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Adaptation of pancreatic lipase to the amount and nature of dietary lipids in the growing pig

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Summary. The purpose of the present study was to examine the adaptation of pancreatic lipase to the amount and nature of dietary lipids in the growing pig. Thirty pigs were distributed into three groups of 10 animals each. They were fed the same amount (1.5 kg/pig/day) of either diet C (3.5 % lard, 3.5 % sunflower oil, 67.7 % starch), diet L (21 % lard, 33.2 % starch) or diet SO (21 % sunflower oil, 33.2 % starch) for 12 days. The diets were isoenergetic and isonitrogenous. Pancreas weight relative to live-weight was highest in group L. The pancreatic lipid content of the latter group exceeded that of groups C and SO by 53 and 39 %, respectively. The pancreatic protein content was similar in the three groups. The specific lipase activity of pancreatic tissue (U per mg of protein) in group SO was about 1.6-fold higher than that of group L and about 3-fold higher than that of group C (31.9, 19 and 11.6, respectively). Specific amylase activity was higher in animals of group C than in those of the other two groups (C : 1689 ; L : 1112 ; SO : 984), whereas no difference was observed in chymotrypsin activity. Specific trypsin activity was lowest in group L.

These results confirm the adaptation of pancreatic lipase and amylase to their respective substrates. Furthermore, it appears that lipase activity was more or less affected by the degree of unsaturation of lipids and that it was much higher for the same amount of triacylglycerols when the latter were rich in unsaturated fatty acids. The mechanisms involved have not been determined yet, but the possible physiopathological consequences of the increased pancreatic lipid content observed in pigs receiving triacylglycerol-rich diets (including especially saturated fatty acids) should be considered.

Introduction.

Pancreatic lipase was long considered as a non-adaptative enzyme (Bucko and Kopec, 1968) but, owing to improved determination techniques, it was demonstrated that lipase did adapt to the amount of lipids ingested in a large number of experiments and in many animal species (Behrman and Kare, 1969 ; Hulan and Bird, 1972 ; Mourot and Corring, 1979 ; Simoes Nunes *et al.*, 1985). Thus, although the effect of dietary amounts of triacylglycerols on pancreatic exocrine secretion has been well established, little is known about the effect of the nature of the triacylglycerols ingested.

Is the adaptative response of the pancreas modulated or not by the degree of unsaturation of triacylglycerol fatty acids ? Up till now only two studies have been

devoted to this question and both in only one animal species, the rat (Deschodt-Lanckman *et al.*, 1971 ; Saraux *et al.*, 1982). Opposite conclusions were drawn by these authors : according to Deschodt-Lanckman *et al.* (1971) unsaturated lipids increased pancreatic lipase activity, whereas Saraux *et al.* (1982) did not find that the degree of saturation of the dietary triacylglycerols affected this enzyme.

The purpose of our study was to examine pancreatic adaptation to the level and nature of dietary lipids by using diets rich in saturated fatty acids (lard) or unsaturated ones (sunflower oil). The experimental design used allowed us to determine whether or not consumption of large amounts of triacylglycerols led to a rise in pancreatic lipid content.

Material and methods.

Thirty growing Large-White pigs (15 males, 15 females) with an initial live weight of 25.5 ± 0.32 kg were used in this experiment.

Three isoenergetic and isonitrogenous diets were each given for 12 days to 10 animals : a control diet (C), a diet rich in saturated fatty acids (L) and a diet rich in unsaturated fatty acids (SO) ; the fatty acid composition of the lard and sunflower oil was analysed by HPLC (table 1). Daily feed intake was 1.2 kg/pig/day the first 5 days and 1.5 kg/pig/day the last 7 days. The daily amount

TABLE 1
Diet composition (p. 100).

