Some quantitative aspects of protein and carbohydrate absorption in the pig*

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A great number of studies have been made the last few years in the fields of gastrointestinal physiology, biochemistry and pathology in the pig. Scientists consider the pig as a valuable animal not only in terms of production, but also as a model resembling the human species more than the rodent does, its feeding behaviour being quite similar (mainly diurnal feeding pattern: Auffray *et al.* 1974) as well as the anatomy of its gastrointestinal system. Owing to several methods developed in the last 20 years, large samplings can be made in vivo in the pig from the whole intestine or segments of the latter allowing a quantification of a certain number of measures. It is thus possible to examine the variation in the digestive contents according to time and space, to distinguish between digesta of exogenous or endogenous origin, to measure their disappearance in the various segments of the digestive tract and their appearance in the body fluids. Several recent reviews dealing with the pig concern either the digestion in general (Kidder & Manners, 1978), or specific problems such as in vivo methodology (Laplace, 1972; Low, 1977, 1980; Rerat *et al.* 1980) or in vitro methodology (Smith, 1980), proteins (Rerat, 1972; Rerat *et al.* 1976; Zebrowska, 1980), carbohydrates and lipids (Sambrook, 1980), minerals (Partridge, 1980), secretions (Corring, 1979, 1980), motricity and transit (Laplace, 1979, 1980).

The present paper presents some new results on the appearance of protein and carbohydrate nutrients in the body fluids. First, however, a description will be made of the technology used for measuring those nutrients.

Methods for measuring the appearance of nutrients in the body fluids

Increase in the amount of the nutrient studied is measured in the portal vein, the thoracic duct or some of their collaterals. Variations in the concentration of nutrients at that level reflect the digestive processes of the feeds (transit, mixture with secretions and desquamations, changes caused by enzymes and microflora) and the possible metabolization in the gut wall. The lymph has been little studied and principally with respect to absorption of lipids (Raulin *et al.* 1966) but also in connection with absorption of protein hydrolysis products (Aliev & Ataev, 1972; Aliev *et al.* 1978). The most studied pathway is that of the blood in particular in the case of absorption of protein hydrolysis products (Rerat *et al.* 1976). A qualitative description of the absorption can be made from the porto-arterial

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differences in the nutrient concentration indicating the degree of enrichment of the portal blood draining the whole gut, relative to the afferent arterial blood of the intestine. A quantitative description of the absorption can be made by measuring simultaneously the blood flow rate in the portal vein. Blood samples can be obtained by permanent catheterizations of the portal vein (Arsac & Rerat, 1962) and the carotid artery (Rerat, 1977). The portal blood flow rate can be measured by means of various techniques, the most currently used in the pig being the electromagnetic flowmeter. The absorption is calculated by combining these two techniques according to the formula: $Q=(Cp-Ca)\,D\,dt$, where $(Cp-Ca)$ represents the porto-arterial differences in the nutrient concentration, D the blood flow rate in the portal vein, and Q the amount absorbed within the time interval dt (Rerat *et al.* 1980).

This measure concerns only the apparent absorption; indeed, some nutrients coming from the intestinal lumen or the arterial blood may be metabolized or catabolized in the intestinal wall. For a given nutrient ingested the absorption balance obtained corresponds to the excess of absorption relative to the metabolization in the gut wall when the porto-arterial difference is positive or to the excess of the metabolization in the gut wall relative to the absorption, when this difference is negative. For a non-ingested nutrient, this method allows to measure its apparent synthesis by the cell wall.

