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Review article

The comparative roles of polyunsaturated fatty acids in pig neonatal development

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The present review focuses on the importance of polyunsaturated fatty acid (PUFA) provision for the normal development of the pig neonate. The review describes first the selected fatty acid composition of a range of porcine tissues including nervous tissues, muscle and adipose tissues, reproductive organs and immune-responsive organs and/or cells. The importance of PUFA to the functioning of the immune system of the neonate is considered briefly and is followed by an in-depth consideration of the sources of PUFA for the neonatal pig. The effects of different categories or specific types of fatty acid (i.e. non-essential, linoleic, α-linolenic, long-chain *n*-6 and *n*-3 PUFA) on various indices of pig neonatal growth are reviewed. The importance of *n*-3 PUFA supply to the fetal and early neonatal pig is underlined and evidence is presented for more attention to be given to the amounts available from maternal sources. Based on the material reviewed, recommendations are made on the dietary intake of PUFA in the gestating pig.

Polyunsaturated fatty acids: Neonatal nutrition: Pig

Essential fatty acids are fatty acids which are required by an organism for the maintenance of normal growth and reproduction, are not able to be synthesized by an organism and are therefore required in appropriate amounts in the diet. The pig has been shown to have a requirement for specific fatty acids within the diet, a requirement which has been said to be overlooked (Stitt & Johnson, 1990). The fact that conventional pig diets contain a predominance of saturated and monounsaturated fatty acids has been reflected to a large extent in the content of fatty acids within the tissues of the pig. However, numerous studies have revealed beneficial effects on important aspects of animal and human health of consuming increased quantities of the *n*-3 polyunsaturated fatty acids (PUFA), in particular the long-chain *n*-3 PUFA eicosapentaenoic acid and docosahexaenoic acid (British Nutrition Foundation, 1992). Beneficial effects of these fatty acids have been observed not only in a range of animal and human disease states (Galli & Simopoulos, 1989) but also, and most importantly for the present review, in the maintenance of optimal pre- and post-natal growth and development (Innis, 1991). The presence of high levels of the long-chain PUFA in vital organs of the developing neonate emphasizes their importance. Knowledge gained from studies with human subjects can be applied to the situation pertaining to the pig. Indeed, the pig has been used frequently as an experimental model to investigate the effects of fatty acids on human growth and development (Bustad *et al*. 1966; Anon, 1984; Miller & Ullrey, 1987; Innis, 1992, 1993).

The newborn pig is subject to a range of life-threatening situations imposed by its weakness and relative shortage of body energy reserves. In a recent review, piglet losses of 13–17·5 % after farrowing were stated (Crawshaw, 1994). The newborn pig has a very low amount of body lipid (Widdowson, 1950) which serves to reduce its chances of survival if an initial food supply is not acquired. The increased recognition of the role of PUFA in the maintenance of optimal development with respect to the pig has the potential to improve the survival of the newborn pig and thus the profitability of pig enterprises.

Nomenclature of fatty acids

Table 1 shows the common or systematic names and respective shorthand designations of a range of fatty acids. A fatty acid consists of a chain of C atoms, the length of which varies according to the particular fatty acid, with a methyl (CH_3) group at one end and a carboxyl (COOH)

Abbreviation: PUFA, polyunsaturated fatty acids.

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Table 1. The common or systematic names of a range of fatty acids and their associated shorthand notations

Common or systematic name	Shorthand notation
Myristic acid	14:0
Palmitic acid	16:0
Palmitoleic acid	16:1*n*-7
Stearic acid	18:0
Oleic acid	18:1*n*-9
Vaccenic acid	18:1*n*-7
Linoleic acid	18:2*n*-6
γ-Linolenic acid	18:3*n*-6
α-Linolenic acid	18:3*n*-3
Eicosanoic acid	20:0
Eicosenoic acid	20:1*n*-9
Dihomo-γ-linolenic acid	20:3*n*-6
Eicosatrienoic acid	20:3*n*-9
Arachidonic acid	20:4*n*-6
Eicosapentaenoic acid	20:5*n*-3, EPA
Erucic acid	22:1*n*-9
Docosatetraenoic acid	22:4*n*-6
Docosapentaenoic acid (*n*-6)	22:5*n*-6
Docosapentaenoic acid	22:5*n*-3, DPA
Docosahexaenoic acid	22:6*n*-3, DHA

group at the other. In the shorthand notation, the chain length is given followed by a colon and the total number of double bonds in the molecule. The position of the last double bond is denoted by *n* (i.e. the number of C atoms in the chain) minus the number of C atoms between the double bond and the methyl group. Detailed information pertaining to the metabolic interrelationships between the fatty acids is to be found in Galli & Simopoulos (1989) and British Nutrition Foundation (1992).

Fatty acid composition of selected oils and fats

Table 2 shows the fatty acid compositions of a range of oils and fats which are currently available for use as components of the pig diet. Tallow (beef fat) and lard (pig fat) are characterized by relatively high contents of oleic acid (approximately 42 g/100 g of total fatty acids) and palmitic acid (approximately 25 g/100 g) but negligible quantities of the long-chain PUFA. Soyabean oil and sunflower oil are notable for the high levels of linoleic acid which they contain (53 and 68 g/100 g total fatty acids respectively). Whilst soyabean oil contains an appreciable quantity of α-linolenic acid, the level of this acid in sunflower oil is almost negligible. The fatty acid composition of rapeseed oil is characterized by a low level of saturated fatty acids, a high content of oleic and α-linolenic acids and a relatively moderate content of linoleic acid (White, 1992). The fatty acid compositions of two commercially available fish oils are presented in Table 2. These oils contain similar quantities of saturated fatty acids in the range of 25–30 g/100 g of total fatty acids. They are notable not only for the relatively high content of palmitoleic acid (approximately 10 g/100 g) but for the high levels of the long-chain *n*-3 PUFA present. Thus, the level of eicosapentaenoic acid in the oils is approximately 19 g/100 g total fatty acids. Whilst the level of docosapentaenoic acid is similar between the two oils, the content of docosahexaenoic acid is higher in the EPAN oil (13·6 g/100 g) than in the BOOST oil (9·3 g/100 g).

Distribution of polyunsaturated fatty acids in porcine tissues

The content of long-chain PUFA in the tissues of a wide range of mammalian species has been the subject of an extensive review by Salem (1989). Tables 3–9 show the principal fatty acid compositions of a wide range of organs, tissues and cell populations for both immature and mature pigs. The tables show the principal essential fatty acids linoleic acid and α-linolenic acid and their longer chain fatty acid metabolites including arachidonic acid, eicosapentaenoic acid and docosahexaenoic acid. The levels of eicosatrienoic acid have been included because levels of this fatty acid have been implicated in essential fatty acid deficiency (Innis, 1991). The levels of saturated and monounsaturated fatty acids have not been included as these fatty acids are not essential and have generally received sufficient consideration elsewhere. Fatty acids analysed were either from the total lipid or from individual lipid fractions, as indicated.

Nerve tissues

The PUFA compositions of brain and retina from porcine tissues as determined by various authors are shown in

Table 2. Fatty acid composition (g/100 g total fatty acids) of various oils and fats of animal or plant origin

Fatty acid	Tallow*	Lard*	Soyabean oil*	Sunflower oil*	Rapeseed oil†‡	EPAN oil§	BOOST oil§
14:0	3·3	1·5	0·1	0·2		7·7	6·8
16:0	25·5	24·8	11·0	6·8	5·0	17·4	15·6
16:1*n*-7	3·4	3·1	0·1	0·1	0·3	10·5	10·4
18:0	21·6	12·3	4·0	4·7	1·4	4·3	2·3
18:1*n*-9	38·7	45·1	23·4	18·6	58·5	13·9	13·5
18:2*n*-6	2·2	9·9	53·2	68·2	21·9	4·0	3·4
18:3*n*-3	0·6	0·1	7·8	0·5	12·7	2·5	6·7
20:4*n*-6	0·4	0·4			0·1	1·9	6·3
20:5*n*-3						18·7	19·5
22:5*n*-3						2·4	2·5
22:6*n*-3						13·6	9·3

* Values from Chow (1992).
† As analysed by authors; oil supplied by The White Sea and Baltic Company Ltd, Hull, UK.
‡ Negligible level of erucic acid.
§ As analysed by authors; oil supplied by Seven Seas Ltd, Hull, UK.

Table 3. Selected fatty acid composition (g/100 g total fatty acids) of pig brain and retina

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-9	20:3*n*-6	20:4*n*-6	20:5*n*-3	22:4*n*-6	22:5*n*-6	22:5*n*-3	22:6*n*-3	Comments	Reference
Brain	PL	0·5	0·7	1·0	0·2	12·0	0·8	4·5		3·8	11·5	Piglet*	Payne (1978)
	PL	0·9	2·1	0·9	1·0	11·2	1·4	5·3	1·4	0·5	11·0	Pig	Payne (1978)
Cerebrum	Total	0·9	0·9	1·5	1·1	12·4		6·9	4·4	0·5	9·4	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
	PE	0·8				17·3		10·8	3·5	1·0	20·5	Plasma membrane from sow milk-fed piglet	Arbuckle & Innis (1992)
Cerebellum	Total	0·3	2·0	1·0	0·8	11·1	0·3	5·1	2·3	0·5	7·9	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
Medulla	Total	0·4	3·2	1·0	0·6	8·2	0·2	5·2	1·3	0·3	5·8	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
Retina	PE	1·4				14·8		3·8	1·5	1·6	31·3	From sow milk-fed piglet	Arbuckle & Innis (1992)

PL, phospholipid; PE, phosphatidylethanolamine.
*Newborn and unsuckled.

