flow rate

Throughout the postprandial period, the mean blood flow rate in the portal vein was not modified either by the diet supplied or the period of adaptation (*table II*). The variations in the flow rate during the postprandial period were similar in both cases.

3.2. Glucose absorption

Figure 2 shows the variation in the blood level of glucose according to the type of treatment. In all cases the meal intake led to the appearance of a glycaemic peak within 60 min which corresponded to more than 200 % of the initial concentration (IC) in the portal blood, but which was much lower (140–165 % IC) in the

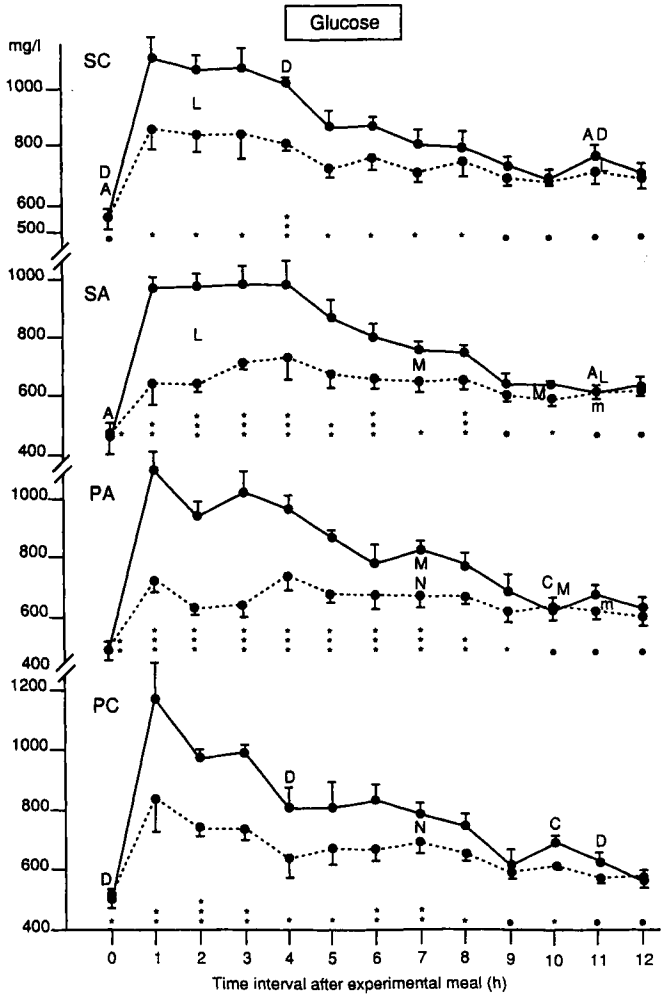

Figure 2. Variations in portal (——) and arterial (- - - -) blood concentrations of glucose (mg/L) after intake of a 800 g meal containing 10 % fibre from wheat bran (S) or dried beet fibre (P) after 30 d habituation (bran: SC versus beet fibre PC) or 5 d habituation (bran: SA versus beet fibre PA). Number of replicates: SC or PC 4; SA or PA 8. Values are means with vertical bars indicating the standard error of the mean. Statistical significance: differences between portal and arterial concentrations for a given treatment • NS * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; differences between portal concentrations: SC versus SA, A: $P < 0.05$; PA versus PC, C: $P < 0.05$; PC versus SC, D: $P < 0.05$; porto-arterial differences: SC versus SA, L: $P < 0.05$; SA versus PA, M: $P < 0.05$, m: $P < 0.01$; PA versus PC, N: $P < 0.05$.

Table II. Mean portal blood flow rate during the postprandial period according to the diet offered to the animals (bran S versus sugar beet fibre P) and to the length of the adaptation (30 d: C versus 5 d: A).

	Mean body weight (kg)	Mean portal blood flow rate mL/min	mL/kg/min
SC	67.0 ± 2.6	2421 ± 51	36.4 ± 2.1
SA	80.0 ± 2.0	2797 ± 71	35.1 ± 1.4
PC	80.0 ± 2.8	2738 ± 123	34.2 ± 0.9
PA	73.0 ± 2.7	2515 ± 74.9	34.7 ± 2.2

arterial blood. This portal peak was not significantly influenced by dietary treatment. The portal concentrations plateaued for a more or less long period according to treatments. For a given period after the meal, they were not significantly different between the dietary treatments and slowly decreased to reach a level which was slightly higher than the initial one (124–138 % IC) 12 h after the meal. For each treatment, the arterial concentrations were significantly lower than the portal concentrations for 8–10 h after the meal. Although the porto-arterial concentration differences at a given time after the meal seemed to be higher for SA and PA than for SC and PC, these differences between treatments only occasionally reached the level of significance (SC versus SA: hour 2; SA versus PA: hours 7, 10; PA versus PC: hour 7).

