Insight on the Profile and Metabolism of Intramuscular Fatty Acids toward Modern Human Consumption: A Review

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Abstract

In regards with fast growing meat consumption in modernizing countries in the 20th Century, recommendations for a public healthier eating were formulated. It is assumed that an increasing consumption of meat, whose fat composition is considered too high in saturated fatty acids (SFA) and too low in PUFA, constitutes a public health issue. This paper aims to collect a comprehensive overview of existing information on some of the most important aspects of intramuscular fatty acid composition and metabolism in farm animals. Trends in healthy eating resulted in selection for leaner animals that has characterized the meat production industries in modern countries, affecting *de facto* meat eating and technological indices. Similar predictions would be drawn for emerging societies thus; more reflections are needed to deal with human health aspects of meat, without however affecting its eating quality and technological processing.

Keywords: Farm animals; Human consumption; Intramuscular fat; Long chain pufa

Introduction

Meat has been identified, often wrongly, as a food having a high fat content and an undesirable balance of fatty acids [1]. This has, in the last half of the 20th Century, attracted considerable investigations on the animal fats, especially for the human consumption safety. Subsequent attention has focussed on the intramuscular fat (IMF) content and composition, as this fat depot is the most closely related to eating quality and healthiness of meat [2]. Efforts have been made in controlling the IMF deposition and its fatty acid composition. Particularly, the IMF long chain (LC) polyunsaturated fatty acids (PUFA) are nowadays focused by research, as they are of particular relevance to human health requirements.

It is assumed that, there is an increasing tendency in the consumption of meat, poultry and other animal products around the globe, following an increasing number of urbanized populations [3]. With meat being considered too high in saturated fatty acids (SFA) and too low in PUFA, particularly in the LC n-3 PUFA, this eating behaviour remains a public health issue. High levels of saturated fatty acids are considered to predispose consumer to several of the so-called `Diseases of Western Civilisation', notably coronary heart disease [4].

Thus, efforts to find ways of controlling *in vivo* the intramuscular composition in farm producing animals, is more that needed to safeguard the healthful consumption

of meat, in modernizing societies. However, trends in healthy eating have created a demand for leaner meat [2] and, this evolution in a decline of the fat content may adversely affect eating quality and further meat processing [2,5].

The aim of this paper was to give a comprehensive overview of existing knowledge on some of the most important aspects of fatty acid composition and metabolism in farm animals, with emphasis on the factors controlling fat deposition, *de novo* synthesis of saturated fatty acids (SFA) and the enzymatic elongation and desaturation pathways, responsible for endogenous synthesis of unsaturated FA. Information was however limited to the major fatty acids in intramuscular fat and to the most important indices used in relation to human health considerations, i.e. the P/S ratio (calculated as (C18:2n-6 + C18:3n-3)/ (C14:0 + C16:0 + C18:0) and the n-6/n-3 ratio (calculated as the sum of n-6 PUFA/ the sum of n-3 PUFA, including longer chain PUFA (C20-C24)).

Brief Description of Fatty Acids in Animal Fats

Fatty acids are hydrocarbons and principal components of most lipids [6]. The naturally occurring fatty acids can be grouped on the basis of the presence of double (=) or sometimes triple (≡) bonds into two broad classes termed saturated and unsaturated fatty acids [7]. The most unsaturated fatty acids (UFA) in meat fat may contain one or more double (ethylenic) bonds and can be separated into monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) (Lobb, 1992)[8]. An UFA with a double bond can have two possible configurations, "*cis*" or "*trans*", depending on the relative position of the alkyl groups. Most naturally occurring UFA have the *cis* orientation [8]. Because of their low melting points, UFAs are essential to maintain the gross fluidity of adipose tissue and the fluidity of phospholipids in membranes [9]. The polyunsaturated fatty acids are generally categorized into ω-6 (n-6) and ω-3 (n-3) families [10], depending on the position of the second double bond being a function of the biochemical system [7,8]. These fatty acids are assembled in different fat (lipid) groups, the most occurring in animal tissues being triacylglycerols, phospholipids and cholesterols [8,9].

Fat Content and Fatty Acid Composition in Muscle Tissues of Farm Animals

Intramuscular fat refers to the fatty acids present in the intramuscular adipose tissue and in the muscle fibres [11]. Fat content and composition in meat and meat products vary greatly according to the animal species, age of the animal, part of the carcass used and animal feeding, with the later offering relatively good results in single-stomached animals, such as pigs and poultry [12,13]. However, it is widely documented that meat fat comprises mostly monounsaturated and saturated fatty acids [13,14].

