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Deposition of dietary fatty acids, *de novo* synthesis and anatomical partitioning of fatty acids in finishing pigs

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Predicting aspects of pork quality becomes increasingly important from both a nutritional and technological point of view. The aim of the present study was to provide quantitative information on the relation between nutrient intake and whole-body fatty acid (FA) deposition. This information is essential to develop mechanistic models predicting the FA content of tissues. A serial slaughter study was carried out in which thirty pigs were slaughtered between 90 and 150 kg. The diet included 15 g/kg soyabean oil and contained 44 g/kg fat. Only 0·31 and 0·40 of the digested *n*-6 and *n*-3 FA were deposited, respectively. Approximately one-third of the *n*-3 supply that was deposited resulted from the conversion of 18 : 3 to other metabolites (i.e. EPA, docosapentaenoic acid and DHA). This proportion was affected by the pig genotype. *De novo*-synthesised FA represented 0·86 of the total non-essential FA deposition, and its average composition corresponded to 0·017, 0·286, 0·025, 0·217 and 0·454 for 14 : 0, 16 : 0, 16 : 1, 18 : 0 and 18 : 1, respectively. Although the average whole-body FA composition was relatively constant during the finishing period, this was not so for the tissues. In the carcass (without backfat), the content of 18 : 1 increased during the finishing period, whereas that of 16 : 0 and 18 : 0 decreased. Backfat captured a proportionally greater fraction of 18 : 2 than did the carcass or the residual tissues. In contrast, a proportionally greater fraction of the dietary 18 : 3 supply was deposited in the carcass compared to other tissues.

Model: Fatty acid deposition: Fatty acid synthesis: Lipid deposition: Pigs

The lipid content and fatty acid (FA) profile of the carcass have an impact on the technological transformation (i.e. a high content of PUFA increases fat softness and the risk of oxidation) and on the nutritional and organoleptic quality (e.g. intra-muscular lipid content, saturated FA content, and *n*-3 to *n*-6 ratio). Deposited lipids originate from dietary FA and *de novo*-synthesised FA. Nutrition is the main factor through which the lipid and FA deposition in pigs may be altered, even if other factors such as genotype, sex, age, slaughter weight and environmental temperature also affect lipid and the FA content (e.g. Wood, 1984; Lebret & Mourot, 1998; Le Dividich *et al.* 1998). Although numerous studies have been carried out studying the relation between nutrition and the FA composition of tissues (e.g. Miller *et al.* 1990; Madsen *et al.* 1992; Wiseman & Agunbiade, 1998; Gatlin *et al.* 2002; Ostrowska *et al.* 2003), these relations are often limited to a single tissue (typically backfat). Consequently, only empirical relationships can be established between nutrition and the FA content of these tissues. In order to define nutritional strategies that modulate the FA profile of tissues, a more mechanistic approach is desirable, describing FA deposition at the whole-animal level.

Mathematical models have been used to predict the consequences of nutritional strategies on pig performance and typically predict whole-body protein and lipid mass (e.g. Whittemore & Fawcett, 1976; Pomar *et al.* 1991; de Lange, 1995). Based on the generic growth model of De Lange (1995), Lizardo *et al.* (2002) developed a first approach with the objective to predict the consequences of different nutritional strategies on FA deposition. Development of this conceptually simple model was hampered by the limited availability of experimental data at the whole-animal level. Especially data concerning the fate of dietary lipids and the composition of *de novo*-synthesised FA was scarce. Danfaer (1999) developed a mechanistic model of carbohydrate and lipid metabolism at the cellular level based on studies of Dunshea *et al.* (1992*a*,*b*). The latter estimated the kinetics of glycogen, glucose and NEFA *in vivo* in the plasma of growing pigs (70 kg body weight (BW)). However, the model proposed by Danfaer (1999) corresponds to the nutrient flow just after ingestion and during a short period of time (a few hours). It is therefore unlikely that it can be used to describe whole-animal FA deposition for prolonged periods of time.

Kloareg *et al.* (2005) further developed the conceptual model of Lizardo *et al.* (2002) and estimated key elements of whole-body FA metabolism related to the efficiency of depositing dietary FA and the composition of *de novo*-synthesised FA. In the absence of a reasonable alternative, Lizardo *et al.* (2002) assumed that tissues would not

Abbreviations: B, backfat compartment; BW, body weight; C, carcass (without backfat) compartment; DPA, docosapentaenoic acid; FA, fatty acid; VHFT, viscera, head, feet and tail compartment.

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preferentially capture specific dietary FA. According to their model, differences in lipid development between tissues (i.e. allometry) in combination with the supply of FA during growth would be the only cause of differences in FA content between tissues. As indicated by Lizardo *et al.* (2002), this simple hypothesis does not seem to hold.

The objective of the present study is to use data from a study of Kloareg *et al.* (2006) to address different aspects of FA deposition in finishing pigs. These aspects include the fate of dietary FA, the composition of *de novo*-synthesised FA and the distribution of FA between different tissues.

Material and methods

Experimental design

Details concerning the experimental design can be found in Kloareg *et al.* (2006). In short, eight blocks of four littermates were used in a factorial design including two genotypes (crossbred Piétrain × (Landrace × Large White) and Large White) and two sexes (females and barrows). From 80 kg BW onwards, animals were offered a diet based on wheat, maize, barley, soyabean meal, which contained also 15 g/kg soyabean oil. The diet contained 153 g/kg crude protein and 44 g/kg lipid. The main FA were 18 : 2, 18 : 1, 16 : 0, 18 : 3 and 18 : 0 (0·54, 0·22, 0·14, 0·045, 0·033 of total FA, respectively). The chemical composition of the diet is given in Table 1. A representative feed sample was obtained by regularly taking samples of the distributed feed. The DM content of the distributed ration was measured weekly. Feed refusals (if any) were collected and weighed daily and sampled to measure the DM content. Pigs were slaughtered at approximately 90, 110, 130 and 150 kg after a 16 h fast.