In the first hour, the amounts of glucose absorbed per hour (*figure 3*) represented 12–13 % of the total amount absorbed for 12 h. They reached the maximum value at hour 2 (15–17 % of the total, diet P) or hour 3 (17 % of the total, diet S) and decreased slowly until they reached a low but not nil value (0.5–3 % of the total) 12 h after the meal. The amounts of glucose appearing in the portal vein per hour after the meal were not different for a given period of adaptation, whether the diet contained sugar beet fibre or wheat bran. However, if the animals were pooled according to the diet independently of the adaptation period, the diet had a significant effect at hours 7 and 8, but not at the other time intervals after the meal. In contrast, amounts of glucose absorbed per hour were higher for a given diet after 5 d than after 30 d of adaptation. However,

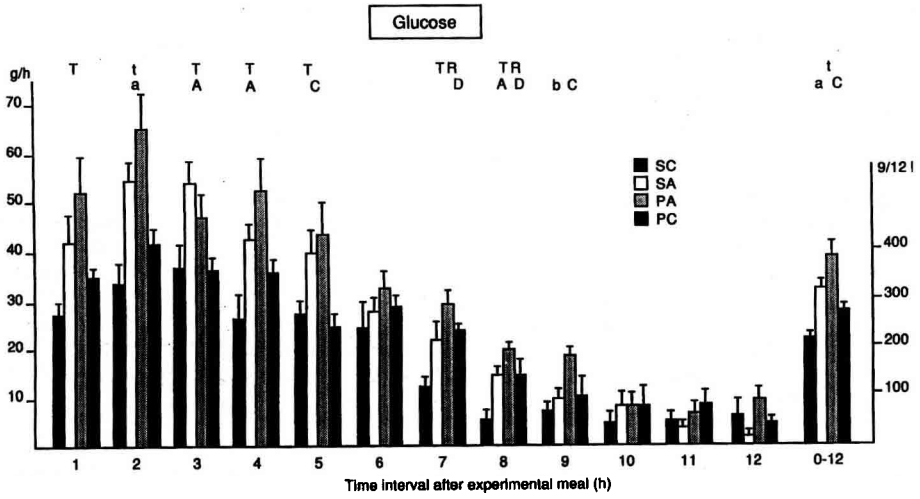

Figure 3. Variations with time in the hourly amounts (g) of glucose appearing in the portal blood after intake of a 800 g meal containing 10 % fibre from wheat bran (S) or dried beet fibre (P) after 30 d habituation (bran SC ■ versus beet fibre PC ■) or 5 d habituation (bran SA □ versus beet fibre PA ▨). Number of replicates: SC or PC 4, SA or PA 8. Values are means with vertical bars representing the standard error of the mean. 0–12 h total amount appearing in the portal blood within 12 h. Statistical significance SC versus SA, A: $P < 0.05$, a: $P < 0.01$; SA versus PA, b: $P < 0.01$; PA versus PC, C: $P < 0.05$; PC versus SC, D: $P < 0.05$. Influence of type of diet, R: $P < 0.05$; influence of habituation, T: $P < 0.05$, t: $P < 0.01$.

these difference reached the level of significance only for some time intervals (hours 2, 3, 4, 8 for diet S; hours 5, 9 for diet P). If the animals were pooled according to the lengh of feeding, amounts of glucose absorbed per hour in animals receiving one of the two diets for 5 d were significantly higher (except at hours 6, 10, 11, 12) than those absorbed from the same diets for 30 d.

The cumulated amounts of glucose absorbed were not significantly different from one diet to another. When the animal performances were pooled according to the diet, i.e. if the length of the adaptation period was not taken into account, the diet had no significant effect on the cumulated absorption of glucose throughout the postprandial period. On the contrary, the cumulated amounts were significantly higher from the 2nd hour for a given diet when the previous adaptation period lasted 5 d in comparison with the 30-d period and this phenomenon persisted throughout the postprandial period which led to marked differences after 12 h (SC 217.3 ± 16.3 g versus SA 321.1 ± 171 g, $P < 0.01$; PC 271.7 ± 14.6 g versus PA 385.8 ± 28.3 g, $P < 0.05$). When the animal performances were pooled according to the adaptation period, the cumulated amounts of glucose absorbed were significantly higher after a short than after a long adaptation period ($P < 0.05$ after 1 h, $P < 0.01$ afterwards). After 12 h, the absorption balances (amounts of glucose absorbed % amounts of glucose ingested) were the following: SC 57.8, SA 85.5, PA 97.5 and PC 68.7 %.

3.3. Amino-nitrogen absorption

Figure 4 shows the variation in the blood level of amino-nitrogen according to the type of treatment. The meal intake led to a marked increase in the blood level of nitrogen which reached a higher maximum value in the portal blood (170–180 % IC) than in the arterial blood (137–147 % IC) within 90 min (except SC: 150 min). Portal concentrations plateaued for a more or less long period according to treatments. They were not significantly different between the treatments for a given period after the meal and slowly decreased to reach a level which was slightly higher than the initial one (in % IC, SC: 128; SA: 138; PA: 135; PC: 132). For each treatment, the arterial concentrations were significantly lower (with a few exceptions) than the portal ones during the whole observation period. For a given treatment and time after the meal, the porto-arterial differences were larger after 5 d than after 30 d (SA > SC; PA > PC) of adaptation but this difference was only significant for some time intervals (between 1 and 3 h after the meal for diet S; after 30 and 90 min for diet P).

In the first hour, hourly amounts of amino-nitrogen absorbed (*figure 5*) represented 9.2 (SC) 9.0 (SA) 10.0 (PA) and 8.7 (PC) % of the total amounts absorbed for 12 h. They reached the maximum value within 2 h (diet P: PA 11.6 %, PC 12.3 % of the total) or 3 h (diet S: SC 11.4 %, SA 12.5 %) and decreased to values representing 6.4 (SC) 3.4 (SA) 4.9 (PA) 3.5 (PC) % of the total after 12 h. Amounts of amino-nitrogen appearing in the portal vein after the meal were quite the same for a given period of adaptation, whether the diet contained sugar beet fibre or wheat bran (except at hour 3: SA > PA, $P < 0.05$). Similarly, if the animals were pooled according to the diet received independently of the adaptation period, the diet had no significant effect. In contrast, hourly amounts of amino-nitrogen absorbed after the meal were higher for a given diet after 5 d of adaptation to this diet than after 30 d, but these differences were only significant with diet S (between hours 2 and 5, and in hours 7 and 8). If the animals were pooled according to the