Table 4. The fatty acid composition (g/100 g total fatty acids) of porcine serum or plasma and blood components

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-9	20:3*n*-6	20:4*n*-6	20:5*n*-3	22:4*n*-6	22:5*n*-6	22:5*n*-3	22:6*n*-3	Comments	Reference
Serum or plasma	Total	14·4	0·5	1·0	0·8	6·7	0·3	1·0	5·8	1·8	tr	Serum from miniature swine fed on 20 g maize oil/kg diet	Hill (1966)
	Total	24·9	0·4		0·6	6·3	tr	0·5	0·1	1·0	0·3	Plasma from sow fed on 50 g tallow/kg diet	Farnworth & Kramer (1989*b*)
	Total	36·9	1·3		0·4	6·0	tr	0·3	tr	1·2	0·3	Plasma from sow fed on 50 g soyabean oil/kg diet	Farnworth & Kramer (1989*b*)
	Total	30·6				12·6	0·6			1·1	0·8	Serum from sow fed on 70 g lard/kg diet	Fritsche *et al.* (1993*b*)
	Total	20·3				5·7	16·2			1·7	4·2	Serum from sow fed on 70 g fish (menhaden) oil/kg diet	Fritsche *et al.* (1993*b*)
Platelet	PL	5·9			1·0	23·4	0·4	2·2	0·3	1·3	0·6	Sow milk-fed piglet (birth to 18 d)	Innis *et al.* (1993)
Erythrocyte	Total	6·6	0·4	0·8	0·7	3·8	0·5	0·4	5·6	0·7	0·7	Washed and frozen	Hill (1966)

PL, phospholipid; tr, trace.

Table 5. Selected fatty acid composition (g/100 g total fatty acids) of major organs and tissues in the pig

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-9	20:3*n*-6	20:4*n*-6	20:5*n*-3	22:4*n*-6	22:5*n*-6	22:5*n*-3	22:6*n*-3	Comments	Reference
Heart	Total	29·5	0·3	1·4	1·2	13·4	0·3	0·9	0·9	0·5	tr	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
	PL	10·2	7·4	1·0	0·8	23·0	1·1	1·8	2·9	1·1	2·3	Piglet*	Payne (1978)
	PC/PE	6·9/5·9	0·2/0·3			6·4/27·5						110-d-old fetus	Farnworth & Kramer (1989*a*)
Aorta	Total	5·7	1·2	0·6	0·2	2·5	tr	0·9	0·1	0·8	0·3	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
Liver	PL	5·9	0·3	1·6	1·4	21·9		1·1	2·5	1·1	8·6	Piglet*	Payne (1978)
	PC/PE	4·1/1·6	0·2/0·2			13·9/25·1						110-d-old fetus	Farnworth & Kramer (1989*a*)
	PL	14·5	0·3		1·9	17·4				2·5	3·1	Pigs fed on 50 g tallow/kg diet	Morgan *et al.* unpublished results†
	PL	20·1	0·6		1·2	14·5	3·6			3·2	4·7	Pigs fed on 50 g soyabean oil and 10 g fish oil/kg diet	Leskanich (1995)
Lung	Total	6·1	0·4	0·7	1·1	8·4	0·2	2·2	0·2	0·3		Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
	PL	3·5	0·3	0·6	0·8	11·9	0·3	1·3	1·3	0·6	2·1	Piglet*	Payne (1978)
	PC/PE	3·0/3·2	0·2/0·4			3·5/21·8						110-d-old fetus	Farnworth & Kramer (1989*a*)
Kidney	Total	12·7	0·9	1·0	1·8	17·6	0·3	2·3	0·2	0·1	0·5	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
	PC/PE	4·0/1·9	0·3/0·4			8·5/28·7						110-d-old fetus	Farnworth & Kramer (1989*a*)
	TAG	6·0	0·6			3·1						110-d-old fetus	Farnworth & Kramer (1989*a*)
Pancreas	Total	12·4	0·8	0·4	0·8	4·9	0·1	0·6	0·1	0·3	0·3	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
Intestine	Total	11·2	0·7	0·6	1·0	9·2		1·9	0·5	0·5	0·5	Miniature pig fed on 20 g diet maize oil/kg	Hill (1966)
	PL	4·7	3·1	0·9	1·6	21·5	0·8	2·1	2·3	1·5	6·2	Piglet*	Payne (1978)

PL, phospholipid; PC, phosphatidylcholine; PE, phosphatidylethanolamine; TAG, triacylglycerol; tr, trace.
*Newborn and unsuckled.
† CA Morgan, RC Noble, M Cocchi and R McCartney.

Table 3. The fatty acid composition of brain is characterized by low levels of linoleic and α-linolenic acid (Dhopeshwarkar & Mead, 1973). However, the levels of the long-chain PUFA arachidonic acid and docosahexaenoic acid are considerably higher at 12 g/100 g of fatty acids in the phospholipid fraction. In addition, appreciable levels of docosatetraenoic acid are observable in the brain. Elevated levels of these fatty acids have been observed in the phosphatidylethanolamine fraction. Some differences in the long-chain PUFA composition of the different brain regions are apparent. The medulla contains less arachidonic acid than the cerebrum or cerebellum and the level of docosahexaenoic acid appears to decrease from the cerebrum to the cerebellum and to the medulla. The fatty acid composition of the phosphatidylethanolamine fraction of the retina is characterized by an extremely high level of docosahexaenoic acid (31 g/100 g) and a high level of arachidonic acid. The fatty acid compositions of other phospholipid fractions of porcine retina have been detailed by Fliesler & Anderson (1983).

Blood and blood components

The fatty acid compositions of serum or plasma, platelets and erythrocytes are shown in Table 4. In most cases, serum or plasma is characterized by high levels (20–37 g/100 g total fatty acids) of linoleic acid accompanied by much lower levels (6–13 g/100 g) of arachidonic acid. The level of linoleic acid was higher in the plasma from sows fed on a soyabean oil diet as opposed to a tallow diet on account of the high level of this fatty acid in soyabean oil (see Kruse *et al*. 1977). In sows fed on either a tallow or a lard diet, the levels of eicosapentaenoic and docosahexaenoic acids were either negligible or very low. However, the inclusion of a fish oil diet markedly increased the levels of eicosapentaenoic and docosahexaenoic acids whilst the levels of linoleic and arachidonic acids were correspondingly decreased. Similar marked alterations in the levels of these fatty acids were observed in the serum of piglets being suckled by sows fed on lard or fish oil (Fritsche *et al*. 1993*b*). The fatty acid composition of platelet phospholipid was characterized by a high content of arachidonic acid and lower levels of the other PUFA. In erythrocytes, a relatively high content of docosapentaenoic acid (*n*-6) was recorded. In newborn piglets during the first week of life, the level of linoleic acid was shown to increase whilst that of oleic acid decreased (Lodge *et al*. 1978).

Major internal organs

The PUFA compositions of the heart, liver, lung, kidney, pancreas and intestine in the pig at various stages of development are presented in Table 5. The fatty acid compositions of the heart and liver are characterized by a high content of arachidonic acid which is detected principally in the phosphatidylethanolamine fraction of the phospholipids. Farnworth & Kramer (1989*a*) observed that phosphatidylethanolamine was consistently the phospholipid class with the highest level of PUFA in fetal pig heart, liver, lung and kidney. The liver contained relatively high levels of docosapentaenoic (*n*-3) and docosahexaenoic acids in the phospholipid fraction. The levels of arachidonic and docosahexaenoic acids were higher in the liver of the newborn and unsuckled piglet than in growing pigs. In the liver of newborn pigs during the first week of life, the levels of linoleic acid and arachidonic acid increased whilst palmitoleic and oleic acids decreased (Lodge *et al*. 1978). As observed for the blood, the type of diet has a marked effect on the fatty acid composition. Thus, in the liver, the levels of the long-chain *n*-3 PUFA increased and arachidonic acid decreased as a result of feeding a soyabean oil + fish oil diet rather than a tallow diet.

The lung and kidney contain relatively high contents of arachidonic acid which, as for the heart and liver, are found most prominently within the phosphatidylethanolamine fraction. The pancreas and intestine contain approximately 12 g linoleic acid/100 g total fatty acids and lower amounts of arachidonic acid. Intestinal wall phospholipid in the newborn piglet contains a high level of arachidonic acid accompanied by docosahexaenoic acid.

Muscle and adipose tissues

The fatty acid compositions of the lipid fractions extractable from the *longissimus dorsi*, *semitendinosus* and *vastus lateralis* muscles have been recorded by various workers and are shown in Table 6. In general, both the triacylglycerol and phospholipid fractions are characterized by high contents of linoleic acid. However, whereas the phospholipid contains approximately 10 g of arachidonic acid/100 g total fatty acids, its level in the triacylglycerol fraction is only approximately 0·6 g/100 g. A marked difference in fatty acid composition arising from the type of oil added to the diet was evident (Leskanich *et al*. 1997). Thus, where diets containing soyabean oil and fish oil were given, the fatty acid compositions of muscle triacylglycerol and phospholipid were characterized by markedly higher levels of linoleic, eicosapentaenoic, docosapentaenoic and docosahexaenoic acids than when a tallow diet was given. The level of α-linolenic acid was more susceptible to change in the triacylglycerol fraction than in the phospholipid fraction, in accordance with the findings of others (Innis, 1991).