Table 1. Chemical composition and nutritional values of the experimental diet (adjusted for a DM content of 873 g/kg)

Ingredients (g/kg)	
Wheat	247·2
Maize	247·2
Barley	247·2
Wheat bran	50·0
Soyabean meal	160·0
Soyabean oil	15·0
Dicalcium phosphate	12·0
Calcium carbonate	11·0
Salt	4·5
Vitamins and mineral mixture	5·0
Chemical composition (g/kg)	
Ash	48
Crude protein	153
Starch	446
Lipid	44
Crude fibre	27
Gross energy (MJ/kg)	16·3
Nutritional values*	
Digestible energy (MJ/kg)	13·7
Metabolisable energy (MJ/kg)	13·2
Net energy (MJ/kg)	9·9
Digestible lysine (g/kg)	6·8
Fatty acid composition (mg for 100 g feed)	
14 : 0	5
14 : 1	2
16 : 0	474
16 : 1	8
18 : 0	110
18 : 1	728
18 : 2	1772
20 : 0	4
18 : 3	150
20 : 1	14
20 : 2	4
22 : 0	10
20 : 4	1
22 : 1	1
20 : 5	5
24 : 0	6
24 : 1	3
22 : 5	1
22 : 6	2
Total fatty acids	3302

* Calculated from Sauvant *et al.* (2002).

Compartments

At slaughter, blood was collected, weighed, sampled and pooled by genotype. The empty digestive tract, kidneys, liver, heart and lungs, spleen, diaphragm, leaf fat, head, feet and tail were weighed and combined as a single compartment (viscera, head, feet and tail (VHFT)). Empty BW was calculated as the sum of the weight of the blood, VHFT and hot carcass. The left half carcass was divided in primal cuts according to the Dutch normalised procedure (Institut Technique du Porc, 1990). Backfat (B) was separated from the loin. The loin (without backfat), shoulder, belly and ham were combined as a single compartment (carcass (C)). The VHFT, B and C compartments were weighed, frozen, ground separately, minced and homogenised. Four samples of each compartment were taken. Two of these were used to determine the DM content. The two other samples were freeze-dried and used for further chemical analysis.

Chemical analyses

The lipid content of feed and carcass were determined by solvent extraction. Lipids in the diet were extracted using chloroform. For the VHFT, B, C and blood samples lipids were extracted with a chloroform and methanol mixture (chloroform–methanol, 2 : 1). All extractions were performed using an automatic extraction system Soxtec Avanti 2050 (FOSS, Höganäs, Sweden) in two steps of 30 min each. First, the sample was immersed in the boiling solvent to dissolve most of the soluble material. In the second step, the sample was raised above the solvent surface to permit efficient washing with solvent from the condensers. During the extraction, solvents were heated to 110°C. As the average lipid content in the blood was 1·7 g/kg, its contribution to lipid and FA deposition was ignored for the remainder of the study. The FA of the lipid extraction in the diet and in VHFT, B and C were transmethylated according to Morrisson & Smith (1964) and the FA profile was obtained by GC using a 30 m long and 0·25 mm wide capillary column. In addition to FA, extracted lipids also contain glycerol, phospholipids and other chloroform- or methanol-soluble components. The FA to lipid ratio in a body compartment was considered constant for all animals and was calculated as the average FA to lipid ratio for each compartment. This ratio was obtained by weighing the lipid extraction used for the transmethylation (approximately 20 mg) to which 2·5 mg heptadecanoic acid (17 : 0) was

added, a FA that does not exist in monogastric animal tissues. The FA profile was expressed as a percentage of identified FA and converted (in g) using the 17 : 0 recovery.

Fatty acids ileal digestibility values

Ileal digestibility values for the dietary FA were not determined but were estimated from literature data. The FA digestibility may be different for FA provided by soya oil compared to those provided by other feed ingredients. The ileal FA digestibilities provided by the basal diet were supposed to correspond to those measured for total lipids, without added oil, by van Milgen *et al.* (2001). This value (0·74) was used for all FA provided by the basal diet. For the ileal digestibility of the soyabean oil FA, the mean values observed by Jørgensen *et al.* (1992) for two diets (basal diet with 5 g/kg crude fat and, respectively, 10 and 20 g/kg added soyabean oil) were used, with different values for each FA. The calculated ileal digestibility for the dietary FA were then 0·77, 0·78, 0·78, 0·80, 0·81, 0·82 and 0·87 for 14 : 0, 16 : 0, 16 : 1, 18 : 0, 18 : 1, 18 : 2 and 18 : 3, respectively. For the other dietary FA, the ileal digestibility was supposed to be 0·95.

Fatty acid deposition

The FA content of the three body compartments was calculated as the lipid content multiplied by their respective FA to lipid ratio and the analysed FA profile. Deposited essential FA (18 : 2 and 18 : 3) originate from the diet only and their deposition rate may be used to estimate the oxidation rate of these FA. However, essential FA may also be used for synthesis of other *n*-6 or *n*-3 FA. For example, 18 : 2 is a precursor for other *n*-6 FA such as dihomolinolenic acid (20 : 3) and arachidonic acid (20 : 4). Similarly, 18 : 3 is a precursor for other *n*-3 FA such as EPA (20 : 5), docosapentaenoic acid (DPA; 22 : 5) and DHA (22 : 6). Thus, in addition to the deposition rates of individual essential FA, the deposition rates for *n*-6 FA and *n*-3 FA were calculated. The digested and deposited 20 : 3 and 20 : 4 were expressed as molar 18 : 2 equivalents required to synthesise these FA and the digested and deposited EPA, DPA and DHA were expressed as molar 18 : 3 equivalents. The balance of individual and *n*-6 and *n*-3 FA were calculated for each period using the comparative slaughter technique (i.e. from 90 to 110 kg, from 110 to 130 kg, from 130 to 150 kg). The period had no significant effect on the results and these results are not presented in the present paper. Because calculated FA balances obtained from successive (relatively) short periods of time results are quite variable, it was decided to analyse the FA deposition for the whole period (i.e. 90–150 kg) through regression. Essential FA (18 : 2 and 18 : 3) and *n*-6 and *n*-3 FA mass were regressed on the digestible intake of these FA consumed since the beginning of the experiment (SAS, 2000). The slope of this regression represents the deposition rate and effects of sex and genotype were tested on this slope.