Available data on muscle and fat tissues indicate that adipose tissue has much higher fatty acid content than muscle fibres but, the fatty acid composition of the two tissues is broadly similar [14,15]. The major lipid class in adipose tissue (>90%) is triacylglycerol or neutral lipid while in muscle fibres, a significant proportion is phospholipid, which has a much higher PUFA content in order to perform its function as a constituent of cellular membranes [14]. As result, long chain n-3 and n-6 PUFA are mainly found in phospholipid but are also detected in pig and sheep muscle neutral lipid and adipose tissue [16,17].

It was reported (Table1) that pigs have much higher proportions of the major PUFA C18:2n-6 in both tissues than cattle and sheep [15,1,14]. Proportions of linoleic acid (LA, C18:2n-6) in pig are however largely reported to be higher in adipose tissue than muscle [18,19] unlike, on the contrary, there were found to be similarly distributed in both tissues by [14]. Subsequently, higher incorporation of LA (C18:2n-6) into pig muscle compared to that of ruminants, produces higher levels of AA (C20:4n-6) by synthesis and, the net result is a higher ratio of n-6/n-3 PUFA in pig compared to beef and lamb (7.22, 2.11 and 1.32 respectively) [15,1,12]. On the other hand, the ratio of all PUFA to saturated fatty acids (P/ S), the target for which is 0.4 or above, is much higher and beneficially so, in pigs (0.58) and other monogastrics, compared with the ruminants (0.11 for beef, 0.15 for lamb) [20,12].

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Fatty Acid	Beef	Lamb	Pork
C12:0 (lauric acid)	2.9	13.8	2.6
C14:0 (myristic acid)	103	155	30
C16:0 (palmitic acid)	962	1101	526
C18:0 (stearic acid)	507	898	278
C18:1-trans	104	231	_
C18:1-cis (oleic acid)	1395	1625	759
C18 :2n-6 (linoleic acid)	89	125	302
C18 :3n-3 (α-linolenic acid)	26	66	21
C20:3n-6	7	2	7
C20:4n-6 (arachidonic acid)	22	29	46
C20:5n-3 (eicosapentaenoic acid)	10	21	6
C22:5n-3 (docosapentaenoic acid)	16	24	13
C22:6n-3 (docosahexaenoic acid)	2	7	8
Total	3835	4934	2255
P/S[1]	0.11	0.15	0.58
n-6/n-3 [2]	2.11	1.32	7.22

[1]P/S: polyunsaturated / saturated fatty acid ratio, i.e. (C18:2n-6 + C18:3n-3)/ (C12:0+C14:0+C16:0)
[2]n-6/ n-3 ratio: calculated as the sum of n-6 PUFA/ the sum of n-3 PUFA, including longer chain PUFA (C20-C24)).
Table1: Fatty acid content of loin muscle (mg/g) in steaks or chops purchased from four supermarkets [15,1].

Ruminant meat is described as the most saturated, as a result of enzymatic bio-hydrogenation of unsaturated dietary fatty acids in the rumen [1,13]. For human consumption safety, recommendations for a healthier FA composition of diets and their constituents have been formulated to meet with meat production requirements, e.g. the PUFA/ SFA ratio (or P/ S ratio) should ideally be above 0.45 and the n-6/n-3 PUFA ratio should preferably be inferior to 4 [4,15].

The second most important PUFA is α-linolenic acid (α-LNA, C18:3n-3), with higher proportions in adipose tissue than muscle [14]. Muscle contains also significant proportions of long chain (C20-22) PUFAs which are formed from α-LNA (C18:3n-3) [9,12]. The important product of this pathway is eicosapentaenoic acid (EPA, C20:5n-3), which has various metabolic roles including eicosanoid production [14]. It has to be mentioned that variations in these values are controlled by genetic or feeding factors, and should thus not be generalised [12].

Values for the fatty acid composition of *longissimus* muscle neutral lipid and phospholipid in pig, indicate that oleic acid (C18:1*cis*-9), the major fatty acid in meat, was much more predominant in neutral lipid. This fatty acid is formed from stearic acid (C18:0) by the enzyme stearoyl Co-A desaturase, a major lipogenic enzyme. On the other hand, LA (C18:2n-6) was found at much higher proportions in phospholipid than neutral lipid [12].

Thus, the C18:2n-6/ C18:3n-3 ratio in membrane phospholipids is generally higher than in triacylglycerols, reflecting the preferential deposition of LA (C18:2n-6) in phospholipids and the more equal partitioning of α-LNA (C18:3n-3) in triacylglycerols and phospholipids, compared to other PUFA [12,21,22]. On the contrary, the overall n-6/n-3 ratio of membrane phospholipids is lower than the C18:2n-6/C18:3n-3 ratio due to the preferential synthesis of longer chain fatty acids of the n-3 series over the n-6 series [22,23].

Fatty Acid Metabolism in Farm Animals

Deposited lipids in farm animals originate mostly from dietary fatty acids and *de novo* synthesized fatty acids [24-26]. However, variations in dietary fat have no significant effect on fatty acid metabolism in pig [27]. Consequently, dietary fat has no influence on the composition of *de novo* synthesized FA throughout growth [26] and by far, on the intramuscular fatty acid content [16].