The fatty acid compositions of adipose tissues taken from various locations in the body are presented in Table 7. Adipose tissue from pigs fed on standard commercial diets is normally characterized by a predominance of oleic acid at a level of approximately 43 g/100 g total fatty acids (Morgan *et al*. 1992; Leskanich, 1995). Among the PUFA shown, the highest percentages were exhibited by linoleic acid followed by α-linolenic acid. The fatty acid composition of adipose tissues is markedly influenced by the fatty acid composition of the diet. Thus, the feeding of a soyabean oil + fish oil diet caused marked increases in the levels of linoleic, eicosapentaenoic, docosapentaenoic and docosahexaenoic acids in both the inner and outer backfats. The feeding of a fish-oil-based diet resulted in marked increases in these fatty acids at the expense of linoleic acid. The fatty acid composition of the skin was similar to that of the adipose tissue.

Table 6. Selected fatty acid composition (g/100 g total fatty acids) of various muscle tissues in pigs

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-6	20:4*n*-6	20:5*n*-3	22:5*n*-3	22:6*n*-3	Comments	Reference
Vastus lateralis (leg muscle)	PL	7·7	0·3	1·1	18·4	0·4	1·0	3·4	Piglet (newborn, unsuckled)	Payne (1978)
	PL	31·8	1·1	0·5	10·9	1·7	2·3	2·4	Pig	Payne (1978)
Longissimus dorsi (loin muscle)	TAG	6·5	0·9	0·3	0·6	–	–	–	Fed on 50 g tallow/kg diet	Morgan *et al.* unpublished results*
	TAG	17·3	2·4	0·1	0·5	0·2	0·3	0·2	Fed on 50 g soyabean oil + 10 g fish oil/kg diet	Leskanich (1995)
	PL	28·5	0·4	1·0	9·1	–	1·8	1·3	Fed on 50 g tallow/kg diet	Morgan *et al.* unpublished results*
	PL	33·5	0·7	1·2	9·2	2·1	2·6	2·0	Fed on 50 g soyabean oil + 10 g fish oil/kg diet	Leskanich (1995)
Semitendinosus (leg muscle)	Total	15·8	1·1	0·8	5·1	tr	0·6	0·4	'Ham muscle' from miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
	TAG	9·6	1·2	0·3	0·2	–	0·1	0·1	Fed on 50 g tallow/kg diet	Morgan *et al.* unpublished results*
	TAG	26·8	3·5	0·2	0·7	0·3	0·5	0·4	Fed on 50 g soyabean oil + 10 g fish oil/kg diet	Leskanich (1995)
	PL	26·3	0·4	1·6	8·6	–	1·6	1·2	Fed on 50 g tallow/kg diet	Morgan *et al.* unpublished results*
	PL	36·3	0·5	1·1	7·6	2·4	2·3	2·7	Fed on 50 g soyabean oil + 10 g fish oil/kg diet	Leskanich (1995)

PL, phospholipid; TAG, triacylglycerol; tr, trace.
* CA Morgan, RC Noble, M Cocchi and R McCartney.

Table 7. Selected fatty acid composition (g/100 g total fatty acids) of porcine adipose tissues and skin

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-6	20:4*n*-6	20:5*n*-3	22:5*n*-3	22:6*n*-3	Comments	Reference
Adipose tissue	Total	7·0	1·2	0·1	0·2	tr	0·1	0·1	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
Inner backfat	TAG	13·8	2·9	0·1	0·3	0·1	0·2	0·2	50 g tallow/kg diet	Leskanich (1995)
	TAG	24·9	3·4	0·1	0·4	0·3	0·4	0·5	50 g soyabean oil + 10 g fish oil/kg diet	Leskanich (1995)
Outer backfat	TAG	14·1	3·0	0·1	0·4	0·1	0·2	0·3	50 g tallow/kg diet	Leskanich (1995)
	TAG	26·1	3·5	0·2	0·4	0·3	0·5	0·5	50 g soyabean oil + 10 g fish oil/kg diet	Leskanich (1995)
Perirenal fat	Total	7·9	1·4		0·3*	0·1	0·4	0·6	Standard diet	Irie & Sakimoto (1992)
	Total	7·5	2·2		0·6*	1·5	1·1	1·9	60 g fish oil/kg diet	Irie & Sakimoto (1992)
Skin	Total	7·4	1·2	0·1	1·1	tr	0·2	0·2	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)

TAG, triacylglycerol; tr, trace.
* Includes the fatty acid 22:1.

Table 8. The fatty acid composition (g/100 g total fatty acids) of various porcine reproductive tissues and fluids

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-9	20:4*n*-6	20:5*n*-3	22:4*n*-6	22:5*n*-6	22:5*n*-3	22:6*n*-3	Comments	Reference
Ovary	Total	13·4	0·7*	tr	26·2	0·2	12·3	0·8	1·5	0·8		Holman & Hofstetter (1965)
Graafian follicle	Total	8·3	0·6*	tr	24·7	0·3	21·1	1·4	3·0	0·9		Holman & Hofstetter (1965)
Testes	Total	5·8	0·3	1·3	23·4		5·7	3·5	0·7	2·7	Miniature pig fed on 20 g maize oil/kg diet	Hill (1966)
	Total	6·4	0·9*	tr	15·5	tr	3·8	12·1	tr	4·4		Holman & Hofstetter (1965)
	PL	1·9	tr		4·5	1·1		24·2		38·1	Testicular or ejaculated spermatozoa	Evans & Setchell (1979); Poulos *et al.* (1973)
	PL	1·7			4·8	–	1·6	29·0	0·3	16·3	Epididymal spermatozoa	Johnson *et al.* (1972)
	NL	2·4	–		1·8			1·2		2·6	Testicular spermatozoa	Evans & Setchell (1979)
Rete testis fluid	PL	3·0	1·5		5·0	5·0		5·0		19·0		Evans & Setchell (1979)
Seminal plasma	PL	3·5	3·0		12·5	3·0		11·0		12·5		Evans & Setchell (1979)

PL, phospholipid; NL, neutral lipid; tr, trace.
* Includes the fatty acid 20:0.

Table 9. Selected fatty acid composition (g/100 g total fatty acids) of porcine organs and cells involved in the immune response

	Lipid fraction	18:2*n*-6	18:3*n*-3	20:3*n*-6	20:4*n*-6	20:5*n*-3	22:4*n*-6	22:5*n*-6	22:5*n*-3	22:6*n*-3	Comments	Reference
Spleen	Total	5·9	0·8	1·0	4·9	0·1	2·2	0·4	0·2	0·9	Miniature swine	Hill (1966)
	Total	7·4		1·2	20·6	0·1	2·7	tr	2·1	2·3	Splenocytes;*	Fritsche *et al.* (1993*a*)
	Total	8·7		1·0	8·8	12·2	0·3	tr	5·3	6·3	Splenocytes;†	Fritsche *et al.* (1993*a*)
Thymus	Total	10·3		1·5	15·3	0·1	2·1	tr	1·5	1·3	*	Fritsche *et al.* (1993*a*)
	Total	9·2		1·6	7·5	6·9	0·3	tr	3·6	5·3	†	Fritsche *et al.* (1993*a*)
Lung alveolar macrophages	Total	5·3		1·0	15·9	0·2	3·4	0·6	2·9	2·2	*	Fritsche *et al.* (1993*a*)
	Total	4·8		0·5	5·7	8·7	0·4	tr	6·5	6·6	†	Fritsche *et al.* (1993*a*)

tr, trace.
* From 21-d-old piglets nursed by sows fed on a diet containing 70 g lard/kg.
† From 21-d-old piglets nursed by sows fed on a diet containing 70 g fish (menhaden) oil/kg.

Reproductive organs and fluid

Table 8 shows the fatty acid compositions of ovarian tissue, testes, rete testis fluid and seminal plasma. Ovary and Graafian follicle contain a relatively high content of arachidonic acid together with the highest content of docosatetraenoic acid (22:4*n*-6) seen in any of the tissues presented. Levels of other long-chain PUFA are relatively low. The phospholipid fraction from spermatozoa is characterized by high contents of docosapentaenoic acid (*n*-6) and docosahexaenoic acid. Rete testis fluid and seminal plasma fluid are also characterized by relatively high contents of these fatty acids with the additional presence of arachidonic and eicosapentaenoic acids. These results are in broad agreement with earlier observations by Holman & Hofstetter (1965).

Immune-responsive organs and cells

The fatty acid compositions of spleen, thymus and lung alveolar macrophages are shown in Table 9. The data are taken almost entirely from the comparative investigations on the tissue fatty acid compositions in piglets being suckled by sows fed on a diet containing either a 70 g lard or 70 g fish oil/kg diet (Fritsche *et al*. 1993*a*). In general, linoleic acid was higher in the thymus than in the spleen or lung alveolar macrophages. Irrespective of diet, the levels of other PUFA were remarkably similar between the tissues although the levels of docosapentaenoic acid (*n*-3) and docosahexaenoic acid tended to be lower in the thymus than in the spleen or macrophages. There were marked diet-related changes in fatty acid composition. Thus, whereas in piglets whose mothers had been fed on a diet rich in lard, arachidonic acid was the dominant PUFA, in piglets supplied with fish oil eicosapentaenoic acid predominated. The levels of docosapentaenoic (*n*-3) and docosahexaenoic acids were also increased in piglets supplied with fish oil.