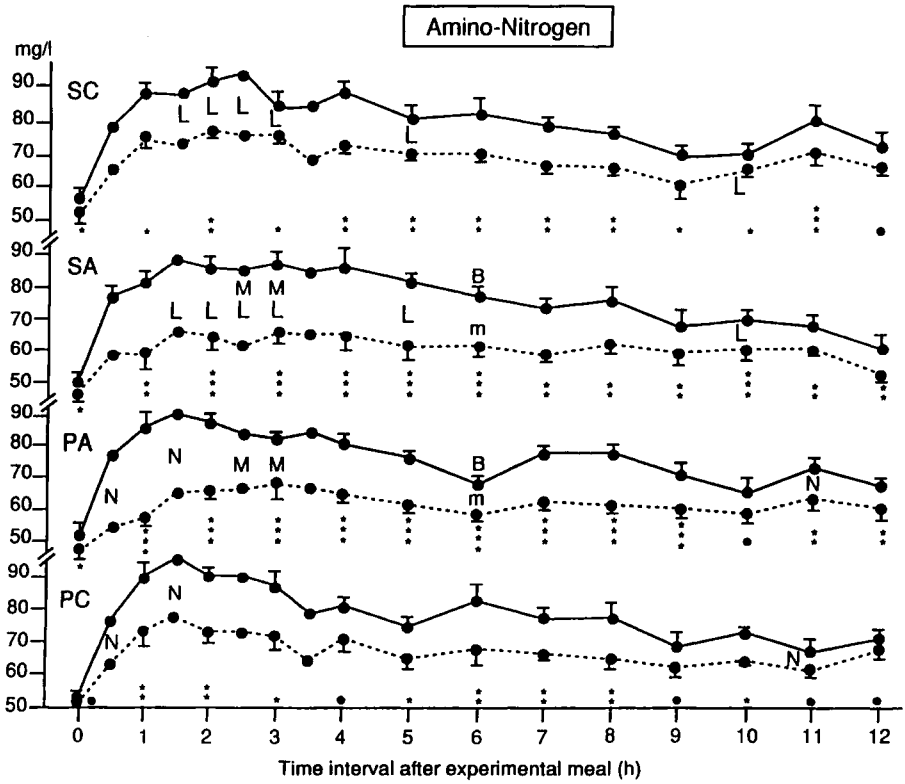

Figure 4. Variations in portal (——) and arterial (- - - -) blood concentrations (mg/L) of amino-nitrogen after intake of a 800 g meal containing 10 % fibre from wheat bran (S) or dried beet fibre (P) after 30 d habituation (bran SC versus beet fibre PC) or 5 d habituation (bran SA versus beet fibre PA). Number of replicates: SC or PC 4, SA or PA 8. Values are means with vertical bars indicating the standard error of the mean. Statistical significance: differences between portal and arterial concentrations for a given treatment • NS, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; differences between portal concentrations: SA versus PA, B: $P < 0.05$; porto-arterial differences: SC versus SA, L: $P < 0.05$; SA versus PA, M: $P < 0.05$, m: $P < 0.01$; PA versus PC, N: $P < 0.05$.

length of feeding, the amounts of amino-nitrogen absorbed per hour in animals receiving one of the two diets for 5 d were significantly higher between the hours 2 and 8 (except for hour 6) than those absorbed from the same diets for 30 d. For a given diet, the cumulated amounts were higher when the adaptation period was short (5 d) than when it was long (30 d) but the differences were only significant for diet S from hour 2. The differences became significant from hour 1 when the animals were pooled according to the length of their period of adaptation to the diet. After 12 h, the absorption balances (amounts of nitrogen absorbed % amounts of nitrogen ingested) were lower after a long (SC: 84.7 %; PC: 96.4 %) than after a short period of adaptation (SA: 128.4 %; PA: 123.6 %).