	Control C	Lard L	Sunflower oil SO
Hydrochloric casein	17.2	17.2	17.2
Maize starch	67.7	33.2	33.2
Lard	3.5	21	—
Sunflower oil	3.5	—	21
Colmacel cellulose	2	10	10
Vermiculite (mica)	2.5	15	15
Minerals	2.5	2.5	2.5
Vitamins	1	1	1
Antioxidant	0.1	0.1	0.1
Crude protejn (%)	15	15	15
Crude energy (Cal/kg)	3944	4007	4007

*Fatty acid composition (in p. 100 of total methyl esters)
of lard and sunflower oil.*

	Lard	Sunflower oil
C 14 : 0	1.3	—
C 16 : 0	29.3	6.1
C 16 : 1	1.9	—
C 18 : 0	15.8	4.1
C 18 : 1	41.1	20.4
C 18 : 2	9.3	69.4
C 18 : 3	—	—
C 20 : 0	1.3	—

of feed was offered in two equal meals at 9.00 and 16.00 h, respectively. Water was given *ad libitum*.

All the animals were sacrificed in the morning of Day 13 of the experiment after a fasting period of 18 h. Immediately after slaughter the pancreas was removed, separated from the connective tissue, weighed and ground in distilled water (6.7 ml H₂O/g of pancreatic tissue). The homogenates thus obtained were used to determine pancreatic protein content as well as lipase, amylase, trypsin and chymotrypsin activities according to methods described elsewhere (Simoes Nunes and Corring, 1979). The total lipid content of the pancreas was measured according to Folch *et al.* (1957).

All data were interpreted statistically by analysis of variance (F-test).

Results.

A. Feed intake, health and weight gain.

All the animals ingested the amounts of feed indicated in the experimental protocol. None of them exhibited clinical symptoms of disease during the study. Daily mean gains (DMG) are reported in table 2 ; those of pigs fed the control diet were significantly higher than those of the animals offered the other two diets. The lowest DMG was recorded in pigs receiving 21 % lard in their diet, but it was not significantly different from that of animals fed the diet containing 21 % sunflower oil (266 ± 45 and 302 ± 34 g/d).

B. Pancreatic characteristics.

1. *Pancreas weight, total pancreatic lipids.* — Pancreas weight relative to live weight was significantly affected by diet composition (table 2) ; it was highest in animals fed 21 % lard and lowest in those receiving the control diet.

TABLE 2

Daily mean gain (DMG), pancreas weight relative to live-weight, total lipid content and pancreatic protein level (expressed in total amount, per g of pancreas and per kg of live weight) according to diet composition.

Parameters	Control (C)	Lard (L)	Sunflower oil (SO)	Statistical significance (F)
DMG (g)	$437 \pm 34^{(1)a(2)}$	266 ± 45^b	302 ± 24^{bc}	a-b P < 0.01 b-c P < 0.05
<u>Pancreas weight (g)</u> Live-weight (kg)	1.80 ± 0.05^a	2.31 ± 0.08^b	2.06 ± 0.07^{bc}	a-b P < 0.001 a-c P < 0.05
<u>Total lipids (g)</u> Pancreas (100 g)	2.98 ± 0.14^a	4.57 ± 0.09^b	3.29 ± 0.05^{ac}	a-b P < 0.001 b-c P < 0.05
<u>Total proteins (mg)</u>	$11\ 084 \pm 532^a$	$12\ 811 \pm 758^a$	$11\ 040 \pm 623^a$	NS
<u>Proteins (mg)</u> Pancreas (g)	202 ± 8^a	186 ± 9^a	188 ± 9^a	NS
<u>Proteins (mg)</u> Live-weight (kg)	363 ± 19^a	453 ± 73^{bc}	389 ± 21^{ac}	a-b P < 0.05

(1) Mean \pm Sem of values obtained.

(2) Values with the same superscript (a, b or c) are not statistically different at the 5 % level.

The pancreatic lipid content of the controls was significantly lower than that of animals fed the diet containing 21 % lard. The pancreas of the latter animals also exhibited a significantly higher lipid content than that of the groups receiving 21 % sunflower oil.