De novo synthesis

A regression analysis was also used to estimate the deposition rates of 14 : 0, 16 : 0, 16 : 1, 18 : 0, 18 : 1, EPA, DPA and DHA. It is not possible to determine the oxidation rate for non-essential dietary FA because deposited FA originate from digested dietary FA and from *de novo*-synthesised FA. Based on results from a previous study (Kloareg *et al.* 2005), it was assumed that 0·70 of dietary non-essential FA were deposited as is.

Only 14 : 0, 16 : 0, 16 : 1, 18 : 0 and 18 : 1 were taken into account in the calculation of *de novo* synthesis because the quantity of long-chain FA synthesised *de novo* is very small. The composition of FA synthesis was used to estimate flow partitioning rates (i.e. elongation and desaturation) of non-essential FA at the whole-animal level (Kloareg *et al.* 2005). Similarly, deposition rates of the long-chain *n*-3 FA (EPA, DPA and DHA) were used to estimate the conversion of dietary 18 : 3 to these FA.

Lipid gain composition and fatty acid anatomical partitioning

To study the FA composition of the lipid deposition in each compartment, allometric relations were used to describe the deposition of a FA in a compartment relative to either the lipid mass of this compartment or relative to the total quantity of this FA deposited in the body:

$$\log(Y) = \log(a) + b \times \log(X),$$

where Y is the FA mass in a body compartment (g) and X is either the lipid mass of that compartment or the total body mass of that FA. The FA composition of deposited lipid (in the whole body or in a compartment) is given by the first derivative of the allometric function relative to lipid mass (i.e. $\mathrm{dFA/d(lipid)} = a \times b \times (\mathrm{lipid})^{(b-1)}$). Similarly, partitioning of FA between anatomical compartments is given by the first derivative of the allometric function relative to total body mass of the FA. The effect of sex or genotype was not estimated on these relations.

Results

Animals were slaughtered between 84 and 154 kg BW. Results concerning performance, weights of compartments and organs, and protein and lipid deposition have been reported by Kloareg *et al.* (2006). On average, C, B and VFHT represented, respectively, 0·694, 0·058 and 0·189 of empty BW and 0·634, 0·183 and 0·183 of whole-body lipid mass. The main results concerning performance and lipid and FA composition are given in Table 2. The FA to lipid ratio was 0·71, 0·80 and 0·58 for C, B and VHFT, respectively. For the whole body, this ratio was 0·70. For some FA, the FA composition was affected by the BW at slaughter (i.e. 90, 110, 130 or 150 kg) and/or by genotype (Table 2).

Metabolism of essential fatty acids

The supply and deposition of *n*-6 FA was almost exclusively as 18 : 2. Consequently, the regression of FA deposition *v.* digestible FA supply gave identical results for 18 : 2 and *n*-6 FA. The slope of this relation was 0·31 (SE 0·03), which means that only 0·31 of the digestible *n*-6 FA supply was deposited in the body. As illustrated in Fig. 1, both sex and genotype affected the deposition rate ($P < 0{\cdot}01$; Fig. 1), resulting in slopes varying between 0·23 and 0·38. Digestible 18 : 3 represented 0·95 of the supply of digestible *n*-3 FA in the diet. On the other hand, deposited 18 : 3 represented only 0·63 of total deposited *n*-3

Table 2. Performance and body composition of finishing pigs slaughtered between 90 and 150 kg†
(Mean values)

	Crossbred		Large White		Target slaughter weight (kg)				Statistical analysis‡	
	Female	Barrow	Female	Barrow	90	110	130	150	RSD	Effects
Number of animals	8	7	8	7	8	8	6	8		
Body weight (kg)	119	115	117	120	89	107	129	149	4	BW***
EBW (kg)	113	110	112	113	84	102	123	142	4	BW***
Feed intake (kg/d)§	3·34	3·13	3·08	3·59	2·96	3·20	3·28	3·41	0·27	BW* S* G*
Body weight gain (kg/d)§	1·05	0·93	0·98	1·13	0·96	1·10	1·04	1·01	0·16	
Body composition										
Lipid (g/kg EBW)	209	232	229	258	188	216	248	277	24	BW*** S** G*
Fatty acids (g/kg body compartment)										
In EBW	147	163	160	181	131	151	174	195	17	BW*** S** G*
In viscera, head, feet, tail	122	138	127	142	102	120	143	166	13	BW*** S**
In carcass without backfat	134	146	151	169	124	141	157	176	16	BW*** S* G**
In backfat	573	592	570	613	561	579	617	596	42	S*
Fatty acids (g/kg total fatty acids)										
14 : 0	14·2	14·4	15·0	15·8	15·5	14·9	14·6	14·3	0·7	BW* G***
14 : 1	0·8	0·7	0·8	0·8	1·0	0·8	0·8	0·6	0·1	BW***
16 : 0	277·5	283·1	278·1	282·0	287·7	281·7	278·7	271·6	7·4	BW**
16 : 1	28·7	29·4	29·2	30·3	34·1	30·2	26·9	25·6	4·2	BW**
18 : 0	166·6	165·7	173·5	175·2	168·4	167·8	178·4	168·4	19·3	
18 : 1	410·8	408·8	394·5	397·8	392·9	406·8	397·9	412·8	17·7	G*
18 : 2	57·0	55·9	66·7	56·6	53·4	57·7	58·2	67·4	9·5	G*
20 : 0	2·3	2·3	2·5	2·6	2·7	2·1	2·3	2·5	0·5	
18 : 3	6·8	6·6	5·3	4·5	3·7	7·4	6·8	5·5	1·7	BW** G**
20 : 1	2·9	4·8	7·2	7·6	6·8	3·8	5·2	6·5	2·7	G**
20 : 2	26·2	23·9	20·5	20·2	28·4	20·9	23·4	18·5	4·8	BW** G*
22 : 0	0·1	0·2	0·4	0·3	0·2	0·2	0·2	0·4	0·2	G*
20 : 4	0·6	0·3	0·6	0·7	0·6	0·7	0·5	0·5	0·3	
22 : 1	0·3	0·3	0·5	0·3	0·3	0·3	0·5	0·5	0·3	
20 : 5	1·7	1·5	2·5	2·3	1·5	1·9	2·4	2·4	0·7	G**
24 : 0	0·3	0·1	0·3	0·2	0·2	0·1	0·2	0·4	0·2	
24 : 1	1·7	0·7	1·0	1·0	0·9	1·0	1·7	1·0	1·0	
22 : 5	0·9	0·9	1·0	1·2	1·4	1·0	0·8	0·8	0·5	
22 : 6	0·6	0·4	0·5	0·7	0·5	0·8	0·6	0·4	0·4	