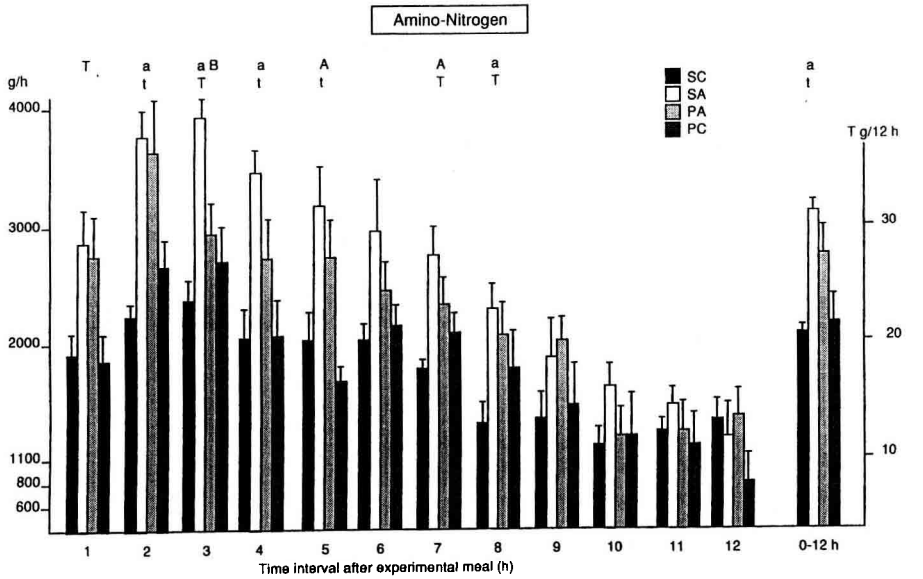

Figure 5. Variations with time in the hourly amounts (g) of amino-nitrogen appearing in the portal blood after intake of a 800 g meal containing 10 % fibre from wheat bran (S) or dried beet fibre (P) after 30 d habituation (bran SC ■ versus beet fibre PC ▩) or 5 d habituation (bran SA □ versus beet fibre PA ▨). Number of replicates: SC or PC 4, SA or PA 8. Values are means with vertical bars representing the standard error of the mean. 0–12 h: total amount appearing in the portal blood with 12 h. Statistical significance: SC versus SA, A: $P < 0.05$, a: $P < 0.01$; SA versus PA, B: $P < 0.05$. Influence of habituation, T: $P < 0.05$, t: $P < 0.01$.

3.4. Volatile fatty acid absorption

Whatever the diet given or the length of the adaptation period, the portal concentrations in total VFA (*figure 6*) were always significantly higher (from 280 to 340 %) than the arterial concentrations. At the time of the meal, the portal concentrations were significantly higher for the sugar beet fibre diet (P) than for the bran diet (S), whatever the length of the adaptation period. Afterwards the differences in favour of the sugar beet fibre diet (P) were only significant for the short period of adaptation (5 d) from hour 4. However, when the animals were pooled independently of the adaptation period, the portal concentrations (*table III*) were always significantly higher after the intake of diet P than after the intake of diet S. On the contrary, the arterial concentrations were significantly higher after the intake of diet P only at some time intervals after the meal (time 0, 1, 4, 5, 6, 8 h after the meal).

The differences in porto-arterial concentrations which were very high during the meal (SC 305 ± µmol/L; SA 337 ± 25 µmol/L; PA 475 ± 57 µmol/L; PC 496 ± 74 µmol/L) decreased to a minimum value between hours 2 and 4 (SC 179 ± 38 µmol/L; SA 179 ± 22 µmol/L; SA 239 ± 25 µmol/L; PC 282 ± 67 µmol/L) and progressively increased to a maximum

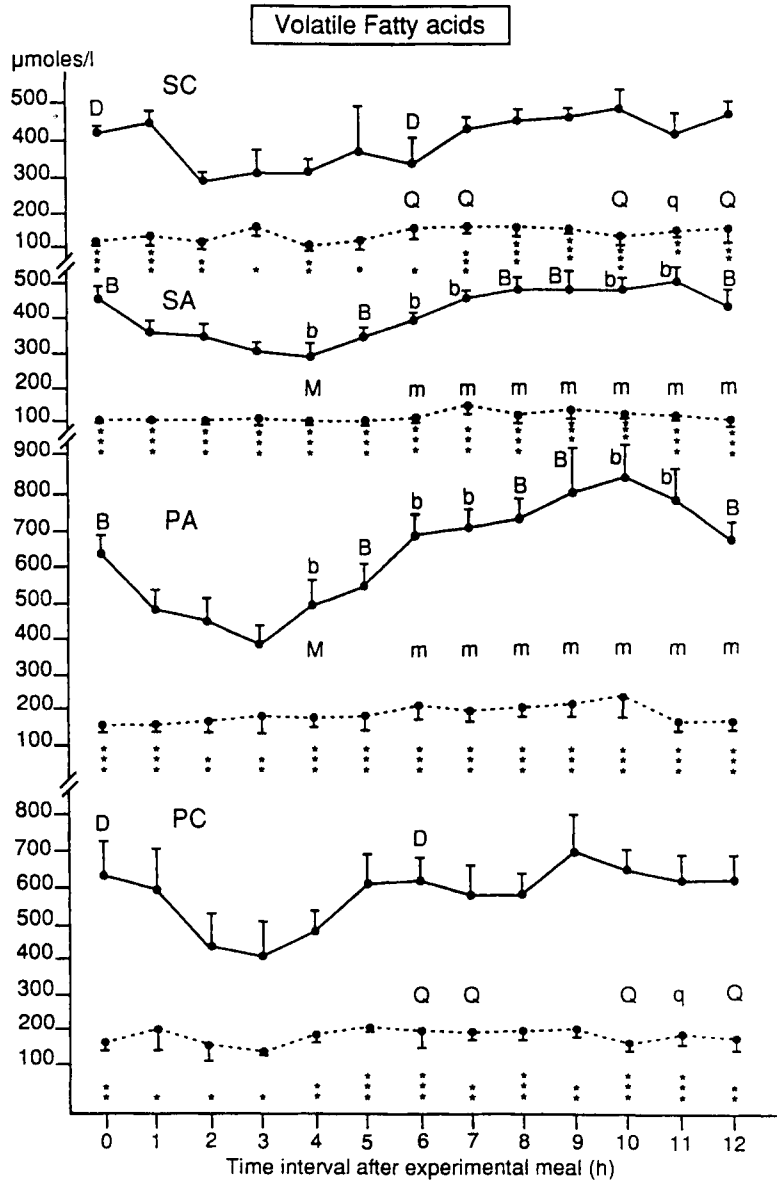

Figure 6. Variations in portal (——) and arterial (- - - -) concentrations of volatile fatty acids (µmol/L) after intake of a 800 g meal containing 10 % fibre from wheat bran (S) or dried beet fibre (P) after 30 d habituation (bran SC versus beet fibre PC) or 5 d habituation (bran SA versus beet fibre PA). Number of replicates: SC or PC 4, SA or PA 8. Values are means with vertical bars indicating the standard error of the mean. Statistical significance: differences between portal and arterial concentrations for a given treatment • NS, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; differences between portal concentrations: SA versus PA, B: $P < 0.05$, b: $P < 0.01$; PC versus SC, D: $P < 0.05$; porto arterial differences: SA versus PA, M: $P < 0.05$, m: $P < 0.01$; SC versus PC, Q: $P < 0.05$; q: $P < 0.01$.