Appearance of nutrients in the body fluids during digestion of carbohydrates and proteins

The transport and absorption of various nutrients have been investigated, especially in the last 10 years, in a great number of species other than the pig. An attempt was generally made in these experiments to describe the hydrolysis and transport processes without, however, the possibility of quantifying them by means of techniques allowing the determination of disappearance of nutrients in vitro (Smith, 1980), or in vivo (Silk, 1977). The advances made in these fields are very important and concern in particular the transport mechanisms of oligopeptides and amino acids (Matthews, 1972, 1977; Munck, 1976) as well as those of simple carbohydrates (Crane, 1968; Gray, 1970, 1975). In the pig, very few studies were made with in vitro techniques although the transport mechanisms do not always seem to be the same as in the other species (Daniels, 1972). Opposite to that some in vivo studies were made on the postprandial appearance of nutrients in the body fluids (blood or lymph) draining the digestive tract. It will thus be possible to understand the factors responsible for the metabolism of nutrients and to determine whether the synchronized supply of nutrients in the tissues play effectively the role defined by Geiger (1950) for amino acids or by Cuthbertson & Munro (1939) for energy and protein.

Absorption kinetics and balance of carbohydrates of various dietary origins

Qualitative aspects. The peripheral glycemia increases as the carbohydrates disappear from the intestinal lumen. This rise is variable according to the

Table 1. *Variations in the amounts of reducing sugars appearing in the pig during a postprandial period of* 8 *h**

(Mean values with their standard deviations; no. of pigs in parentheses)

	Period after meal (h)							
	2		4		6		8	
Food intake:	Mean	SD	Mean	SD	Mean	SD	Mean	SD
400 g								
Cerelose (6)	77	10	177	30	228	43	241	40
Sucrose (10)	84	11	175	25	229	34	257	40
Lactose (5)	40	3	79	7	103	7	119	9
Maize starch (7)	69	9	131	25	176	29	214	30
800 g								
Cerelose (4)	157	21	345	43	483	36	592	27
Sucrose (5)	118	17	287	25	432	24	521	28
Lactose (4)	32	10	62	20	88	28	113	35
Maize starch (5)	102	10	220	33	302	49	360	55

*Rerat (1977) and Rerat *et al.* (1978).

carbohydrate ingested and changes with the age of the animal which conditions its enzyme capacities (Dollar *et al.* 1957; Cunningham, 1959; Kidder *et al.* 1963; Ly & Velasquez, 1970). Systematic studies made in 3-month-old animals (Aumaitre *et al.* 1973, 1975; Rerat *et al.* 1977) show that the portal blood level of reducing sugars increases rapidly. The magnitude of the level reached as well as the time elapsed to reach it and to decrease are highly variable from one carbohydrate to another. The arterial glycemia follows the portal fluctuations and sometimes increases in large proportions. Thus, according to the sugar ingested the liver is more or less able to retain the flux of nutrients reaching this organ. The porto-arterial differences are highly marked for glucose and sucrose; less marked but persistent for maize starch and very small for lactose.

Quantitative aspects—absorption balance of reducing sugars during a postprandial period of 8 *h.* The amounts of reducing sugars appearing in the body during a postprandial period of 8 h vary according to the sugar ingested (Rerat *et al.* 1974; Rerat *et al.* 1977). Except for lactose, they increase simultaneously with the ingestion level, but the over-all pattern is different for each sugar according to the amounts ingested (see Table 1). Cerelose and sucrose are digested more rapidly than starch. In the case of lactose there is no relationship between the amounts of sugars appearing in the portal vein and the amounts ingested and the rather low absorption coefficient is almost reduced to half when the intake level is doubled. Accordingly, there is a limiting factor probably involving either the hydrolysis of lactose or the absorption of its hydrolysis products. The differences between the various sugars and levels appear very early. A comparison of gastric emptying values for starch (Cuber & Laplace, 1979*b*) and the values concerning the

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portal appearance of reducing sugars after intake of an analogous amount of a semi-synthetic diet based on starch shows that the processes of starch hydrolysis and the absorption of the hydrolysis products do not seem to be able to follow the very rapid gastric emptying of starch which accumulates in the intestine during the first hours after the meal. Thus, the starch digestion rate seems to be limited by the process of degradation and absorption.