De novo synthesis of fatty acids

Fatty acids are synthesized *in vivo* from anybody component "primer" which yields a two-carbon acetyl unit during its metabolism [9], as displayed below;

$$CH_3CO\text{-}S\text{-}CoA + 7HOOC\text{-}CH_2\text{-}CO\text{-}S\text{-}CoA + 14NADPH + 14H^+ \longrightarrow C_{15}H_{31}COOH + 7CO_2 + 6H_2O + 8CoASH + 14NADP+$$
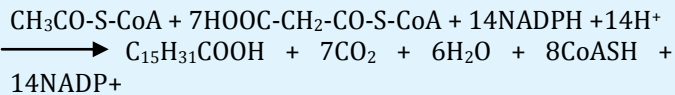
Figure1: Overall equation for de novo fatty acid synthesis [9].

De novo lipogenesis occurs in the cytosol [25], in which two enzymes are involved: acetyl-CoA carboxylase (ACC) and fatty acid synthetase (FAS) [9,25]. Both of them are complexes and catalyze multiple reactions [7]. Acetyl-CoA carboxylase adds carbon dioxide to acetyl-CoA (also to 3-hydroxybutyrate in lactating mammary gland of ruminants) to yield malonyl-CoA. The malonyl group and an acetyl group are then transferred from CoA to the fatty acid synthetase complex and condensed to give acetoacetyl-S-enzyme with the release of the carbon dioxide. The enzyme system then carries out sequentially the reduction of the ketoacyl group, dehydration of the hydroxyacyl group and reduction and hydrolysis of an enoyl group [9,25]. The main sites of lipogenesis are adipose tissues and liver, where the major product is palmitic acid [9,28]. In pigs, the lipogenesis activity is more intense in liver than in adipose tissue for piglets before weaning age [29], but this becomes the inverse after weaning, where more than 80 % of fatty acids are synthesised *de novo* in adipose tissues, from dietary glucose [30-32]. In this view, the pig is distinguished from other monogastric species, where *de novo* lipogenesis is mostly occurring in river tissue.

The Enzymatic Synthesis of Mono-Unsaturated Fatty Acids

Role of the stearoyl-CoA desaturase (Δ9 desaturase) enzyme: The Δ9 desaturase complex (EC1.14.99.5), a microsomal enzyme **[9,33]** catalyses, in microsomes and peroxisomes, the conversion of SFA in their corresponding MUFA, e.g. palmitic acid (C16:0) and stearic acid (C18:0) to cis-9 palmitoleic acid (cis-9 C16:1) and cis-9 oleic acid (cis-9 C18:1) respectively [34,35]. The reaction requires acyl-CoA, NADH, NADH-reductase and cytochrome b_5 (Strittmatter et al., 1974) [36], and shows the maximum velocity on the stearic acid [9,33]. For this reason, acetyl-CoA desaturase (Δ9 desaturase enzyme) is often referred to as stearoyl-CoA desaturase (SCD). The major product of Δ9 desaturation in animal tissues is oleic acid, with smaller quantities of palmitoleic acid [9]. Acetyl-CoA carboxylase is under short-term metabolic control and longer-term hormonal and dietary regulation [37,9,30].

Role of the elongase enzyme: Since palmitic acid is the major product of fatty acid synthetase, except in the mammary gland, other mechanisms are required to produce longer or shorter fatty acids [9]. Two elongation pathways exist which extend the chain by 2C unit at a time, predominantly in the endoplasmic reticulum membrane. In the mitochondria, the elongation system uses acetyl-CoA and NADH or NADPH for reduction and fatty acyl-CoA substrates in the range of C10 – C14, while in the microsomes, it uses malonyl-CoA and NADPH as source of two additional carbon atoms, acting on C16 and longer chain fatty acids [9,31,32]. The microsomal fraction, unless using malonyl-CoA, is distinct from fatty acid synthetase which is a cytosolic enzyme [9]. Fatty acids can also undergo shortening by sequential removal of two carbon units [9].

Omega-3 and omega-6 long chain PUFA metabolism

The most important PUFA belong to n-6 and n-3 PUFA groups, and are derived from their respective metabolic precursors linoleic acid (LA, C18:2n-6) and α-linolenic acid (α-LNA, C18:3n-3) [10]. Vertebrates lack Δ12 and Δ15 (ω3) desaturases and so cannot form C18:2n-6 and C18:3n-3 from C18:1n-9. Therefore, C18:2n-6 and C18:3n-3 cannot be synthesized *de novo* by animal cells and hence, must be provided as essential fatty acids (EFA) in the diets [9,10,38]. These dietary essential fatty acids can be further desaturated and elongated to form the physiologically essential C20 and C22 PUFA, arachidonic acid (AA, C20:4n-6), eicosapentaenoic acid (EPA, C20:5n-3) and docosahexaenoic acid (DHA, C22:6n-3) [10,34]. Two possible routes for the production of C22:6n-3 from C20:5n-3 and C22:5n-6 from C20:4n-6 are described (Figure 4), where Δ6, Δ5 fatty acid desaturases and malonyl-CoA-dependant chain elongase are critical enzymes [10,39,40].