Polyunsaturated fatty acids and the immune status of the pig neonate

The involvement of fatty acids in the immune response has been reviewed by various authors (Gurr, 1983; Johnston, 1985). In both human subjects and laboratory animals, the long-chain *n*-3 PUFA eicosapentaenoic acid and docosahexaenoic acid have been associated with the partial alleviation of the symptoms arising from a number of autoimmune diseases including rheumatoid arthritis and systemic lupus erythematosus (British Nutrition Foundation, 1992). These effects have been associated, in part, with a reduction in the formation of pro-inflammatory eicosanoids, most notably leukotriene B_4. It may be questioned, therefore, whether the effects of these fatty acids on chronic, autoimmune diseases could also apply to the alleviation of acute, infectious diseases and more specifically to those infectious diseases which are of relevance to the pig. Diseases caused by *Escherichia coli* bacteria in pigs are well known and account for a high proportion of deaths and reduced growth rates. *E. coli* infestation has been shown to cause septicaemia in neonatal piglets and diarrhoea in sucking and newly-weaned piglets (Whittemore, 1993; Bertschinger, 1995). A compromised health status is also more likely to occur in piglets of low birth weight (Whittemore, 1993).

The wide-ranging effects of fatty acids on the functioning of the immune system have been reviewed recently (Calder, 1998; Miles & Calder, 1998). Several reports have described the effects of the long-chain *n*-3 PUFA on the response in pigs to infectious disease challenge; these reports have presented evidence of ameliorating effects of fish-oil fatty acids on the pig's immune responses. For example, in a study by Fritsche *et al*. (1993*a*), sows were fed on a diet containing 70 g/kg either lard or menhaden fish oil from day 107 of gestation until 3 weeks post-partum. In consequence, the serum, liver and immune-responsive tissues (thymus, splenocytes and lung alveolar macrophages) from 3-week-old piglets exhibited a marked enrichment in eicosapentaenoic acid at the expense of arachidonic acid (see Table 9). Experiments *in vitro* showed that the basal release of prostaglandin E, thromboxane B and leukotriene B from alveolar macrophages was 60–70 % lower in the piglets maternally-supplied with fish-oil fatty acids. Although no comparative measurements of disease incidence or mortality of the piglets were indicated, the possibility of beneficial effects on disease resistance was alluded to. In another study (Murray *et al*. 1993), pigs were fed for 8 d on either a basal diet, an *n*-6 fatty acid-enriched (maize oil) diet or an *n*-3 fatty acid-enriched (fish oil) diet containing 80, 180 and 180 g dietary fat/kg respectively. On the ninth day, the pigs were injected intravenously with 0·3 mg endotoxin (*E. coli*)/kg. As observed by others (see Fritsche *et al*. 1993*a*,*b*), the fatty acid composition of the blood was significantly enriched in *n*-3 fatty acids resulting from the inclusion of dietary fish oil. Furthermore, the responses of the fish-oil-fed pigs and the pigs fed on the basal and maize-oil diets were different. The plasma levels of thromboxane B_2 and 6-ketoprostaglandin $F_{1\alpha}$ which have been implicated in the response to infectious disease were lowest in the fish-oil group. Physiological indicators of infection were also modifed by the fish-oil diet. Thus, whereas in the basal and maize-oil groups there were decreases in arterial O_2 concentration, this was not affected in the fish-oil group. The fish-oil group also exhibited a more normal arterial blood pressure and pulmonary vascular resistance in response to the endotoxin than the basal or maize-oil groups. These workers, therefore, concluded that *n*-3 fatty acids attenuated the response to sepsis. In a different study, it was demonstrated that the severity of lung lesions in pigs incurred as a result of intratracheal *Mycoplasma hyopneumoniae* inoculation was inversely related to the ratio *n*-3 : *n*-6 fatty acids in alveolar macrophage lipids (Turek *et al*. 1996); these findings were in overall agreement with previous work undertaken by the same group (Turek *et al*. 1994). In contrast to these observations, the feeding of fish oil to rabbits (D'Ambola *et al*. 1991) and mice (Chang *et al*. 1992) appeared to reduce the effectiveness of the response to bacterial challenge.

Sources of polyunsaturated fatty acids for the neonatal pig

Lipid synthesis de novo

Non-essential fatty acids are readily obtained by the fetus either by synthesis from appropriate precursors or by

absorption via the placenta. Lipogenic (i.e. lipid-forming) activity has been demonstrated to occur *de novo* in both porcine fetal adipose tissue (Kasser *et al*. 1981) and fetal pig liver (Mersmann, 1971). It appears that, before birth, the lipogenic activity of the liver is greater than that of the adipose tissue, whereas postnatally the adipose tissue assumes the greater role (Mersmann *et al*. 1973). However, compared with other mammals, the potential for lipid synthesis in the newborn pig is lower and is associated with a limited degree of free fatty acid mobilization. Free fatty acids are released into the plasma from triacylglycerol in adipose tissue stores. In the newborn unfed pig shortly after birth there is only a twofold increase in plasma free fatty acid release compared with a sixfold increase in unfed lambs and human infants (Seerley, 1984). The low level of free fatty acid mobilization is probably related to the fact that the newborn, unsuckled pig contains only 10–30 g total lipid/kg body weight (Manners & McCrea, 1963; Farnworth & Kramer, 1987) which, as Seerley (1984) points out, is probably in the form of structural fat and therefore not available for mobilization. In contrast, by 4 weeks of age, the proportion of fat in the piglet fed on sow's milk has risen to 180 g/kg of body weight (Manners & McCrea, 1963). Unlike neonatal ruminants (Noble, 1979), the neonatal pig contains no brown adipose tissue (Pond & Houpt, 1978).

The relative contributions to lipid accretion in the fetal pig of *de novo* lipogenesis and preformed fatty acid taken up via the placenta have not been assessed fully. However, from a number of observations it appears that *de novo* lipogenesis is the principal mechanism of fatty acid accretion but that the extent of this synthesis is low. Also, in general the transfer of fatty acids across the placenta is relatively low. The observations supporting these statements are as follows: (1) the newborn pig is born with a very low quantity of body lipid (Manners & McCrea, 1963; Filer *et al*. 1966); (2) efforts to increase the fat content of newborn piglets to improve survivability have not been successful (Pettigrew, 1981); (3) the contents of triacylglycerol and free fatty acid in fetal porcine plasma are 35 and 20 % of the respective maternal blood levels (Ramsay *et al*. 1991), thus, although the levels of triacylglycerol and free fatty acid increased significantly in maternal plasma as a result of consuming a diet containing 150 g tallow/kg, their levels in the fetal plasma were not significantly affected; (4) the fatty acid composition of the fetus is relatively refractory to changes in the fatty acid content of the maternal blood (Farnworth & Kramer, 1989*b*); (5) overall, there is a low rate of placental transfer of fatty acids (Thulin *et al*. 1989). However, this apparent deficit in body lipid content at birth is largely rectified through the piglet's access to a rich lipid source in the form of colostrum.

The low level of lipid synthesis exhibited by the pig fetus does not appear to be related to a lack of substrate availability from maternal sources but rather to innate hormonal control of lipogenesis (Kasser *et al*. 1983). *De novo* lipogenesis and triacylglycerol synthesis in the porcine fetus are enhanced by insulin (Kasser *et al*. 1981) and are affected by various hormones arising from the central nervous system, in particular the hypothalamus and pituitary glands (Martin *et al*. 1985) with growth hormone appearing to have an inhibitory effect on these processes (Kasser *et al*. 1983). The molecular mechanisms relating to the synthesis of fatty acids and principal lipid classes including triacylglycerols and phospholipids have been reviewed elsewhere (Farnworth & Kramer, 1987).

The role of the placenta in the provision of polyunsaturated fatty acids

The placenta allows the transfer of nutrients from the maternal plasma to the fetal plasma and the reverse transfer of waste products of fetal metabolism. The anatomy of the porcine placenta is of the diffuse and epitheliochorial type (Flood, 1991). Early studies using ^{14}C-labelled fatty acids in rats indicated the existence of 'biomagnification' of long-chain fatty acids of the *n*-6 and *n*-3 series (Crawford *et al*. 1976). Thus, levels of these fatty acids increased in ascending order from maternal liver to placenta to fetal liver and ultimately to fetal brain. Similar observations were made by Noble *et al*. (1978*a*,*b*) in neonatal lambs. Interesting data on mechanisms controlling interrelated transfer and accumulation of essential fatty acids in fetal tissues have been obtained recently using an avian embryo model system (Noble & Speake, 1997). From the fact that porcine placenta contains only a low amount of total lipid it would appear that provision of fatty acids to the fetus does not involve any prior storage. Ramsay *et al* (1991) observed that maternal and fetal regions of the placenta contained 11 and 16 g lipid/kg dry weight respectively and that the presence or absence of 150 g tallow/kg in the sow diet had no significant effect on these levels.

The fact that the placenta is itself a fast-growing, highly vascular organ has prompted suggestions that it too places a demand for PUFA. Thus, Crawford *et al*. (1989) noted that the contents of arachidonic and docosahexaenoic acids in human umbilical cord plasma phospholipid were significantly higher in cases where placental weight was classed as high than where it was classed as low. A beneficial effect on birth weight was also implicated as placental weight and birth weight were positively related. Crawford *et al*. (1989) hypothesized that a deficiency of essential fatty acids and their long-chain metabolites could lead to sub-optimal blood flow conditions in the growing placenta, as supported by their observations of vascular lesions and inflammation in placentas associated with low-birth-weight babies. Findings related to fetal pig growth which could be seen to support this hypothesis have been recorded. Thus, Dyck & McKay (1986) studied the relationship between fetal pig weight and eleven factors related to fetal environment in over 900 fetuses. It was found that the uterine weight of the area of placental attachment accounted for most of the variation in fetal weight, thereby underlining the importance of the placenta in fetal pig growth.