In conclusion, large amounts of maize starch and of lactose still subsist in the digestive tract 8 h after the meal, whereas the digestion of glucose or sucrose is much advanced. This is confirmed by the concordance between the duration of gastric emptying after ingestion of starch (Laplace, 1979) and the persistence of the porto-arterial differences in the concentration of reducing sugars (Rerat, 1977). Consequently, the digestive tract of the pig is able to store large amounts of energy for a long period after ingestion of meals based on maize starch or lactose. Moreover, as these carbohydrates are present in the gut for a long time they may constitute substrates for the microbial proliferation leading to the formation of useful or noxious substances.

Absorption of protein hydrolysis products

In the pig only few investigations have been made using the lymph to study protein absorption. According to Aliev & Ataev (1972) and Aliev *et al.* (1978) the substances absorbed do not only appear in the organism in the form of free amino acids, but also in the form of proteins synthesized in the intestinal cell wall and thereafter conveyed to the portal blood and the lymph.

Concerning the blood route, it is well known that the amino acidemia increases after a protein meal, but more markedly in the portal than in the systemic blood. This increase occurs rapidly and lasts for a long or short time according to the quality and nature of the protein ingested (Rerat *et al.* 1976).

The last few years, quantitative investigations have been made systematically in the pig. Some information on the comparative absorption rates of proteins, carbohydrates and their hydrolysis products will be given.

Table 2. *Relationships between the amounts of amino acids* (Y/*g*) *and reducing sugars absorbed* (Y′/*g*) *and the amounts of crude protein* (X/*g*) *and sugars ingested* (X′/*g*)

	Period after meal (h)	*n*	Regression equation	*r*	$\bar{X}$	$\bar{Y}$	Statistical significance of difference
Wheat	8	16	$Y=0{\cdot}459\,X+14{\cdot}244$	0·805	117·6	68·2	**
Barley	8	12	$Y=0{\cdot}302\,X+9{\cdot}230$	0·842	74·5	31·2	**
Wheat	8	16	$Y'=0{\cdot}366\,X'+56{\cdot}925$	0·821	626·9	286·4	**
Barley	8	16	$Y'=0{\cdot}309\,X'+47{\cdot}047$	0·880	475·4	193·9	**

**$P<0{\cdot}01$.

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Comparison between absorption rates of protein and carbohydrate hydrolysis products. Some results referring to the digestion of two cereals, wheat and barley, are given in Table 2 (Rerat, Vaissade *et al.* 1979). The relationships between amounts absorbed during a postprandial period of 8 h and the amounts ingested can be described by 1st degree equations (Table 2). Wheat proteins exhibit the highest digestion rate. The slopes of the regression lines at 8 h are significantly different between wheat and barley proteins, and between protein and reducing sugars of wheat. Conversely, there is no difference either between reducing sugars of the two cereals or between reducing sugars and proteins of barley. This possibility of a differential digestion of proteins and carbohydrates may have important nutritional consequences, especially for the valorization of N retention by the energy supply.

Composition of the amino acid mixture absorbed after ingestion of various proteins. Using as a basis the amounts of each amino acid absorbed at various time intervals after the meal, it is possible to determine the composition of the amino acid mixture absorbed and to compare it with that of the proteins ingested. This composition may be expressed in the form of patterns of amino acids absorbed, either relative to the sum of essential amino acids or relative to the sum of non-essential amino acids. By comparison with the profile of essential and non-essential amino acids of the proteins ingested (in this case, wheat, barley, fish) it is possible

Table 3. *Composition of the essential amino acids absorbed* (%) *and difference from composition of amino acids ingested* (%) *during a period of* 8 *h after the intake of wheat, barley or fish meal*

(No. of pigs/diet in parentheses)

	Amino acids absorbed (%)			Difference from mixture ingested (%)		
	Wheat (7)*	Barley (7)*	Fish (11)†	Wheat	Barley	Fish
Histidine	8·3	8·2	4·9	138	161	112
Lysine	6·6	8·1	12·7	89	90	86
Phenylalanine	14·3	13·0	9·3	118	109	109
Leucine	16·4	16·2	18·4	101	101	109
Isoleucine	10·2	9·1	10·8	114	108	102
Methionine	5·4	4·8	4·9	126	117	80
Valine	12·3	11·8	12·7	111	97	104
Threonine	8·0	7·5	9·3	114	98	103
Arginine	6·3	8·0	7·7	50	65	67
Cystine	2·8	2·7	2·4	43	54	138
Tyrosine	9·4	10·1	7·2	129	139	171
Sulphur amino acids	8·1	8·1	7·0	76	83	89
Aromatic amino acids	23·7	23·7	16·5	122	121	129

*From Rerat, Vaissade *et al.* (1979).
†From Rerat, Kande *et al.* (1979).