2. *Pancreatic protein content.* — The protein content of the pancreas, expressed in total amount or in mg per g of pancreas (table 2), was very constant in the three groups of animals and did not show any significant difference. The pancreatic protein content expressed per kg of live weight, was highest in the group ingesting 21 % lard, but this was mainly due to the low live weight of these animals at the end of the experiment.

3. *Chymotrypsin and trypsin activities.* — Chymotrypsin activity — either total, specific (per meg of protein) or per g of pancreas — was very similar and not different statistically in the three experimental groups (table 3).

Whatever the diet offered, total trypsin activity was similar in the three groups. Specific trypsin activity or per g of pancreas was lowest in pigs receiving 21 % lard, the difference being statistically significant as compared to pigs ingesting the diet containing 21 % sunflower oil.

4. *Amylase activity.* — The activity of this enzyme was very high in the controls, low in the pigs fed 21 % lard and even lower in the group ingesting 21 % sunflower oil (table 3). Whatever the mode of expression of amylase activity (total, specific or per g of pancreas), there was always a statistical difference between the control and the 21 % sunflower oil groups. Because of the wider dispersion of the values in the control group and the lower final weight of the 21 % lard group, the differences observed between the amylase activity of the latter group and that of the two others were not always significant.

5. *Lipase activity.* — Significant differences were observed between the lipase activity of the three groups (table 3).

The activity of the pancreatic lipolytic enzyme was very high in pigs receiving 21 % sunflower oil, moderate in those fed the diet containing 21 % lard and low in the controls. These observations concerned all forms of expression of enzyme activity (total, specific or per g of pancreas).

Discussion and conclusion.

In the present experimental conditions, growing pigs fed lipid-rich diets over a 12-day period showed lower mean gains than pigs fed a control diet. This was particularly marked with the diet containing 21 % lard. However, it was found that the growth rate increased in pigs ingesting a peanut-rich diet as compared to those fed a lower lipidic diet (Henry and Rérat, 1964 ; Henry, 1974). This is in contradiction with the results of our experiment but this contradiction is only apparent, as the energy level of our three diets was the same, so that the higher growth rate recorded by the former authors can be imputed to an increase in the

TABLE 3

Enzyme activities of chymotrypsin, amylase, lipase and trypsin according to diet composition.

Parameters	Control (C)	Lard (L)	Sunflower oil (SO)	Statistical significance (F)
<i>Total enzyme activities (U)</i>				
Chymotrypsin	111 475 ± 17 354 ^{(1)a(2)}	117 980 ± 15 617 ^a	120 140 ± 10 797 ^a	NS
Amylase	19 208 454 ± 2 998 792 ^a	14 350 168 ± 1 369 439 ^a	10 783 589 ± 708 183 ^b	a-b P < 0.05
Lipase	132 298 ± 19 112 ^a	244 708 ± 20 286 ^b	355 489 ± 38 722 ^c	a-c P < 0.001 a-b P < 0.005 b-c P < 0.05
Trypsin	19 591 ± 2 778 ^a	17 041 ± 2 259 ^a	20 216 ± 1 828 ^a	NS
<i>Specific enzyme activities (per mg of protein)</i>				
Chymotrypsin	9.8 ± 1.1 ^a	9.1 ± 0.99 ^a	10.9 ± 0.8 ^a	NS
Amylase	1 689 ± 186 ^a	1 112 ± 63 ^b	984 ± 57 ^{bc}	a-c P < 0.005 a-b P < 0.05
Lipase	11.6 ± 1.2 ^a	19 ± 0.7 ^b	31.9 ± 2.3 ^c	a-b b-c P < 0.001
Trypsin	1.72 ± 0.21 ^a	1.3 ± 0.13 ^{ab}	1.8 ± 0.09 ^{ac}	a-c b-c P < 0.01
<i>Enzyme activities (U)</i>				
Pancreas (g)				
Chymotrypsin	2 017 ± 293 ^a	1 816 ± 244 ^a	2 037 ± 155 ^a	NS
Amylase	349 398 ± 52 111 ^a	219 198 ± 18 645 ^b	184 544 ± 8 758 ^{bc}	a-c P < 0.01 a-b P < 0.05
Lipase	2 390 ± 311 ^a	3 732 ± 250 ^b	5 992 ± 493 ^c	a-c P < 0.001 a-b b-c P < 0.005
Trypsin	354 ± 47 ^a	257 ± 30 ^{ab}	342 ± 24 ^{ac}	b-c P < 0.05

(1) and (2) : see legends of Table 2.

energy level of the diet used and hence to a larger ingestion of digestible energy.