EBW, empty body weight.
† For details of procedures, see pp. 36–37.
‡ From ANOVA; RSD, residual standard deviation; BW, effect of body weight; G, effect of genotype; S, effect of sex. Levels of significance: *$P<0·05$; **$P<0·01$, ***$P<0·001$.
§ Between 80 kg and the target slaughter weight. Feed intake was adjusted for 873 g DM/kg.

FA; the remainder was deposited as 20 : 5, 22 : 5 and 22 : 6. The slopes of the relations between the deposited and the digested FA was 0·24 (SE 0·06) for 18 : 3 and 0·40 (SE 0·05) for *n*-3 FA (Fig. 1). This means that 0·40 of the digestible *n*-3 FA supply was recovered in the body and that 0·60 remained unaccounted for. The slopes of the relation between deposited and digestible EPA, DPA and DHA supply were 4·2 (SE 0·6), 1·5 (SE 0·9) and 1·1 (SE 0·5), respectively. The corresponding profile of *n*-3 FA that were synthesised was 0·909, 0·060 and 0·031 for EPA, DPA and DHA, respectively. These results allow the estimation of the partitioning of 18 : 3 that could be accounted for. The metabolism of 18 : 3 first occurs through a successive desaturation, elongation and again a desaturation to EPA. As indicated earlier, 0·24 of the supply of digestible 18 : 3 was deposited as is, and 0·13 was further metabolised, first to EPA. Most of this supply (0·114) was deposited as EPA, whereas the remainder (0·0114) was elongated to DPA. Approximately two-thirds of this (0·0075) was deposited as DPA and one-third (0·0039) was metabolised further and deposited as DHA.

Genotype affected the deposition rate of 18 : 3 ($P=0·01$). The slope of the relation between deposited and digestible 18 : 3 supply was 0·19 for the Large White and 0·33 for the crossbred. As the deposition rate of *n*-3 FA was not affected by genotype ($P=0·40$), this means that Large White pigs convert a greater proportion of 18 : 3 to EPA, DPA and/or DHA than do the crossbred (0·15 *v.* 0·08 of digestible 18 : 3). Moreover, the deposition rate of EPA is greater for Large White than for crossbred ($P=0·004$), whereas the deposition rates of DPA and DHA are not affected by genotype. Consequently, the *n*-3 synthesis profile is affected by genotype (0·922, 0·051 and 0·027 for Large White *v.* 0·859, 0·093 and 0·048 for crossbred for EPA, DPA and DHA, respectively).

Metabolism of non-essential fatty acids

The slopes of the relation between the deposited and digestible non-essential FA were 19·9 (SE 1·6), 4·2 (SE 0·3), 18·0 (SE 2·6), 11·8 (SE 1·1) and 4·2 (SE 0·3) for 14 : 0, 16 : 0, 16 : 1, 18 : 0 and 18 : 1, respectively. These values indicate that, in this experiment, the *de novo* synthesis was several times greater than the dietary supply of these FA. In fact, assuming that 0·70 of digestible, dietary non-essential FA were deposited as is, the *de novo* synthesis represented on average 0·86 of the non-essential FA deposition. The corresponding profile of *de novo*-synthesised FA was 0·017, 0·286, 0·025, 0·217 and 0·454 for 14 : 0, 16 : 0, 16 : 1, 18 : 0 and 18 : 1, respectively. Sex and