Delivery of fatty acids to the placenta. The transfer of fatty acids across the placenta from the maternal to the fetal blood supply occurs with fatty acids in the free, unesterified form (see review by Noble, 1979; Kuhn & Crawford, 1986). Such free acids may be present within the blood bound to plasma proteins such as albumin (Brossard *et al*. 1997) or α-fetoprotein (Innis, 1991). However, as most fatty acids in the maternal blood are esterified as triacylglycerols (Thulin *et al*. 1989), their transfer requires the liberation of the free

acids by the enzyme lipoprotein lipase (*EC* 3.1.1.34). Placental lipoprotein lipase activity has been reported to be high in the pig (Ramsay *et al*. 1991) and there is evidence from studies on guinea-pig placenta to suggest that the enzyme's activity may increase from early to late gestation with increasing fetal demand for fatty acids (Thomas & Lowy, 1987). Furthermore, it appears that this lipoprotein lipase is located only on the maternal side of the placenta, presumably in order to prevent the reverse transfer of fatty acids from the fetal to the maternal circulation (Thomas *et al*. 1984). A preferential release of PUFA from maternal adipose tissue stores has been suggested from the results of several studies. This has implications for the supply of fatty acids to the developing fetus either directly in the free fatty acid form or following metabolic manipulation via the liver. A preferential release of eicosapentaenoic acid and arachidonic acid has been observed in hormonally stimulated rat adipocytes (Hollenberg & Angel, 1963; Raclot & Groscolas, 1993). Similarly, Gavino & Gavino (1992) observed that cultured and stimulated preadipocytes released more *n*-6 and *n*-3 fatty acids than saturated fatty acids. A preferential release of docosahexaenoic acid from chick embryo adipose tissue has also been observed (Cerolini *et al*. 1996).

The form in which fatty acids are transported within the blood and delivered to the placenta may also be important. As a percentage of particle mass, triacylglycerols are present in largest amounts in chylomicrons and VLDL. Chylomicrons are formed in the intestinal wall and transport dietary fat whereas VLDL are formed in the liver and may contain fatty acids which have been 'processed' to some degree. However, in the placenta it appears that only triacylglycerol from VLDL and not chylomicrons is hydrolysed (McBride & Burton, 1964; Thomas & Lowy, 1987). This may be a mechanism both to protect the fetus from potentially injurious changes in dietary fatty acids and to facilitate the increased delivery of long-chain PUFA to the fetus (Dutta-Roy *et al*. 1996). In the pig, a marked increase in the level of VLDL in the plasma during the last 8 weeks of pregnancy has been shown to occur (Wright *et al*. 1995). An increase in the proportion of docosahexaenoic acid in liver phospholipid has been shown to coincide with the fetal brain growth 'spurt' in the guinea-pig (Burdge & Postle, 1994) which would suggest that fatty acids destined for the brain are accumulated and released from the liver. Recent data on the avian embryo have underlined the existence of a specific relationship between the adipose tissue and the liver for the delivery of long-chain PUFA (Noble & Speake, 1997).

Preferential transfer of fatty acids across the placenta. Early studies speculated that transfer rates across the placenta depended on differences in fatty acid concentration (Noble, 1979; Kuhn & Crawford, 1986) and that transfer involved, as in intestinal fatty acid absorption, an intermediate (re)esterification step followed by lipolysis for the release of free fatty acids into the circulation (Coleman, 1986; Ramsay *et al*. 1991). It was also believed that this intermediate esterification could be one of the factors responsible for the low level of fatty acid transfer across the porcine placenta. However, after adding [^{14}C]palmitic acid to placental tissue incubations, Ramsay *et al*. (1991) noted that only a low level of esterification was exhibited; other factors were purported to be limiting, such as the fatty acid binding proteins. More recently it has become apparent that fatty acid binding proteins are important in placental fatty acid uptake (Dutta-Roy *et al*. 1996). Furthermore, the long-chain PUFA are selectively or preferentially taken up by the placenta (Campbell *et al*. 1996; Dutta-Roy, 1997). Indeed, a similar preference for fatty acids of increasing unsaturation is known to exist for the fatty acid binding protein within the intestinal enterocyte (British Nutrition Foundation, 1992).

Colostrum and milk as effective sources of polyunsaturated fatty acids

The newborn piglet receives its nourishment from the first milk or colostrum which persists for the first 3–4 d of lactation. The colostrum supplies the newborn piglet with a range of nutrients as well as antibodies, the latter of which are virtually absent from the blood due to the apparent inability of antibodies to cross the placenta (Pond & Houpt, 1978). It is the consumption of colostrum and milk, with their high fat content, that is responsible for the marked increase in the fat content of the piglet after birth (Lee & Kauffman, 1974*a*; Mersmann, 1974). In addition to fat, the colostrum provides other nutrients including lactose, a range of vitamins and various minerals (Braude *et al*. 1947). By noting differences in piglet weight, Fraser & Rushen (1992) observed that, during the first hour after establishing successful suckling, newborn pigs consumed 75 g colostrum and later (3rd to 4th hours) consumed it at approximately 20 g/h.

Various changes in the blood and body composition and enzyme activities occur following birth in relation to the consumption of colostrum and milk. Before sucking, the newborn pig is dependent on large carbohydrate (glycogen) stores in both the liver and muscle tissues (Mersmann, 1974) but after the start of sucking, carbohydrates are supplied by the milk as reflected by an increase in the level of blood glucose (Lodge *et al*. 1978). Similarly, increases in plasma lipid levels have been observed contingent on the start of sucking (Noble *et al*. 1971). The accumulation of fat from colostrum and milk by both muscle and subcutaneous adipose tissue is enabled by the increasing activities of lipoprotein lipase in these tissues from birth, with the activity of this enzyme being much higher in the subcutaneous adipose tissue than in the muscle (Lee & Kauffman, 1974*a*,*b*). Lee & Kauffman (1974*a*) showed that the accumulation of fat in the piglet during the first 4 weeks of life is entirely due to the deposition of fatty acids derived from milk fat, the activities of lipogenic enzymes (malic enzyme (*EC* 1.1.1.40) and citrate cleavage enzyme (*EC* 4.1.3.8)) being negligible during this period.

Sow colostrum has been shown generally to contain less fat (approximately 40 g/l) than post-colostrum milk (40–80 g/l) (Braude *et al*. 1947; de Man & Bowland, 1963; Frobish *et al*. 1967; Friend, 1974) although Schuld & Bowland (1968*b*) observed no difference in the level of fat between colostrum and milk. This contrasts with the situation in the ruminant in which a markedly higher fat content has been recorded in colostrum than in late milk (Noble *et al*. 1970). Fat supplementation of the sow diet

Table 10. Fatty acid composition (major fatty acids, g/100 g total fatty acids) of colostrum, milk and backfat of sows fed on a standard diet (from de Man & Bowland, 1963)

Fatty acid	Colostrum	Milk	Backfat
10:0	–	0·2	–
12:0	–	0·3	–
14:0	1·4	3·3	1·0
16:0	22·5	30·3	23·7
16:1*n*-7	5·0	9·9	2·8
18:0	5·7	4·0	14·6
18:1*n*-9	41·7	35·3	44·4
18:2*n*-6	20·9	13·0	13·2
18:3*n*-3	2·4	2·5	–
Unidentified	0·4	1·2	0·3

during late gestation and lactation has been shown to increase both milk production and the fat content of colostrum and milk (Bowland, 1966; Pettigrew, 1981). The total amount of lipid in sow's milk does not appear to be affected by differences in the level of unsaturation of the dietary fat (cod-liver oil supplement *v*. 'control': Taugbøl *et al*. 1993; menhaden fish oil *v*. lard: Fritsche *et al*. 1993*b*). The overall composition of sow's milk has been described in detail (Braude *et al*. 1947; Bowland, 1966; Miller *et al*. 1971).

The fatty acid composition of sow's colostrum has been shown to differ from that of mature milk in several important respects (see Table 10). Most notably, the level of linoleic acid in colostrum is considerably higher than that of mature milk (Schuld & Bowland, 1968*b*; Miller *et al*. 1971). The levels of myristic, palmitic and palmitoleic acids are correspondingly lower. Fritsche *et al*. (1993*b*) observed that the level of total *n*-3 polyunsaturates in sow colostrum was similar to that in mature milk. This is in contrast to the situation in man where the levels of long-chain metabolites of linoleic and α-linolenic acids in colostrum have been shown to be double the levels found in mature milk (Gibson & Kneebone, 1981).

Sow's milk is characterized by a predominance of oleic acid followed by palmitic, linoleic and palmitoleic acids. The short-chain fatty acids butyric (4:0), caproic (6:0) and caprylic (8:0) acids are not present in the milk under any dietary conditions whilst capric (10:0) and lauric (12:0) are present only in trace amounts (Witter & Rook, 1970). The fatty acid composition of the milk is influenced extensively by the fatty acid composition of the sow diet. Thus, feeding maize oil resulted in higher levels of linoleic acid in the milk (Miller *et al*. 1971) and feeding fish oil increased the levels of the long-chain *n*-3 PUFA (Taugbøl *et al*. 1993; Fritsche *et al*. 1993*a*,*b*). As shown in Table 11, the levels of saturated fatty acids have been shown to be relatively resistant to dietary alteration. Significant increases of the long-chain *n*-3 PUFA in the milk brought about by the fish oil and mixed lard–fish oil treatments occurred primarily at the expense of oleic acid. Levels of linoleic and arachidonic acids in the milk were not markedly affected by dietary alteration. The lack of response by arachidonic acid within the milk even under widely fluctuating dietary levels of arachidonic acid or its precursor linoleic acid has been observed elsewhere (Innis, 1991; British Nutrition Foundation, 1992).