The utilization of either 21 % lard or sunflower oil in the diet led to an increase in pancreas weight relative to live weight (less marked with 21 % sunflower oil). These differences were to a great extent due to the variable total lipid content of the pancreas. Thus, it appeared that ingestion of lipid-rich diets (especially those rich in saturated fatty acids) significantly increased the total lipid content of the pancreas. The possible long-term physiopathological consequences of this should be envisaged, as food for human consumption in most industrialized countries is very lipid-rich.

Many studies on the adaptation of pancreatic amylase and lipase to dietary carbohydrates and lipids were made with diets in which not only the supply of carbohydrates and lipids, but also of proteins, was different. Now, variations in the protein supply have not only a specific effect on pancreatic proteases (mainly chymotrypsin in pigs), but also a non-specific effect on all pancreatic hydrolases (Vandermeers *et al.*, 1968 ; Corring and Saucier, 1972). In the present study, the dietary protein level was the same in all the experimental groups ; only the supply of carbohydrates and lipids as well as the nature of the latter varied. This allowed us to clearly show the sensitivity of pancreatic amylase and lipase to changes in the proportions of their specific substrates in the diet. Pancreatic protein content and chymotrypsin activity were not modified by the diets used. These findings are in agreement with previous observations by Mourot and Corring (1979) and Simoes Nunes (1982).

The enzyme activity of trypsin in pigs is generally little affected by variations in the dietary protein supply, *i.e.* in its specific substrates (Corring and Saucier, 1972 ; Simoes Nunes, 1982). Ingestion of the diet containing 21 % lard led to a particularly low trypsin activity. Such an effect was not observed either with 21 % sunflower oil or with diets including similar levels of peanut oil administered to growing pigs (Mourot and Corring, 1979 ; Simoes Nunes, 1982). It seems that lard exerts a depressive effect on the activity of trypsin.

It has been well established that amylase adapts to dietary starch content, and our data confirm its inductibility by its substrate in pigs (Corring, 1975 ; Mourot and Corring, 1979 ; Simoes Nunes, 1982). In parallel, it appears that pancreatic amylase activity is also sensitive to the nature of dietary triacylglycerols. Amylase activity was low with the diet containing 21 % sunflower oil. In rats, Deschodt-Lanckman *et al.* (1971) and Saraux *et al.* (1982) also observed that unsaturated fatty acid-rich triacylglycerols had a depressive effect on pancreatic amylase activity.

It appears to be essential to consider lipase activity determination in order to be able to separate the phenomenon of pancreatic lipase adaptation (under diet action) from a possible and isolated increase of the colipase level. The assay of lipase activity used concerns the determination of enzyme activity before and after the addition of colipase of pig origin. In previous studies and in the present one, we systematically observed that the values of lipase activity obtained before and after the addition of exogenous colipase were the same, *i.e.* that all the lipase activity present in the pancreatic tissue was measured. According to this, the observed variations of lipase activity with the diets offered to the pigs were the result of an increase in enzyme activity and not the indirect result of colipase

adaptation. However, it must be remembered that in the pig, colipase also adapts to the fat content in the diet, but this is less evident than in the case of lipase (Mouroit and Corring, 1979).