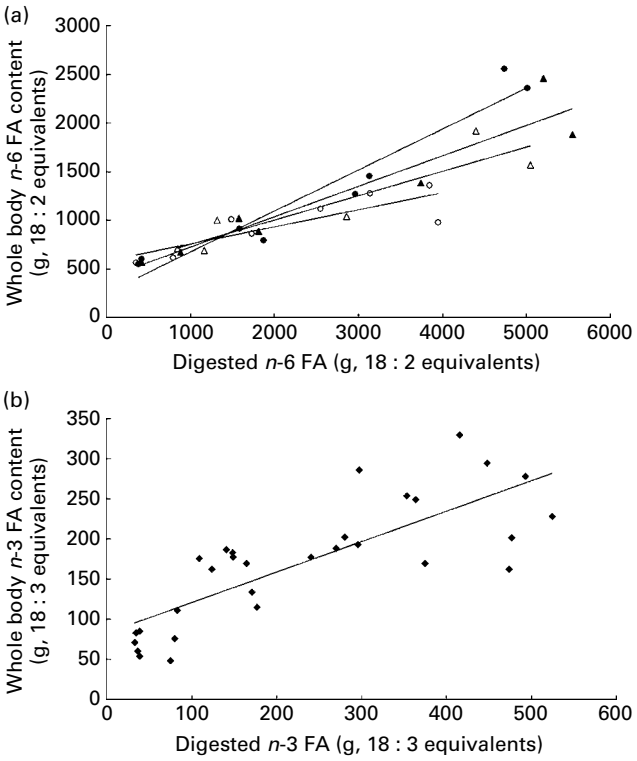

Fig. 1. Relation between deposited *n*-6 and *n*-3 fatty acid (g) and digestible fatty acid supply since 80 kg of BW (g). Sex and genotype affected the slope of the relation for *n*-6 fatty acids ($P = 0{\cdot}005$; (a): 0·38 for Large White females (•), 0·31 for Large White barrows (▲), 0·27 for crossbred barrows (△) and 0·23 for crossbred females (c). Sex and genotype had no effect on the slope for *n*-3 fatty acid deposition ((b); 0·40).

genotype affected the ratio between deposited and digested FA ratio for 14 : 0, 16 : 0 and 18 : 1 ($P < 0{\cdot}05$), suggesting that the *de novo* synthesis is affected by both sex and genotype. The composition of *de novo*-synthesised FA is given in Table 3 for the four groups. Boars tend to deposit slightly more 16 : 1 than gilts, whereas Large White deposit more 18 : 0 and less 18 : 1 than the crossbred. Nevertheless, differences in the profiles of *de novo*-synthesised FA remain small.

The present results allow estimation of the partitioning of *de novo*-synthesised FA. Of the total flow of 16 : 0 that is used in the *de novo* synthesis, 0·286 will be deposited as is, 0·017 will be shortened to 14 : 0, 0·025 will be desaturated to 16 : 1 and 0·671 will be elongated to 18 : 0. Similarly, 0·324 of the *de novo*-synthesised 18 : 0 will be deposited as is and 0·676 will be desaturated to 18 : 1.

Table 3. Calculated composition of *de novo*-synthesised fatty acids in finishing pigs*

	Crossbred		Large White	
Fatty acid	Female	Barrow	Female	Barrow
14 : 0	0·015	0·015	0·017	0·018
16 : 0	0·281	0·288	0·279	0·291
16 : 1	0·025	0·025	0·023	0·027
18 : 0	0·211	0·190	0·226	0·228
18 : 1	0·467	0·483	0·455	0·436

* It was assumed that 0·30 of the digestible dietary fatty acids supply was oxidised. For details of the calculation method, see p. 37.

Composition of lipid deposition and anatomical partitioning of fatty acids

In Table 4, the average FA composition of the total FA gain is given for the whole body and for the different tissues. The results indicate that, relative to the whole-body FA gain, the FA gain in C has a slightly higher 18 : 1 and a lower 18 : 2 content. The FA gain in B contains less 16 : 0 and 18 : 1, but considerably more 18 : 2 and 18 : 3 compared to the whole-body FA gain. Finally, VFHT contains less 18 : 1 and 18 : 2, but more of the saturated FA 16 : 0 and 18 : 0.

Parameter estimates of the allometric relationships between the different FA masses and whole-body lipid mass are given in Table 4. The shape parameter *b* of the allometric relations indicates the change in FA mass relative to the lipid mass. A constant composition would result in a shape parameter of 1. The shape parameter was close to 1 for most non-essential FA, with the exception of 16 : 1 ($b = 0{\cdot}716$ (SE 0·070)) suggesting that the 16 : 1 content decreases with lipid mass. In contrast, in the present experiment the proportion of essential FA in lipid mass increased with lipid mass ($b = 1{\cdot}188$ (SE 0·072) for 18 : 2; $b = 1{\cdot}243$ (SE 0·207) for 18 : 3).

Table 4 also lists the parameter estimates of the allometric relation between FA and lipid mass in the three body compartments. It appears that for 16 : 0 and 18 : 0, B and VFHT follow a similar development pattern. For 18 : 1, deposition occurs relatively early for VHFT and relatively late for C. The most striking difference occurs for the essential FA. The shape parameter *b* for C is much greater than those observed for B and VFHT, indicating that deposition of essential FA in C increases during the later stages of growth.

In the preceding analysis, FA mass of a compartment was related by an allometric relation to the total lipid mass of that compartment. An alternative approach is to relate the FA mass of a compartment to the total mass of that FA in the body. The results are given in Table 5. On average, 0·60 of the total FA gain was deposited in C, 0·25 in B and 0·15 in VHFT. This partitioning is variable for the different FA, especially for essential FA. Of the total 18 : 2 deposition, 0·48 was deposited in C, 0·44 in B and only 0·08 in VFHT. In contrast, for 18 : 3, 0·71 was deposited in C, 0·21 in B and 0·08 in VFHT. The proportion of total FA deposited in B increases during growth, as well as the proportions of non-essential FA at the expense of the deposition of essential FA. The reverse is seen for C.