Table 11. Fatty acid composition (major fatty acids, g/100 g total fatty acids) of the milk from sows fed on diets containing 70 g lard/kg, 70 g fish oil/kg or 35 g lard + 35 g fish oil/kg (from Fritsche *et al.* 1993*b*)

Fatty acid	Lard	Lard + fish oil	Fish oil
14:0	2·9	3·4	3·4
16:0	26·8	25·9	25·6
16:1*n*-7	8·0	8·0	8·1
18:0	4·6	4·8	5·1
18:1*n*-9	39·2	32·4	32·0
18:2*n*-6	13·1	12·6	11·3
18:3*n*-3	0·6	0·8	0·9
20:4*n*-6	0·7	0·5	0·7
20:5*n*-3	0·5	2·3	3·3
22:5*n*-3	0·4	1·1	1·3
22:6*n*-3	0·6	2·4	3·5
SFA	34	34	34
MUFA	47	41	40
PUFA	17	20	22
Total *n*-6 : total *n*-3	7·0	2·1	1·4

SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids.

Positional distribution of fatty acids in milk triacylglycerols. Milk fat is made up almost entirely of triacylglycerol, which accounts for 98 % of the fat. The fatty acids within the milk triacylglycerols of the sow are distributed on the glycerol moiety (i.e. on position *sn*-1, *sn*-2 or *sn*-3) in a manner similar to that found in depot fat. Thus, most notably, palmitic acid is preferentially esterified to the *sn*-2 position of the glycerol moiety (Freeman *et al*. 1965; Duncan & Garton, 1966). The *sn*-1 position is occupied mostly by oleic, palmitic and stearic acids and the *sn*-3 position by oleic and linoleic acids (Christie & Moore, 1970; Parodi, 1982). This distribution is similar to that found in human milk (Goedhart & Bindels, 1994). Stinson *et al*. (1967) observed that, in terms of the positional distribution of fatty acids, the colostrum fat of the sow resembled body fat more than milk fat. Also, no difference in sow milk fatty acid positional distribution was observed between milk from the first or the third week of lactation. Only very limited information is available on the stereospecific distribution of the long-chain PUFA within the triacylglycerols. However, it would be reasonable to suppose that their distribution is similar to that observed in human milk in which arachidonic and docosahexaenoic acids are found primarily at the *sn*-2 and -3 positions (Martin *et al*. 1993; Goedhart & Bindels, 1994). Similarities in fatty acid positional distribution in the milk from a wide range of mammalian species have been observed (Parodi, 1982).

Phospholipid represents approximately 1 % of the fat component of milk. Its function appears to be in providing a structural framework with cholesterol and proteins for retaining the milk triacylglycerols in the aqueous surroundings (Innis, 1991). In sow milk, the major phospholipid species is phosphatidylethanolamine (37 %) followed by sphingomyelin (35 %) and phosphatidylcholine (22 %) whilst phosphatidylserine and phosphatidylinositol are present at a level of 3 % each (Morrison, 1968). The distribution of the phospholipid species in the milks from a wide

range of mammals has been shown to display a remarkable uniformity (Morrison, 1968). Although the milk phospholipids account for some 50 % of the total *n*-6 and *n*-3 long-chain PUFA, diet-induced changes in milk fatty acids occur mostly in the triacylglycerols rather than in the phospholipids (Innis, 1991).

Temporal changes in lipid composition of sow's milk. Various changes in the lipid composition of sow's milk have been observed depending on the stage of lactation. The total fat content has been observed to decrease by approximately 20 % from early to late lactation (Braude *et al*. 1947) although Miller *et al*. (1971) observed no significant change in total milk fat with stage of lactation. Perrin (1954) observed that the milk fat content increased during the initial 3 weeks then decreased over the remainder of the lactation period. Furthermore, considerable day-to-day variation was noted. In the rat, milk triacylglycerol content tended to increase from early to late lactation, the extent of the changes decreasing with up to four parities (Huang *et al*. 1992).

In addition, some workers have observed changes in the fatty acid content of milk during the course of lactation. Miller *et al*. (1971) observed a number of changes in fatty acids in pigs fed on isoenergetic diets with or without 100 ml maize oil/kg. Thus, during lactation, myristic, palmitic and palmitoleic acids were observed to increase in control sows but not in the maize oil group. Oleic acid decreased during lactation in both diet groups. Notably, linoleic acid decreased in the control group from the beginning to 5 weeks of lactation, whereas, in the maize oil diet linoleic acid decreased up to 2 weeks but increased thereafter. Stinson *et al*. (1967) observed no difference in sow milk fatty acid composition between milk from the first or the third week of lactation under normal dietary conditions. From the first to the third week of lactation in the sow, the levels of arachidonic and eicosapentaenoic acids tended to decrease; these changes were reflected by similar reductions in the plasma levels of these fatty acids (Fritsche *et al*. 1993*b*). The decrease in eicosapentaenoic acid occurred even when the level of this acid in the diet was elevated by the inclusion of a high level of fish oil. Similarly, reductions in *n*-6 and *n*-3 PUFA levels in sow milk during lactation have been reported by Taugbøl *et al*. (1993). In rats, the levels of *n*-6 fatty acid metabolites (γ-linolenic acid, dihomo-γ-linolenic acid and arachidonic acid) in milk fat declined progressively (Huang *et al*. 1992).

Digestion of sow milk fat. The digestibility of the fat in sow's milk is high at over 95 % (Frobish *et al*. 1967). The enzymic digestion of milk triacylglycerols is effected by lipases which principally hydrolyse the fatty acids at the *sn*-1 and *sn*-3 positions thereby giving rise to *sn*-2 monoacylglycerols (Small, 1991; Innis *et al*. 1995). As reviewed by Aumaitre (1972), the measured *in vitro* lipase activity in the gut of the newborn pig is very high and increases slightly with age. It was concluded that sufficient lipase activity exists to digest all incoming fats. In spite of the known resistance of the long-chain PUFA to lipase hydrolysis (Bottino *et al*. 1967), the extent of digestion of fats rich in such acids has been shown to be high (over 95 %) in neonatal piglets (Chiang *et al*. 1989). Furthermore, it appears that the level of lipase activity may be affected by the level of lipid but not by the type of lipid in the diet (Armand *et al*. 1990). Not only are lipases secreted from the pancreas but 'pre-duodenal' sources of the enzyme have been identified. Thus, in the neonatal pig, lipases have been shown to be secreted in the milk (milk lipase), the mouth (lingual lipase) and the stomach (gastric lipase) with the hydrolytic activity not occurring until the acidic environment of the stomach is encountered (Borgström & Brockman, 1984).

Fatty acids and reproductive performance

Non-essential fatty acids

Several investigations have been undertaken on the general effects of dietary fat on the reproductive performance of pigs (Wiseman, 1984; Pettigrew & Moser, 1991). Overall, however, little attention has been paid to the constituent fatty acid composition of the fat being fed. Thus, the generic term 'fat' has been used most frequently and often without reference to the kind of fat and much less to the dietary fatty acids being fed. Indicators of reproductive performance have included such measurements as number of piglets born alive or dead, number alive at 3 weeks or at weaning (Kruse *et al*. 1977) and birth and weaning weights (Pettigrew & Moser, 1991; Fritsche *et al*. 1993*b*).

Supplemental dietary fat fed to sows during late gestation has been shown to increase the fat content of piglets only to a very limited extent and apparently of insufficient magnitude to have effects on reproductive variables. Thus, in a review of a number of investigations, Pettigrew & Moser (1991) noted that fat supplementation during late pregnancy had no effect on pig birth weight or the rate of stillbirths. However, beneficial effects on reproductive performance of feeding sows supplemental fat during lactation have been observed, albeit to a moderate degree. Thus, litter weaning weight was increased by supplemental dietary fat given to the sow during lactation, such increases being greatest for sows given 100–150 g added fat/kg diet (Pettigrew & Moser, 1991). This is presumably related to the increased milk yield and milk fat content which has been observed in sows given added dietary fat (Pettigrew, 1981). Although increased survival of piglets from birth to weaning has been observed in piglets sucking sows given supplemental fat, the improvement was only found to be 3 percentage units (Pettigrew & Moser, 1991). These authors noted that the improvement in survival was greater in situations where piglet survival rate was between 70 and 80 % than where it was less than 70 %. It was also noted that there was little difference in response to vegetable and animal fats although the actual type of fat included was not stated in their review.

The feeding of cholesterol has been shown to have an effect on the growth of the piglet. Thus, Schoknecht *et al*. (1994) observed that pigs supplemented with dietary cholesterol had an improved growth rate which was possibly due to a low endogenous synthesis of cholesterol.