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to determine the relative absorption rate of the essential amino acid relative to the mixture of the essential ones and that of the non-essential amino acids relative to the mixture of non-essential ones (Rerat, Vaissade *et al.* 1979).

In these conditions, the profile of the mixture of amino acids absorbed within 8 h (Table 3) closely depends on the profile of the essential amino acids ingested without completely resembling it. Thus, whatever the protein ingested, the over-all absorption rate of the ramified amino acids and threonine is close to that of the mixture; the absorption rate of histidine and aromatic amino acids is much faster; contrary to that, the total cumulated absorption of lysine, sulphur amino acids and especially arginine is slower. Although the concentration of lysine is much higher in fish than in cereal proteins and that of aromatic amino acids much lower in fish than in cereal proteins, the behaviour of these amino acids relative to the mixture of essential amino acids is the same for the three proteins (wheat, barley, fish) as if there is an identical chronology in the degradation and absorption of their essential amino acids whatever the concentration of the latter.

The mixture of non-essential amino acids absorbed (Table 4) undergoes marked changes in the same direction for the three proteins, but of variable extent according to the protein considered. Thus, a large excess of alanine and glycine is observed particularly in cereals and large aspartic and glutamic acids deficiencies especially in fish. These modifications correspond to the transaminations occurring in the gastrointestinal cell wall as shown previously by Neame & Wiseman (1958) and Pion *et al.* (1964).

These results clearly show that although digestion is a more or less rapid and early process according to the protein considered, the sequence of release of the various amino acids does not seem to depend on their relative proportion in the protein.

Table 4. *Composition of the mixture of non-essential amino acids absorbed* (%) *and difference from composition of amino acids ingested* (%) *during a period of* 8 *h following the intake of wheat, barley or fish meal*

(No. of pigs/diet in parentheses)

	Non-essential amino acids absorbed (%)			Difference from mixture ingested (%)		
	Wheat (7)*	Barley (7)*	Fish (11)†	Wheat	Barley	Fish
Aspartic acid+asparagine	7·3	10·1	11·3	80·8	88·6	52
Proline+hydroxyproline	17·4	14·1	12·8	88·5	68·4	122
Serine	10·1	8·4	7·5	128·8	111·1	93
Glutamic acid+glutamine	13·7	7·2	2·3	28·2	16·2	7
Glycocolle	11·6	11·8	14·2	168·1	147·9	105
Alanine	26·5	31·4	36·7	472·2	397·8	255
Citrulline	6·61	8·33	9·6	—	—	—
Ornithine	3·28	3·85	3·4	—	—	—

*From Rerat, Vaissade *et al.* (1979).
†From Rerat, Kande *et al.* (1979).

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Due to lack of space, very important aspects of the digestive processes are not given in this paper and will be discussed elsewhere (Rerat, 1980). This is particularly the case for the gastrointestinal secretions and their regulation, the role of the stomach in digestion, and digestion of proteins and carbohydrates in the different parts of the gut (small intestine, hind-gut) and subsequent disappearance of their hydrolysis products. Results are only given concerning kinetics and balance of appearance in the portal blood of hydrolysis products of some proteins (wheat, barley, fish meal) and carbohydrates (cerelose, sucrose, lactose, maize starch).

A systematic use of this methodology is very promising as it contributes to a better understanding of the results obtained by other techniques aiming at measuring the segmental or total disappearance of the hydrolysis products in the gastrointestinal tract. It may help to estimate the role of the 'time-factor' when the nutrients arrive at the site of protein synthesis.

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