Discussion

Fatty acid oxidation

In the present study, 0·31 of *n*-6 and 0·40 of the digestible *n*-3 FA supply was recovered in the body. The remainder (0·69 for *n*-6 FA and 0·60 for *n*-3 FA) could not be accounted for and was supposed to be oxidised or converted to non-FA metabolites. The serial slaughter technique used in the present study does not distinguish between physiological processes that may be involved in the metabolism of *n*-3 FA (i.e. postprandial oxidation, oxidation due to the turnover of the lipid mass or further synthesis of metabolites such as hormones or prostaglandins). Moreover, the results are directly affected by the (assumed) ileal digestibility of essential FA, which were estimated from literature data (0·82 and 0·87 for 18 : 2

Table 4. Allometric development of the fatty acid (FA) mass relative to the lipid mass in different body compartments in finishing pigs*

	Whole body		C		B		VHFT	
Average lipid mass (g)	26 668		16 755		4988		4925	
Average composition of fatty acid gain (g/kg FA gain)†								
Main non-essential FA	921		941		859		960	
14 : 0	14		15		12		17	
16 : 0	275		276		254		308	
16 : 1	21		22		16		24	
18 : 0	180		170		175		229	
18 : 1	431		458		402		382	
Essential FA	79		59		141		40	
18 : 2	72		53		132		36	
18 : 3	7		5		9		3	
Scale (*a*) and shape (*b*) parameters of the allometric relations	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
Main non-essential FA	0·623	1·001	0·718	0·990	0·528	1·026	0·510	1·006
14 : 0	0·017	0·954	0·023	0·924	0·010	0·994	0·006	1·048
16 : 0	0·304	0·957	0·420	0·925	0·161	1·022	0·171	1·000
16 : 1	0·358	0·716	0·550	0·671	0·036	0·891	0·072	0·825
18 : 0	0·087	1·031	0·169	0·965	0·039	1·132	0·040	1·124
18 : 1	0·193	1·038	0·148	1·070	0·341	0·992	0·317	0·958
Essential FA	0·00656	1·190	0·00017	1·521	0·355	0·879	0·05828	0·900
18 : 2	0·00614	1·188	0·00014	1·530	0·349	0·873	0·05241	0·900
18 : 3	0·00032	1·243	0·00031	1·234	0·011	0·957	0·00234	0·976

B, backfat; C, carcass without backfat; VHFT, viscera, head, feet and tail.
* The allometric relation $Y = aX^b$ was used between 80 and 150 kg live weight, where Y is the fatty acid mass (g) and X the lipid mass (g) of the compartment.
† The first derivative of the allometric relation was used to calculate the average composition: the d*F*A/d*X* was calculated for the average lipid mass and multiplied by the FA to lipid ratio for each compartment.

and 18 : 3, respectively). For example, if the assumed digestibility of 18 : 2 decreases from 0·82 to 0·72, the recovery rate increases from 0·31 to 0·36. Nevertheless, both estimates of oxidation are considerably higher than those found in the literature, particularly for *n*-6 FA. Using also the slaughter technique, Flanzy *et al.* (1970) estimated an average net oxidation rate of 18 : 2 of 0·50 in pigs between 45 and 100 kg BW. Average daily gain of the animals affected this value, with estimates varying between 0·35 (for a high daily gain) to 0·66 (for a low daily gain; Flanzy *et al.* 1970). This may be due to the higher turnover rate of *n*-6 FA turnover and the relative importance of hormone synthesis at low growth rates. The results of the present study may be compared to those having a high growth rate in the study of Flanzy *et al.* (1970), for which the 18 : 2 net oxidation varied between 0·35 and 0·43. Using the comparative slaughter technique, Kloareg *et al.* (2005) estimated a net oxidation of 0·31 for *n*-6 and 0·52 for 18 : 3 FA. These values were not affected by feeding level. Chwalibog *et al.* (1992) concluded that, based on data obtained in respiration chambers, all digestible dietary lipids were stored (i.e. they concluded that there was no oxidation of dietary FA). Crespo & Esteve-Garcia (2002*b*) observed oxidation rates between 0·07 and 0·30 for *n*-6 and *n*-3 FA in chicken. Using ^{14}C-labelled medium-chain FA and essential PUFA, Leyton *et al.* (1987) estimated whole-body oxidation rates during a 24 h period in weanling rats. The oxidation rates (measured as expired $^{14}CO_2$) were 0·48 for 18 : 2 and 0·64 for 18 : 3. Little information is available in the literature about factors affecting *n*-6 or *n*-3 oxidation that could explain these differences. Stage of

Table 5. Anatomical partitioning of fatty acids (FA) and lipids between the three compartments*

		Partitioning†			C		B		VHFT	
X	Average *X* (g)	C	B	VHFT	*a*	*b*	*a*	*b*	*a*	*b*
Lipids	26 668	0·596	0·222	0·182	1·113	0·944	0·021	1·212	0·211	0·987
FA	18 743	0·599	0·252	0·149	1·165	0·939	0·027	1·208	0·186	0·979
Main non-essential FA	16 808	0·608	0·238	0·155	1·239	0·934	0·018	1·243	0·177	0·987
14 : 0	276	0·616	0·207	0·177	1·022	0·924	0·042	1·244	0·109	1·074
16 : 0	5214	0·600	0·235	0·165	1·350	0·915	0·015	1·294	0·135	1·021
16 : 1	529	0·670	0·174	0·155	1·046	0·939	0·014	1·355	0·120	1·035
18 : 0	3207	0·569	0·245	0·186	1·487	0·894	0·014	1·319	0·112	1·055
18 : 1	7582	0·633	0·236	0·131	0·811	0·975	0·053	1·151	0·336	0·905
Essential FA	1251	0·494	0·431	0·075	0·060	1·260	1·615	0·836	0·665	0·734
18 : 2	1141	0·479	0·444	0·077	0·056	1·265	1·743	0·827	0·572	0·751
18 : 3	110	0·714	0·209	0·077	0·096	1·353	2·467	0·580	0·230	0·804

B, backfat; C, carcass without backfat; VHFT, viscera, head, feet and tail.
* The allometric relation $Y = aX^b$ was used were Y is the lipid or fatty acid mass deposited in each compartment (g) and X is the whole-body lipid or fatty acid mass (g).
† The first derivative of the allometric relation was used for the average value of *X*.

development undoubtedly will affect the results. Whereas a growing animal will deposit some of the dietary energy supply, mature animals will be (almost) in energetic equilibrium and thus catabolise all dietary energy. Pigs used in the present study were still depositing considerable quantities of energy and lipid and it is unlikely that stage of development may explain the high oxidation rate observed in the present study. Also diet composition, and especially the lipid content and FA composition, may affect the oxidation of FA. It has been shown in chickens that the dietary 18 : 2 and 18 : 3 contents increase the oxidation of these FA (Crespo & Esteve-Garcia, 2002*a*,*b*; Newman *et al.* 2002). The 18 : 2 and 18 : 3 contents in the diet used in the present study were higher than those used by Kloareg *et al.* (2005). Although this may have contributed to the observed difference in oxidation rates, the magnitude of the difference is considerable.