Polyunsaturated fatty acids

An essential role for linoleic acid has long been established (Burr & Burr, 1930; Guarnieri & Johnson, 1970) with

deficiency symptoms of reduced growth, scaly dermatitis, increased permeability of skin, fatty liver, kidney damage and impaired reproduction (Holman, 1968, 1970; Rivers & Frankel, 1981). Following the identification of the essentiality of linoleic acid, an essential role for α-linolenic acid has been indicated although not without some degree of scientific debate (Chapkin, 1992). The long-chain PUFA including arachidonic acid, eicosapentaenoic acid and docosahexaenoic acid have been classified as 'conditionally essential' (British Nutrition Foundation, 1992), being required to redress nutritional requirements occurring under specific conditions. According to the British Nutrition Foundation (1992), an example of such a situation is premature human infant birth, where the infant has missed out on the placental supply of long-chain PUFA at late gestation when the brain is undergoing rapid development. It is under such conditions that a supply of pre-formed long-chain PUFA becomes critical to normal brain development. At other times, the presence of sufficient amounts of the precursor fatty acids linoleic and α-linolenic acid is deemed to be sufficient for the formation of the longer chain metabolites. However, in the literature there is a need to define more clearly the circumstances in which these fatty acids are essential *per se* and when they are not.

Linoleic acid

In a study by Kruse *et al*. (1977), an attempt was made to determine the effects of increasing dietary linoleic acid on pig reproductive performance. Sows were fed on diets, over three successive pregnancies, containing levels of linoleic acid of 1·4, 2·2 or 4·8 % of total dietary energy, which were supplied by 0, 20 and 40 g soyabean oil/kg diet, respectively. All the diets contained approximately 240 g of soyabean meal/kg which contributed to the levels of linoleic acid observed in the diets. The levels of linoleic and α-linolenic acid in sow plasma, colostrum and milk and piglet plasma were increased with the increasing dietary soyabean oil supplied to the sows. The levels of eicosatrienoic acid (20 : 3*n*-9) in the plasma of piglets and sows increased with decreasing dietary supply of soyabean oil fatty acids. An increasing level of eicosatrienoic acid relative to arachidonic acid (triene:tetraene ratio) has been stated to be indicative of essential fatty acid deficiency (Holman *et al*. 1979). There was no effect of dietary linoleic acid supply to the sow on the survival rate or growth of the piglets. The authors were able to show that even the basal diet was linoleate-sufficient. However, this was to be expected given that the present-day linoleate requirement is 1 g/kg diet (National Research Council, 1988, see p. 100) and that the diet supplied 5 g linoleate/kg. In another study, the feeding of lard or maize oil either with or without 100 mg α-tocopheryl acetate/kg diet to sows throughout gestation and lactation had no effect on reproductive performance (Malm *et al*. 1976). Similarly, Farnworth & Kramer (1988) observed that the fetuses from sows fed on diets containing no added fat, 50 g soyabean oil/kg or 50 g tallow/kg had no differences in the size or total lipid contents of heart, liver, lung or kidney nor in overall carcass proximate composition.

α-Linolenic acid

Studies which have examined specific effects of α-linolenic acid and its longer chain derivatives on pig reproductive performance are few in number, resulting in calls for research in this area (Schuld & Bowland, 1968*a*; Stitt & Johnson, 1990). Studies in both mice (Rivers & Davidson, 1974) and monkeys (Sinclair *et al*. 1974) have shown that dietary deprivation of α-linolenic acid causes adverse metabolic changes. After feeding mice on an α-linolenic acid-deficient diet based on safflower oil, Rivers & Davidson (1974) observed that the fasting metabolic rate was increased and that the offspring from adult mice fed on the linolenate-deficient diet weighed 17 % less at weaning than offspring from mice fed on control (linolenate-sufficient) diets. This difference in weight was found to persist after weaning onto a standard diet, suggesting that growth was permanently impaired (see also Dickerson *et al*. 1967; Widdowson, 1974). In monkeys fed on maize oil diets, severe skin lesions were observed after approximately 2 years (Sinclair *et al*. 1974). That these lesions were caused by a deficiency of α-linolenic acid was confirmed by subsequently feeding linseed oil which is high in linolenate and which resolved the lesions. In spite of these and other findings (see Tinoco, 1982) which indicate an essentiality of α-linolenic acid, debate still exists as to the validity of this claim (Chapkin, 1992).

Long-chain n-*6 and* n-*3 polyunsaturated fatty acids*

The long-chain PUFA arachidonic, eicosapentaenoic and docosahexaenoic acids have more recently come to be regarded as essential to fetal and neonatal development due to their critical role in the normal growth and development of the brain and retina (Innis, 1991; British Nutrition Foundation, 1992). The brain requires significant quantities of both arachidonic and docosahexaenoic acids at a period of rapid neonatal brain development known as the 'brain growth spurt'. A shortage in the supply of these fatty acids or their precursors, namely linoleic and α-linolenic acids has been shown to cause deleterious changes to the developing brain manifesting in a reduced brain responsiveness and visual acuity (Neuringer *et al*. 1988; British Nutrition Foundation, 1992; Carlson *et al*. 1993*b*).

Several studies have examined the effect of feeding fish oil containing the long-chain fatty acids, eicosapentaenoic and docosahexaenoic acids, on pig reproductive performance. Fritsche *et al*. (1993*b*) fed diets containing 70 g lard or fish oil/kg or a mixture of 35 g each lard and fish oil from day 107 of gestation until 3 weeks postpartum. Samples of milk and serum from the sows and piglet serum were collected weekly from the day of farrowing. As a result of feeding fish oil, there were marked and highly significant increases in the levels of eicosapentaenoic acid, docosapentaenoic acid (*n*-3) and docosahexaenoic acid in the plasma and milk of the sows and consequently in the plasma of the piglets sucking those sows. There was no effect of diet on the number of live pigs born per litter, piglet birth weights or age-adjusted weaning weights. Similar observations were made by Taugbøl *et al*. (1993) who fed a daily supplement of 50 ml cod-liver oil to sows from day

107 of gestation until the resulting piglets were weaned. No noticeable effect on overall piglet mortality or piglet weight gain was observed although it was noted that the health and productivity record of all the animals was very high. This may be attributed to the fact that the basal diet contained rapeseed meal and herring meal at the levels of 30 and 15 g/kg diet respectively. A disadvantage of the studies of both Fritsche *et al*. (1993*b*) and Taugbøl *et al*. (1993) may have been the relatively low number of sows used. The addition of a unique fish oil containing a high level of docosahexaenoic acid to pregnant sow diets was investigated to determine if any effects on resulting piglet behavioural characteristics could be elicited (Bland *et al*. 1997). However, no such effects were found. In a different study, the feeding of a diet containing 50 g fishmeal/kg to a large number of sows resulted in a prolonged gestation length, an increased litter birthweight and a reduced number of postnatal deaths (Edwards & Pike, 1997).

In other mammals besides the pig, a beneficial growth effect of dietary long-chain polyunsaturates has been observed. Thus, Yeh *et al*. (1990) observed that weight gain was 5–10 % greater in rats sucking dams fed on fish oil as opposed to maize oil. In premature (human) infants, plasma arachidonic acid associated with the phosphatidylcholine fraction was found to correlate positively with growth rate in the first year (Carlson *et al*. 1993*a*). Crawford *et al*. (1990) observed that there were positive and statistically significant correlations between human birth weight or head circumference and arachidonic acid or docosahexaenoic acid in the phosphatidylethanolamine fraction of tissue sections taken from the umbilical artery. There were also significant negative correlations between weight or head circumference and the eicosatrienoic : arachidonic acid ratio (20:3*n*-9/20:4*n*-6) or the docosapentaenoic : docosatetraenoic acid ratio (22:5*n*-6/22:4*n*-6) of the umbilical arterial sections. However, various workers have found no effect of long-chain PUFA on neonatal growth weights. Thus, Arbuckle & Innis (1992) observed no difference in body or cerebrum weight of piglets after feeding diets differing in *n*-3 PUFA from birth to 15 d of age. In human infants, Clandinin *et al*. (1992) observed no differences in birth weight, body length or head circumference between babies given breast milk or infant formula with or without added C20 and C22 *n*-6 and *n*-3 PUFA. Carlson *et al*. (1992) observed that very-low-birth-weight infants supplemented with marine oil had lower normalized weight and length during the first year of life than those fed on infant formula. However, in a study using 194 infants, the addition of docosahexaenoic acid and arachidonic acid to preterm infant formula enhanced growth compared with control formula (Hansen *et al*. 1997).

Quantification of pig polyunsaturated fatty acid requirements

Recommendations on the intake of essential fatty acids for pigs have been restricted almost wholly to consideration of the intake of linoleic acid (Agricultural Research Council, 1981; National Research Council, 1988; Stitt & Johnson, 1990). Recommendations on the intake of arachidonic acid have been made by the Agricultural Research Council (1981). It is apparent from studies involving a wide range of animals including the pig (Holman, 1960; Holman & Peifer, 1960; Tinoco *et al*. 1977; Wall *et al*. 1992) that a deficiency in a particular essential fatty acid can be accelerated by the presence of high levels of non-essential and/or other essential fatty acids or other lipids (e.g. saturated fatty acids, cholesterol).

Linoleic acid

A requirement for linoleic acid of 1 g/kg diet has been stated for pigs of all ages including sows in gestation and lactation; this equates to 0·3 % of digestible energy intake per day (National Research Council, 1988). However, the Agricultural Research Council (1981) recommended that higher levels of linoleic acid should be given and be adjusted according to the age of the animal. Thus, for young pigs up to 30 kg, 15 g/kg diet (or 3 % of digestible energy or 3·8 % of total energy) should be linoleic acid but the level should be halved for pigs weighing from 30 to 90 kg. The Agricultural Research Council values are more in line with that of approximately 2 % of total dietary energy as linoleic acid stated by Kruse *et al*. (1977).