Table III. Changes in arterial and portal concentrations of volatile fatty acids (µmol/L), mean ± standard error of the mean with time after the meal according to the diet offered to animals (bran S versus sugar beet fibre P) and independently of the length of adaptation (30 d: C; 5 d: A).

Time	Portal blood			Arterial blood		
(h)	SC + SA		PC + PA	SC + SA		PC + PA
0	430 ± 18	***	638 ± 50	121 ± 8	*	157 ± 14
1	392 ± 25	*	522 ± 50	123 ± 7	*	173 ± 18
2	332 ± 20	*	450 ± 49	114 ± 10	NS	164 ± 25
3	312 ± 20	*	401 ± 36	110 ± 13	NS	148 ± 19
4	307 ± 26	***	499 ± 41	122 ± 10	**	184 ± 18
5	369 ± 40	**	590 ± 50	119 ± 11	*	181 ± 21
6	381 ± 23	***	692 ± 43	134 ± 14	*	211 ± 30
7	452 ± 18	***	691 ± 41	167 ± 15	NS	199 ± 20
8	486 ± 24	***	712 ± 37	146 ± 14	*	205 ± 21
9	490 ± 40	**	788 ± 77	155 ± 14	NS	218 ± 32
10	501 ± 23	***	796 ± 69	135 ± 17	NS	218 ± 46
11	489 ± 35	**	746 ± 62	149 ± 13	NS	184 ± 20
12	442 ± 32	***	673 ± 37	145 ± 14	NS	176 ± 16

Statistical significance: NS not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

value between hour 9 and 12 after the meal (SC 356 ± 13 µmol/L; SA 370 ± 43 µmol/L; PA 623 ± 55 µmol/L; PC 506 ± 87 µmol/L). The porto-arterial differences were always higher after the intake of diet P than after the intake of diet S but this difference was only significant ($P < 0.01$) from hour 6 for the short adaptation period and significant but less so ($P < 0.05$) in hours 6, 7, 10, 11 and 12 for the long adaptation period. When the animals were pooled according to diet without taking into account the adaptation period, the porto-arterial differences were always significantly higher ($P < 0.01$ to $P < 0.001$) after the intake of diet P than after the intake of diet S, except during hours 1, 2 and 3 after the meal.

The distribution of individual VFA in the total mixture present in the portal blood was characterized by a high level of acetic acid (69–73 %), a moderate level of propionic acid (19–23 %) a relatively low level of butyric acid (5–7 %) and a very low level of isovaleric and valeric acids (0.5–2.5 %). In contrast, the VFA mixture present in the arterial blood contained almost only acetic acid (90–100 %). The proportions of VFAs in the portal blood did not change between hours 1 and 12 (*table IV*), but was different according to the diet ingested. Thus, the mixture of VFA contained more acetic acid and less propionic acid after the intake of diet P than after the intake of diet S. The differences were significant for the short adaptation period (SA versus PA: acetic acid $P < 0.05$ after 12 h; propionic acid $P < 0.05$ after hours 1 and 12) and for the overall comparison (PC + PA versus SA + SC).

Amounts of volatile fatty acids absorbed per hour (*figure 7*) relatively high at the time of the meal (46 to 48 mmol/h in hour 1 for diet S and 63–69 mmol/h for diet P), decreased during the first 3 h to a minimum value

Table IV. Distribution (%) of individual volatile fatty acids in the portal and arterial blood, according to time after the meal, the type of fibre (bran S versus beet fibre P) the length of adaptation (30 d: bran SC versus beet fibre PC; 5 d: bran SA versus beet fibre PA).

	Time after feeding							
	1 h				12 h			
Item	SC	SA	PA	PC	SC	SA	PA	PC
Portal blood								
Acetic acid %	71.9 ± 1.6^{a}	68.9 ± 1.8^{a}	73.5 ± 1.2^{a}	73.5 ± 0.8^{a}	69.5 ± 2.5^{ab}	69.2 ± 1.3^{a}	73.9 ± 1.4^{b}	73.6 ± 1.8^{ab}
Propionic acid %	19.9 ± 1.7^{a}	23.9 ± 0.9^{b}	20.4 ± 1.1^{a}	19.2 ± 1.0^{a}	22.2 ± 2.8^{ab}	23.4 ± 0.8^{a}	19.5 ± 1.0^{b}	20.3 ± 0.7^{b}
Butyric acid %	5.6 ± 0.2^{a}	5.4 ± 1.4^{a}	4.9 ± 0.4^{a}	5.7 ± 0.5^{a}	6.3 ± 0.5	5.4 ± 0.5	5.5 ± 0.5	7.3 ± 0.5
Isovaleric %	2.6 ± 0.7^{a}	1.8 ± 0.4^{a}	1.2 ± 0.6^{a}	1.6 ± 0.5^{a}	2.2 ± 0.9	2.1 ± 0.6	1.0 ± 0.3	0.4 ± 0.3
Arterial blood								
Acetic acid %	100 ± 0	95.0 ± 2.0	97.9 ± 1.1	100	100	96.3 ± 1.9	89.9 ± 5.0	100
Total VFA (μmoles)								
Portal blood	412 ± 34^{ab}	365 ± 26^{a}	487 ± 46^{b}	595 ± 121^{b}	394 ± 40^{a}	466 ± 43^{ac}	691 ± 43^{b}	634 ± 72^{bc}
Arterial blood	130 ± 18^{a}	119 ± 7^{a}	172 ± 30^{a}	198 ± 30^{a}	172 ± 32	132 ± 14	164 ± 29	178 ± 37
Statistical significance:								
SC + SA versus PC + PA : Acet. acid $P < 0.05$					SC + SA versus PC + PA: Acet. acid $P < 0.01$			
: Prop. acid $P < 0.05$					: Prop acid $P < 0.05$			

Means on the same line not sharing a common superscript differ ($P < 0.05$).