De novo synthesis

The deposition of dietary FA is small compared to FA synthesis and represented in the present study 0·86 of the FA deposition. Consequently, errors in the assumed oxidation rate of non-essential dietary FA (0·30) have little effect on the calculation on the *de novo*-synthesised FA.

The profile of *de novo*-synthesised FA calculated in the present study were similar to those obtained by Kloareg *et al.* (2005) for pigs fed *ad libitum* at thermoneutrality between 24 and 65 kg BW. The most important differences were found for 16 : 0 (0·286 *v.* 0·311) and 18 : 0 (0·217 *v.* 0·177). Consequently, estimation of the rates with which 16 : 0 is metabolised further or deposited were similar in both studies. The composition of *de novo*-synthesised FA is also similar to that found by Hilditch & Williams (1964); Leat *et al.* (1964) and Flanzy *et al.* (1970), who used lipid-free diets. Flanzy *et al.* (1970) estimated that the FA synthesis composition was 0·28, 0·14 and 0·58 for 16 : 0, 18 : 0 and 18 : 1, respectively, for the slow growth rate group and 0·28, 0·18 and 0·53 for the high growth rate group.

The present results suggest that the composition of *de novo*-synthesised FA is relatively constant in most experimental conditions. Moreover, the shape parameter *b* of the allometric development of FA relative to the whole-body lipid mass was close to 1 for most non-essential FA (Table 4). The only exception was 16 : 1, which had an allometric shape parameter considerably lower than 1. Nevertheless, its contribution to the profile of *de novo*-synthesised FA is low (0·027 of synthesised FA). Therefore, this does not necessarily invalidate the assumption of Lizardo *et al.* (2002), who assumed that the composition of *de novo*-synthesised FA was constant throughout growth.

Although the composition of *de novo*-synthesised FA is relatively constant at the whole-animal level, this is less so for the body compartments. For example, the allometric shape parameter for 18 : 1 is higher for C than for the whole body, whereas that for 18 : 0 and 16 : 0 is lower. Obviously, the inverse is seen for B and VFHT relative to the whole body.

There are also external factors known to affect the composition of *de novo*-synthesised FA. Kloareg *et al.* (2005) showed that ambient temperature and feeding level affected the *de novo* FA composition: a reduction in feed intake increased the 16 : 0 elongation rate, whereas the increase in temperature reduced the 18 : 0 desaturation rate. Others have shown that the dietary 18 : 2 and 18 : 3 content affects the composition of *de novo*-synthesised FA. In backfat, the activity of the stearyl-CoA desaturase, involved in the desaturation of both 16 : 0 and 18 : 0, decreases when the dietary 18 : 2 and 18 : 3 content increases (Kouba & Mourot, 1998; Kouba *et al.* 2003). This could explain the slightly lower 16 : 1 and 18 : 1, and higher 16 : 0 and 18 : 0 content in the *de novo*-synthesised FA in the present study compared to Kloareg *et al.* (2005).

n-3 fatty acid synthesis

Linolenic acid (18 : 3) can be converted to other *n*-3 FA (mainly to EPA and DPA and, to a lesser extent, DHA) and to hormones and prostaglandins. No quantitative information concerning the efficiency of 18 : 3 conversion was found in the literature for pigs. In adult man, the apparent conversion of 18 : 3 to EPA is limited (less than 0·08) and is even less for DHA (less than 0·04) (Burdge & Wootton, 2002; Burdge *et al.* 2002). Results of the current study indicated that only 0·40 of the dietary supply of 18 : 3 could be recovered in the body. Of the 18 : 3 that was deposited, more than one-third was deposited as EPA, DPA and DHA, suggesting that the conversion of 18 : 3 to these metabolites is more efficient in pigs than in man. Genotype affected this proportion and a greater conversion rate of 18 : 3 to EPA was observed for Large White pigs relative to the crossbreds (0·13 of digestible 18 : 3 *v.* 0·06, respectively). No information about the effect of genotype on *n*-3 FA metabolism was found in the literature. Nevertheless, the fact that in the present study a considerable fraction of essential FA could not be recovered in the body (compared to results of other studies) makes it difficult to draw general conclusions, as the efficiency of conversion of 18 : 3 to EPA, DPA and DHA may be affected by the rate of recovery of 18 : 3.

Anatomical partitioning of fatty acid gain

The FA composition varies between adipose tissues (e.g. Leat, 1983). In their model, Lizardo *et al.* (2002) supposed that the FA deposition in different tissues was the result of tissue development combined with differences in FA supply (i.e. tissues would capture FA relative to the development rate of the tissues). For example, perinephric tissue develops relatively late and it was hypothesised that its constituent FA are mainly those ingested or synthesised during the finishing phase. As indicated by the authors, differences in FA composition between tissues could only partly be explained by differences in tissue development (Lizardo *et al.* 2002). Results of the current study confirm that differences in development between tissues are insufficient to explain differences in FA composition between tissues. As indicated in Table 4, the shape parameter of the allometric relation between FA and total lipid for a compartment differs from unity for several FA. This means that the profile of FA deposition changes during growth. The same conclusion can be drawn from the results presented in Table 5. This means that some FA are preferentially deposited in some tissues. Consequently, the FA gain in backfat is not necessarily representative for the FA gain in the other adipose tissues, or for whole-body FA deposition.