Recent studies using the piglet as a model for determining the adequacy of fatty acids in human infant formulas have proposed requirements for linoleic acid for the newborn piglet based on the fatty acid composition of brain and retina phospholipid as indicators of essential fatty acid status (Innis, 1993). These and other results indicated much higher requirements of 5–10 % dietary energy as linoleic acid in a ratio of 5 : 1, linoleic : α-linolenic acid. A similar ratio of 6 : 1 has been stated as optimum for human intake (British Nutrition Foundation, 1992).

The range of recommended linoleic acid intakes of 1–4·8 % total energy for man (Rivers & Frankel, 1981; Galli & Simopoulos, 1989; Department of Health, 1991; Innis, 1991; British Nutrition Foundation, 1992) is similar to that stated for the pig by the Agricultural Research Council (1981) but clearly lower than that stated by Innis (1993). Recommendations for human intake of linoleate have made distinctions in terms of age and reproductive status and have used knowledge of the composition of human breast milk as a standard of reference (British Nutrition Foundation, 1992). Therefore, as stated by the British Nutrition Foundation (1992), human infants, children and adults should consume a minimum of 3 % dietary energy as linoleic acid which is at the low end of the range of linoleic acid contents of 3–12 % (mean 4 %) total energy content recorded in breast milk. A higher requirement of 10 % dietary energy as linoleic acid has been stated for premature babies (Farrell *et al*. 1988). Higher requirements for linoleic acid during pregnancy and lactation in the order of 4·5 and 5–7 % total energy respectively, have been stated (Mendy *et al*. 1986).

α-Linolenic acid

No recommendations for α-linolenic acid in pig diets can be found in frequently used nutritional guidelines by the Agricultural Research Council (1981) and the National Research Council (1988) nor in a comprehensive text pertaining to swine nutrition (Miller *et al*. 1991). Only

nutritional guidelines concerning human intake of α-linolenic acid or studies which have used the pig or other mammals as a model for human (infant) nutrition are available. Pudelkowicz *et al*. (1968) showed that approximately 0·5 % dietary energy intake as α-linolenic acid was required to support the normal growth of rat pups. Arbuckle *et al*. (1994) cite a number of studies in rats, chicks and human subjects suggesting that acquisition of normal levels of docosahexaenoic acid in the brain required a dietary intake of α-linolenic acid in the range 0·75–1 % energy. The minimum advised content of this fatty acid in the human diet has been stated as 1·0 (Galli & Simopoulos, 1989; Innis, 1991), 0·2 (Department of Health, 1991), 0·4 (Bourre *et al*. 1989) and 0·5 % total dietary energy (British Nutrition Foundation, 1992). In human milk, α-linolenic acid supplies approximately 0·4 % of the total energy (British Nutrition Foundation, 1992).

Recent studies using the piglet to assess the effects of altering the fatty acid composition of human infant formulas have provided recommendations on α-linolenic acid intake. Thus, Arbuckle & Innis (1992) observed that piglets given 2 % total dietary energy as α-linolenic acid in a linoleic : α-linolenic acid ratio of 4 : 1 had levels of docosahexaenoic acid in brain and retina similar to those of sow milk-fed piglets. These workers also noted that α-linolenic acid was only 24 % as effective as C20 and C22 *n*-3 fatty acids as a source of docosahexaenoic acid. That the optimal dietary linoleic : α-linolenic acid ratio for the formation of docosahexaenoic acid in the piglet is approximately 4 : 1 is supported by the findings of Gibson *et al*. (1997). On the basis of a range of observations, Innis (1993) proposed that the requirement for α-linolenic acid in the sucking pig should be regarded as 0·8–2·0 % dietary energy in a linoleic : α-linolenic acid ratio of 5 : 1. However, subsequently (Arbuckle *et al*. 1994), the feeding of approximately 2 % dietary energy in the form of α-linolenic acid was claimed to significantly reduce the brain weight of the piglets.

Long-chain n-*6 and* n-*3 polyunsaturated fatty acids*

There is little or no mention of required levels of the long-chain *n*-6 and *n*-3 PUFA (i.e. arachidonic, eicosapentaenoic and docosahexaenoic acids) in guidelines for pig diets. As mentioned earlier, the fatty acid compositions of the brain and retina have been used as reference points for judging the suitability of fatty acid intakes (Innis, 1991). Furthermore, whereas the triene : tetraene ratio has been used as an indicator of essential fatty acid deficiency, the ratio docosahexaenoic acid : docosapentaenoic acid (*n*-6) has been found to be a more appropriate measure of dietary *n*-3 adequacy (Galli *et al*. 1974; Arbuckle *et al*. 1994). With respect to the long-chain *n*-6 PUFA arachidonic acid, the Agricultural Research Council (1981) recommended that it should be fed at the level of 2 % digestible energy (or 10 g/kg diet or 2·6 % total dietary energy) for pigs up to 30 kg live weight. From 30 to 90 kg, the level of feeding should be halved, as for linoleic acid. Arbuckle & Innis (1992) showed that milk formula containing 0·4 % energy as C20 and C22 *n*-3 PUFA was equally or more effective than sow's milk in supporting the deposition of docosahexaenoic acid in piglet brain and retina. It was also observed that the feeding of 1·7 % dietary energy as α-linolenic acid resulted in a similar level of docosahexaenoic acid in the growing piglet synaptic plasma membrane and retina as feeding 0·4 % dietary energy as C20 and C22 *n*-3 PUFA. Thus, it would appear that sufficient levels of long-chain PUFA can be obtained either from feeding high levels of linoleic and α-linolenic acids in an appropriately balanced manner or from feeding comparatively low levels of the preformed long-chain fatty acids.

Human dietary recommendations have proposed a consumption of 0·27 % energy in the form of eicosapentaenoic acid + docosahexaenoic acid with a total *n*-6 fatty acids : total *n*-3 fatty acids ratio of 4 : 1 (Galli & Simopoulos, 1989). It is of note that the ratio of these fatty acids in the milk of sows fed on a diet containing 70 g lard/kg is 22 : 1 (Fritsche *et al*. 1993*b*). Although recommending an increase for man in the consumption of long-chain *n*-3 PUFA, the British Nutrition Foundation (1992) did not state a minimum amount of consumption.

Authors' recommendations for pig polyunsaturated fatty acid intakes

By taking into account the data presently available an attempt can be made to estimate the fatty acid requirements for the pig for fatty acids of both the *n*-6 and *n*-3 series (i.e. linoleic, α-linolenic, arachidonic, eicosapentaenoic and docosahexaenoic acids) (see Table 12). The present estimations have incorporated more recent findings on the role of essential fatty acids in normal tissue growth obtained from studies where the piglet was used as a model for the human infant. The level of 8 % dietary energy for linoleic acid is mid-way within the range of 5–10 % energy as linoleic acid proposed by Innis (1993) but is double that stated by the Agricultural Research Council (1981). Unlike the Agricultural Research Council (1981), we have not stated a recommendation for arachidonic acid, a sufficiency of which would probably be derived from the adequate quantity of linoleic acid provided and its subsequent metabolism. The recommendation for α-linolenic acid at 0·8 % dietary energy is at the low end of the scale of 0·8–2 % suggested by Innis (1993) but, in contrast to that of Innis, the estimation includes an allowance for eicosapentaenoic and docosahexaenoic acids in the pig diet. The suggestion for α-linolenic acid is therefore close to those which have been made for man. The present estimation for eicosapentaenoic and docosahexaenoic acids is based on the data available for

Table 12. Proposed dietary polyunsaturated fatty acid requirements for pigs

	Requirement		
Fatty acid	% total dietary energy	kJ/d*	g/d
Linoleic acid	8·0	4535·9	115·3
α-Linolenic acid	0·8	453·5	11·5
Eicosapentaenoic + docosahexaenoic acid	0·2	113·4	2·9

* Based on values from the National Research Council (1988) for pigs within the live-weight range 50–110 kg with an expected gross energy intake of 56·7 MJ (13 551 kcal)/d and assuming a digestible energy/gross energy value of 0·78 as stated by the Agricultural Research Council (1981).

normal healthy human adults. The linoleic acid : α-linolenic acid ratio presently advised is 10 : 1 which is higher than the 6 : 1 recommended for man (British Nutrition Foundation, 1992). Arbuckle & Innis (1992) observed normal brain and fatty acid profiles in piglets when a formula with a linoleate : α-linolenate ratio of 26 : 1 but a total *n*-6 : total *n*-3 fatty acid ratio of 11 : 1 was fed. It would appear, therefore, that the inclusion of preformed long-chain *n*-3 PUFA enables the feeding of a higher linoleate : α-linolenate ratio. The presently advised α-linolenic acid : (eicosapentaenoic acid + docosahexaenoic acid) ratio of 4 : 1 is exactly that which has been advised by Galli & Simopoulos (1989) in man. Due to the lack of sufficient information available, estimations based on different age categories of pig are not able to be made.

Conclusion

The lack of recognition of PUFA other than linoleic acid could be seen to predispose to a sub-optimal reproductive performance in pigs. Sow gestation and lactation diets presently in use are generally characterized by a high content of linoleic acid and a low content of α-linolenic acid and the long-chain *n*-3 PUFA. Based on a number of studies, it can readily be suggested that *n*-3 PUFA supplementation of sow gestation or lactation diets could improve the situation with respect to: (1) growth of the placenta thereby improving nutrient supply to the fetus; (2) the accumulation of fatty acids necessary for the normal growth and development of the neonate, particularly at critical phases of development; (3) the immune status of the neonate. Supplementation of the sow diet with *n*-3 fatty acids could be met by the relatively simple addition of specific fish, vegetable or microbial oils or appropriate mixtures of the same to achieve a perceived optimum intake of these fatty acids.

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