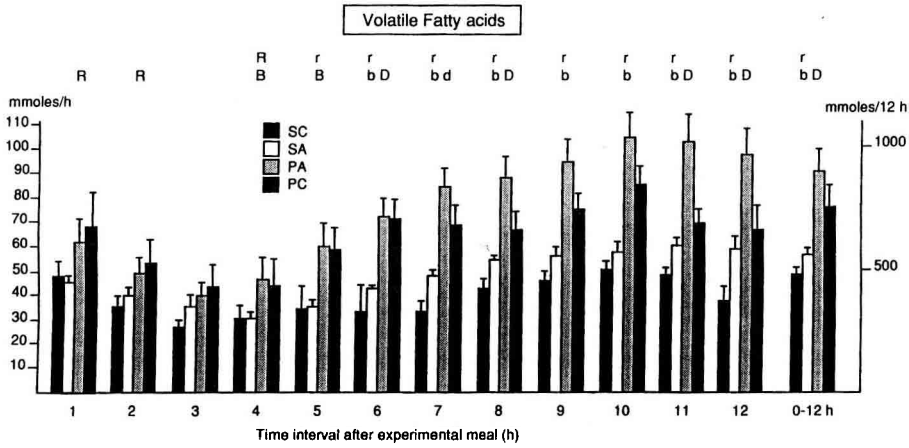

Figure 7. Variations with time in the hourly amounts (mmol/h) of volatile fatty acids appearing in the portal blood after intake of a 800 g meal containing 10 % fibre from wheat bran (S) or dried beet fibre (P) after 30 d habituation (bran SC ■ versus beet fibre PC ■) or 5 d habituation (bran SA □ versus beet fibre PA ▨). Number of replicates: SC or PC 4, SA or PA 8. Values are means with vertical bars representing the standard error of the mean. 0–12 h: total amount appearing in the portal blood within 12 h. Statistical significance: SA versus PA, B: $P < 0.05$, b: $P < 0.01$; PC versus SC, D: $P < 0.05$, d: $P < 0.01$; influence of type of diet, R: $P < 0.05$, r: $P < 0.01$.

(28–30 mmol/h for diet S, 41–42 mmol/h for diet P) and then progressively increased to a maximum value during the last 3 h of the study. This maximum value (mean of the last 3 h) was lower after the long period of adaptation (SC 96 % of the first hour, PC 103 %) than after the short period (SA 126 %, PA 160 %). The hourly amounts of VFAs absorbed were higher after the intake of diet P than after that of diet S for the same length of adaptation. The differences became significant for the short period from hour 4, and only from the hour 6 for the long period (except at hours 9 and 10, NS). Pooling the animals according to the diet independently of the adaptation period showed that the diet had a significant effect ($P < 0.05$ to 0.001) throughout the postprandial period (except at hour 3, NS), the absorption of volatile fatty acids being higher after the intake of diet P. Moreover, it was observed that the VFA absorption tended to be higher after the meal when the animals were only accustomed to their diet for a short period (5 d) but the differences for all animals whatever the diet were not significant.

Throughout the postprandial period, the cumulated amounts of VFA absorbed within 12 h were higher after the intake of diet P than after that of diet S, whether the adaptation period was short (SA 566.2 ± 20.3 mmol versus PA 906.1 ± 92.3 mmol, $P < 0.01$) or long (SC 470.2 ± 32.9 mmol versus PC 752.6 ± 101.8 mmol, $P < 0.05$). The diet effect was thus highly significant for diet P ($P < 0.001$). However, the 'adaptation period' effect was not significant even if VFA tended to be more absorbed after a short period of adaptation.

The differences recorded for individual VFA were similar to those recorded for total VFA (*table V*). Thus, the amounts of acetic and propionic acid absorbed

Table V. Amounts (mmol) and distribution (%) of individual volatile fatty acids appearing in the portal blood within 12 h after the meal according to the type of fibre in the diet (bran S versus beet fibre P) and the length of adaptation (30 d: bran SC versus beet fibre PC; 5 d: bran SA versus beet fibre PA).