No explanation for the difference in the spatial distribution of FA was found in the literature. Although differences between tissues are observed, it is not clear whether this is due to differences in the synthesis or capture of FA. It is known that different tissues possess different capacities of FA synthesis. For example, elongation is faster in bovine subcutaneous adipose tissue compared to liver (0·42 *v.* 0·15 nmol/min per mg protein) whereas desaturation was observed only in adipose tissue (0·21 nmol/min per mg protein; St John *et al.* 1991). Consequently, the contribution of different tissues in FA synthesis is not necessarily indicative for differences in FA deposition between tissues.

Although the present results do not explain the differences observed in FA spatial distribution, they can be useful for modelling FA deposition in the body. In the future, there will be an increased need to control FA composition in different tissues (e.g. to increase the *n*-3 and *n*-6 FA content in lean meat, while ensuring firmness of backfat). Lizardo *et al.* (2002) proposed a model of FA deposition in different tissues. Their approach was generic in that it could be linked to any growth model that predicted lipid deposition. Although few mechanistic models of lipid metabolism exist (e.g. Danfaer, 1999; Halas *et al.* 2004), practical application of such a model probably calls for a simpler and more empirical approach. The results of Tables 4 and 5 cannot be used directly in modelling the FA deposition in growing pigs as the (absolute values of the) partitioning of FA is specific for the current experimental conditions. For example, the parameters of the allometric relation for 18 : 2 and 18 : 3 in Table 4 will depend on the essential FA content of the diet. For the essential FA, a 'push' approach seems most appropriate where the supply of essential FA is partitioned between the tissues (after accounting for digestion and oxidation). In Table 5, the first derivative of the allometric function directly gives the partitioning of essential FA supply between tissues.

For non-essential FA, the approach is somewhat different as there is no need to partition a dietary supply of FA. Lizardo *et al.* (2002) used a 'pull' approach for FA deposition, where whole-body lipid deposition was determined by an external model (which determined the partitioning of energy between protein deposition and lipid deposition). In the approach of Lizardo *et al.* (2002), the composition of *de novo*-synthesised FA did not vary with development or between tissues. Fig. 2 shows two hypotheses concerning the driving forces for non-essential FA deposition in tissues. In Fig. 2(a), tissue FA deposition of a compartment is driven by the total lipid or total FA deposited in this tissue. The corresponding allometric relations given in Table 4 describe this partitioning. In Fig. 2(b), the distribution of each FA in the anatomical compartments is driven by the total FA deposited in the body and the allometric relations given in Table 5 describe this partitioning. Although both representations can be considered as empirical approaches to FA modelling, they nevertheless reflect fundamental differences in the perception of metabolism. In Fig. 2(a), it is the tissue itself that controls autonomously its composition. The model represented in Fig. 2(b) reflects a view in which there is a centralised perception of FA that have been deposited.

Conclusions

The main objective of the present study was to estimate parameters of a modelling approach that relates nutrition and animal development to FA composition at the whole-animal level. The major elements include the deposition of dietary FA (relative to oxidation) and the composition of

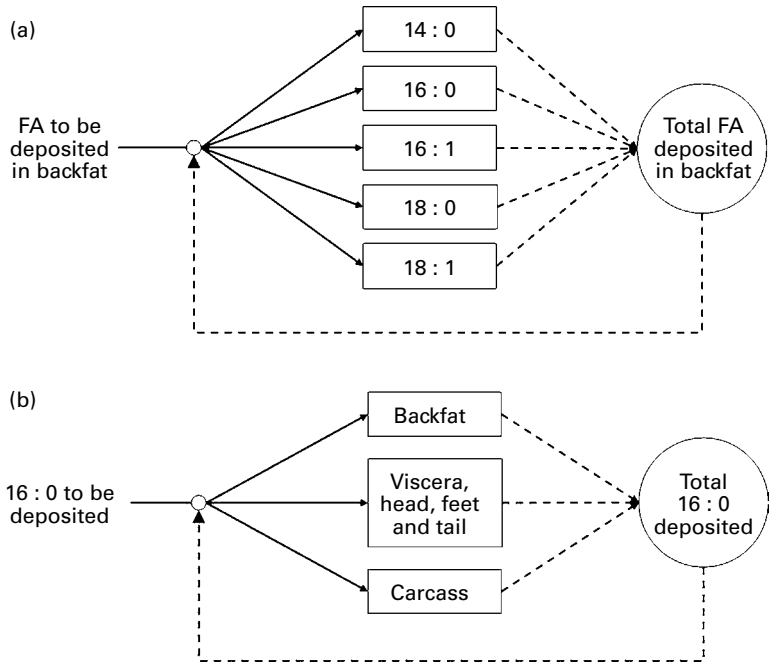

Fig. 2. Possible hypotheses concerning the driving forces for the anatomical partitioning of *de novo* synthesised fatty acids (FA). (a) The partitioning is driven locally by the fatty acid mass of the tissue. Whereas in (b), there is a central control for the partitioning of fatty acids between tissues.

de novo-synthesised FA. In addition, partitioning of FA between the carcass, backfat and non-carcass components was addressed. Only 0·31 of the digested *n*-6 FA was retained by the animal, a value much lower than that obtained in previous studies. At this point in time, it appears difficult to quantify the deposition of dietary FA as a function of the nutritional strategy or stage of development of the animal. Due to the importance of *de novo* FA synthesis in pigs, this issue mainly concerns essential FA. Nutrition and stage of development seem to have little effect on the composition of whole-body *de novo*-synthesised FA although the deposition of non-essential FA differs between tissues. Different empirical approaches were proposed to partition the FA between different tissues. Their generality for use under other circumstances remains to be proven.

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