Pancreatic lipase was highly affected by the content and nature of dietary lipids. As compared to the control diet, its activity was 1.6 and 3-fold higher with diets containing 21 % lard and 21 % sunflower oil, respectively. Accordingly, there was a specific effect of the quality and quantity of dietary triacylglycerols on pancreatic lipase. The inductibility of lipase by the dietary lipid content confirmed previous data also obtained in pigs (Corring, 1975 ; Mouroit and Corring, 1979 ; Simoes Nunes, 1982). Differences in the ability of triacylglycerols (saturated or unsaturated) to stimulate pancreatic lipase have only been studied in rats by Deschodt-Lanckman *et al.* (1971) and Saraux *et al.* (1982). Contradictory conclusions were drawn from these studies on differences in the sensitivity of lipase to the degree of unsaturation of the fatty acids of dietary triacylglycerols. Thus, Deschodt-Lanckman *et al.* (1971) showed that the inductibility of lipase by triacylglycerols was higher with those containing unsaturated fatty acids, while Saraux *et al.* (1982) did not observe such an effect. The results of our study seem to show that pig pancreatic lipase is not only specifically sensitive to the content but also to the nature of dietary triacylglycerols.

It may be concluded that the enzyme composition of the pig pancreas adapts to the carbohydrate and lipid content of the diet. The inductibility of pancreatic lipase also depends on the degree of unsaturation of the triacylglycerol fatty acids, *i.e.* inductibility is higher when the triacylglycerols are rich in unsaturated fatty acids (sunflower oil) than when they are rich in saturated fatty acids (lard).

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Résumé. *Adaptation de la lipase pancréatique à la teneur et à la nature des lipides alimentaires chez le porc.*

L'objectif du travail rapporté a été d'examiner, chez le porc en croissance, l'adaptation de la lipase pancréatique à la quantité et à la nature des lipides du régime alimentaire. Trente porcs de $25,5 \pm 0,32$ kg de poids vif initial ont été répartis en trois groupes de dix animaux chacun. Ils ont reçu respectivement le régime C (3,5 % de saindoux ; 3,5 % d'huile de tournesol ; 67,7 % d'amidon), le régime L (21 % de saindoux ; 33,2 % d'amidon) et le régime SO (21 % d'huile de tournesol ; 33,2 % d'amidon). Les trois régimes (isoénergétiques et isoprotéiques) ont été alloués aux animaux en quantité égale (1,5 kg/jour/porc) pendant douze jours. Sur le tissu pancréatique, prélevé à la fin de l'expérience, différents paramètres ont été déterminés.

Le poids du pancréas relatif au poids vif s'est montré le plus élevé dans le lot L. Le contenu en lipides totaux du pancréas de ces animaux était supérieur de 53 % et de 39 % respectivement à celui des lots C et SO. La teneur en protéines pancréatiques est apparue identique dans les trois groupes d'animaux. L'activité spécifique (U/mg de protéines) de la lipase dans le lot SO était environ une fois et demie celle du lot L et environ trois fois celle

du lot C (SO : 31,9 ; L : 19 et C : 11,6). L'activité spécifique de l'amylase a été plus élevée chez les animaux C que chez ceux des deux autres groupes (C : 1689 ; L : 1112 et SO : 984), tandis qu'aucune différence ne s'est révélée dans l'activité de la chymotrypsine. La trypsine a présenté l'activité spécifique la plus faible dans le lot L.

Ces résultats confirment, d'une part, l'adaptation de la lipase et de l'amylase pancréatiques à leurs substrats respectifs et montrent, d'autre part, que l'activité de la lipase pancréatique est plus ou moins inductible selon le degré d'insaturation des lipides. L'activité enzymatique de la lipase est beaucoup plus élevée chez le porc, pour la même quantité de triacylglycérols alimentaires, quand ceux-ci sont riches en acides gras insaturés. Les mécanismes impliqués dans ce phénomène restent à déterminer. Les éventuelles conséquences physiopathologiques de l'augmentation du contenu en lipides totaux du pancréas, observée chez le porc nourri avec des régimes riches en triacylglycérols (surtout saturés), méritent aussi d'être envisagées.

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