	Amounts				Distribution (% of Total VFA)			
	SC	SA	PA	PC	SC	SA	PA	PC
Acetic acid	292.1 ± 18.5[a]	331.9 ± 13.4[b]	584.7 ± 63.9c	448.5 ± 64.6[c]	58.3 ± 2.3[a]	58.6 ± 1.1[a]	64.3 ± 1.7[b]	62.2 ± 2.5[ab]
Propionic acid	149.0 ± 12.0[a]	182.9 ± 7.8[b]	241.9 ± 23.0[c]	207.1 ± 26.4[bc]	28.7 ± 1.7[a]	32.2 ± 0.3[b]	27.2 ± 1.2[a]	27.9 ± 1.9[a]
Butyric acid	39.4 ± 5.0[a]	38.9 ± 4.3[a]	61.8 ± 10.1[a]	71.2 ± 20.8[a]	8.4 ± 0.7[a]	6.9 ± 0.7[a]	6.9 ± 0.7[a]	7.7 ± 1.6[a]
Isovaleric acid	13.0 ± 5.8	12.3 ± 2.5	13.0 ± 2.8	15.3 ± 8.2				
Valeric acid	0.4 ± 0.2	0.8 ± 0.4	2.7 ± 1.0	12.1 ± 1.0	4.7 ± 1.2[ac]	2.2 ± 0.4[b]	1.7 ± 0.3[b]	2.1 ± 1.2[bc]
Total	494.0 ± 39.6[a]	566.9 ± 19.9[b]	904.2 ± 90.3[c]	754.2 ± 101.2[c]				

Statistical significance:

SC + SA versus PC + PA: Acet. acet. $P < 0.001$; Acet. prop. $P < 0.005$; Acet. butyr. $P < 0.05$

SC + SA versus PC + PA : Acet. acet. $P < 0.01$; Acet. prop. $P < 0.01$; Acet. butyr. NS

Means on the same line not sharing a common superscript differ ($P < 0.05$).

within 12 h were higher after the intake of diet P than after the intake of diet S whether the adaptation period was short (SA versus PA: $P < 0.01$ for acetic acid; $P < 0.05$ for propionic acid) or long ($P < 0.05$ for acetic and propionic acid), even more for the overall comparison of the two diets (SC + SA versus PC+PA: acetic acid $P < 0.001$; propionic acid $P < 0.005$). On the contrary, the difference for butyric acid was only significant ($P < 0.05$) for the overall comparison. The VFA mixture appearing within 12 h in the portal blood contained a higher percentage of acetic acid and a lower percentage of propionic acid after the intake of diet P than after that of diet S. This was significant for the short adaptation period (SA versus PA) and for the overall comparison of the data (SC + SA versus PC + PA). Despite changes in composition, the weight of total fatty acids absorbed within 12 h remained lower after the intake of diet S (SC 32.20 g; SA 38.20 g) than after that of diet P (PC 50.48 g; PA 60.21 g). The cumulative absorption of volatile fatty acids for 12 h led to an energy supply much lower after the intake of diet S (SC: 142.9 cal/12 h, SA 165.7 cal/12 h) than after that of diet P (PC 217.0 cal/12 h; PA 254.9 cal/12 h). This energy absorption during the first 12 h after the meal represented 3.8 (SC) to 4.4 % (SA) of the ingested crude energy from the bran diet and 5.9 (PC) to 6.9 % (PA) for the sugar beet fibre diet.

4. DISCUSSION

The aim of this study, using the pig as a model for humans, was to analyse the influence of the type of dietary fibre on the absorption of nutrients released by the enzymes in the small intestine and by the microflora (VFAs) in the large intestine after the intake of a diet similar to that consumed by humans. Hence, nutrients such as potato flour, fish proteins, groundnut oil and sucrose were mixed in proportions close to those found in human diets.

The limits of the method used to quantify absorption kinetics have already been discussed [24, 26]. The main limitation of this method is related to the metabolism in the epithelial cells which can take up a part of the nutrients released in the intestinal lumen (glucose and amino acids: Rérat et al. [33]), but also metabolites produced by microbial fermentation [18]. Additionally, this method also has limitation in terms of adequacy between the volume of blood sampled and the length of the period necessary for sampling. Thus, it was difficult to obtain blood samples representative of the whole period of digestion and absorption without affecting the blood volume and the haematocrit. It has been well established that the enzymatic digestion of large amounts of starch can last for 15 to 18 h for large meals [23]. Moreover, the length of the food transit in the proximal gastro-intestinal tract up to the ileocaecal valve ranges from 4 to 14–18 h depending on whether the first or the last fractions of the meal are considered [7]. According to Hecker and Grovum [11], an additional period of 30 h is necessary for the transit in the large intestine; consequently, the mean retention time in the total digestive tract ranges from 20 to 53 h, depending on whether the first or the last fractions of the meal are considered. Thus, to study the total absorption of nutrients originating from the enzymatic digestion, the establishment of intestinal balances for a given meal would require blood samplings for 18 h during the postprandial period. However, according to the variation in the postprandial concentrations of these nutrients the porto-arterial differences generally became low or nil after hour 12 and more than 90 % of the absorption of nutrients occurred during the first 12 h after the meal. Therefore, the absorption of nutri-

ents after this period can be considered negligible. On the contrary, studying the total absorption of microbial metabolites originating from a given meal would require blood samplings for 48 to 50 h. Moreover, the fermentable material present in the large intestine corresponds to residues from several successive meals [29] and only experimental devices such as radio isotopes would make it possible to separate the fermentation products of the experimental meal from the others. Hence, only partial balances can be established and only comparisons on a relatively short period after the experimental meal (12–24 h) can be made when the maximum fermentation originating from the experimental meal takes place, the products of which add to those in smaller amounts originating from previous meals [29]. Thus, the experimental design constitutes a compromise for obtaining data for VFA during maximum fermentation over the 12 to 24 first hours after the experimental meal, and for glucose and amino-nitrogen over the 12 first hours following a new experimental meal, after 24 h fast for avoiding residual absorption from preceding meals.

The portal flow rate expressed relative to the animal weight (mL/kg/min) was slightly lower than in previous studies [25, 33]. This difference can be explained by the fact that, in the present experiment, the animals were heavier than in the previous ones. Moreover, it is well established that, from 40 kg live weight, there is a negative allometry between the increase in the weight of the viscera (and consequently the blood volume which irrigates them) and the weight of the animal [17].

The variation in the portal and arterial concentrations of glucose is similar to that found after the intake of starch-rich diets in previous studies [9, 27]. It should be emphasized that, with the type of diet used, the porto-arterial differences at the 12th hour were almost nil or even negative corresponding to the end of the enzymatic digestion of starch. The percentage of glucose appearing in the portal blood during the enzymatic digestion represented only 58–97 % of the carbohydrates ingested, what is left corresponding to the volume of residues emptied towards the large intestine plus the glucose uptake by the gut wall. The negative influence of the presence of large amounts of fibre on the digestibility of starch could thus be indirectly estimated. The glucose absorption seemed to be only slightly modified by the type of fibre in this case since absorption coefficients after 12 h were not different whatever the diet and whether the period of adaptation was long (SC 58 % versus PC 69 %) or short (SA 86 % versus PA 97 %). In contrast, shortening the adaptation period seemed to increase the enzymatic digestion of carbohydrates and glucose absorption with a subsequent increase in hourly amounts absorbed during the first hours as well as in the total amounts. The possible cause for the more efficient absorption after a short period of adaptation is the possible slowing down of the transit time in the proximal small intestine when feeding an unusual fibre-rich diet without a previous adaptation. This could lead to a prolonged contact between feeds and enzymes and between the nutrients released and the absorptive walls thus enhancing both the enzymatic degradation and the absorption. In support of this hypothesis, Entringer et al. [8] suggested that digestibility increased with a decreasing transit rate in the small intestine.

The variation in the arterial and portal concentrations of amino-nitrogen observed in the present trial was similar to that described in previous studies using similar types of diets [30]. The total absorption coefficients within 12 h were very high (85–128 %), although the absorption process was not completed, the porto-arte-

rial differences being still found significant after 12 h. The absorption of larger amounts of amino-nitrogen than those ingested accounted for the recycling of endogenous nitrogen which can be very marked [31–33]. Similarly to the absorption of glucose, that of amino-nitrogen did not seem to be modified by the type of fibre since the absorption coefficients after 12 h were not different for either diet, whether the period of adaptation was long (SC 85 % versus PC 96 %) or short (SA 128 % versus PA 124 %). In contrast, shortening the adaptation period led to a more rapid and increased appearance of amino-nitrogen in the portal blood, as in the case of glucose. The influence of the period of adaptation was significant for the hourly amounts absorbed during the first hours and for the total amounts absorbed within 12 h. An explanation similar to that given for glucose can be provided for amino-nitrogen.

The concentrations of volatile fatty acids in the portal blood decreased until hour 3 or 4 in all cases, whereas the arterial concentrations remained stable. This phenomenon can be attributed to the decrease in easily fermentable substrates originating from the last meal ingested the day before [29]. The subsequent increase in the portal concentration corresponded to the arrival of fresh residues at the level of the large intestine. It has long been established that the transit time of the first fractions of a meal in the small intestine is approximately 4–6 h [7]. From hour 6, the porto-arterial differences however were much larger after the intake of the sugar beet fibre diet than after that of the bran diet. After 4 h, these differences led to the absorption of larger amounts of volatile fatty acids after the intake of the sugar beet fibre diet than after that of the bran diet. The same was observed for the total amounts of volatile fatty acids absorbed within 12 h. In contrast, the adaptation period had no significant influence on the absorption of volatile fatty acids. This result was not in agreement with the data of a previous experiment [9] which showed a higher VFA absorption when the adaptation period was extended from 21 to 28 d. The experimental conditions, especially the type of fibre and the length of the periods considered, were different in this other work.

Unlike in portal blood, the mixture of individual VFA present in the arterial blood was almost exclusively composed of acetic acid. This provides further evidence for the large uptake of propionic, butyric, isovaleric and valeric acid by the liver [29]. A major fraction of acetic acid was also taken up by the liver since the concentration in the arterial blood was 2 to 4 times lower than in the portal blood according to sampling time, but a portion of it escapes liver metabolism by being taken up by peripheral tissues, particularly muscles [21]. The type of fibre introduced into the diet can modify the composition of the VFA mixture absorbed. Replacing wheat bran by sugar beet fibre led to an increase in acetic acid and a decrease in propionic acid. Modifications in the composition of VFA produced were also observed when using other fibres [3] or when hydrogenated sugars were introduced into the diets [34]. The proportion of butyrate seems to be lower in the pig (7–15 %) than in humans (20 %), but this could be due to the type of fibre.

As regards energy, the production of volatile fatty acids during the 12 h following the meal corresponded to 0.17–0.18 kcal/h/kg live weight for diet S and to 0.25–0.27 kcal/h/kg live weight for diet P. These values, which were much lower than those found with other diets [9, 24, 29, 39], could be explained by a difference in the ileal digestibility of the carbohydrates present in the different diets.

In conclusion, the type of fibre present in pig diets (wheat bran versus sugar beet fibre) at an inclusion level of 10 % pro-

duced a change in the amounts of volatile fatty acids appearing in the portal blood following the meal, but did not modify the absorption of nutrients originating from enzymatic hydrolysis in the small intestine. Diets containing sugar beet fibre led to the absorption of larger amounts of volatile fatty acids than those containing wheat bran. The proportion of acetic acid in the mixture absorbed was higher and that of propionic acid lower. Shortening the period of adaptation (5 d versus 30 d) did not cause any modification in the production of volatile fatty acids whereas it led to an increase in the absorption of nutrients originating from the enzymatic digestion in the small intestine.

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