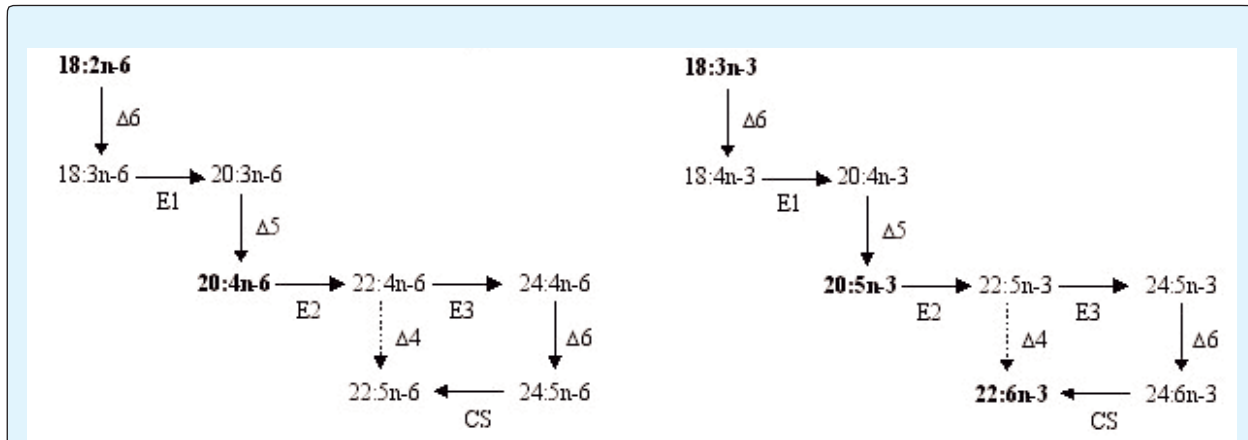Ntawubizi M. Insight on the Profile and Metabolism of Intramuscular Fatty Acids toward Modern Human Consumption: A Review. J Vet Sci Res 2016, 1(1): 000106

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Figure2: Pathways for the biosynthesis of C20 and C22 PUFA from C18:2n-6 and C18:3n-3 [10,38,39,40].

Δ6, Δ5 and Δ4 represent microsomal fatty acyl desaturase activities, E1, E2 and E3 denote microsomal fatty acyl elongase activities and CS denotes peroxisomal chain shortening (*β-oxidation*). The dotted lines indicate secondary pathways for which there is no direct evidence in vertebrates [25,38].

Reactions occur in the microsomal fraction of the adipose cells and the same enzymes act on the n-3 and the n-6 fatty acid series [10,25]. Originally the insertion of the last, Δ4, double bond in C22:6n-3 was assumed to occur through direct Δ4 desaturation of its immediate precursor C22:5n-3 [38]. It has been however shown in rat liver that, the C22:5n-3 is further chain elongated to C24:5n-3 which is then converted by Δ6 desaturase enzyme to C24:6n-3, then by a chain shortening reaction in the peroxisomes, to C22:6n-3 [39]. This pathway has also been demonstrated in pigs, in baboons and in human [41]. There is a competition for desaturase and elongase enzyme activities between n-6 and n-3 PUFA, with however a preference for the n-3 PUFA synthesis pathway [42], in which Δ6 desaturase appears to be the rate-limiting step [35,39,41]. Long chain PUFA are important in membrane structure as major components of phospholipids for the integrity and fluidity of intracellular and plasma membranes. In this regard, they modulate activity of membrane-bound receptors, enzymes, molecule carriers and ionic channels [10,43].

Inner Factors Affecting the Variation in Intramuscular Fatty Acid Composition in Farm Animals

Effect of fat content on intramuscular fatty acid composition

The overall fat content of the animal and muscle have an important impact on fatty acid proportions because of the different fatty acid compositions of neutral lipids and phospholipids [14]. In pig, IMF content was reported to be positively related to the total and most of the individual SFA and MUFA proportions, while showing a negative relationship with all PUFA proportions, except C18:3n-3, leading to a decrease in the P/ S ratio [11,12]. In lean animals or animals fed a low energy diet, the lower cis-9 C18:1 and higher C18:2n-6 content of phospholipids has a major influence on total muscle fatty acid composition [14].

There are evidences that animals with a lower IMF content do have lower *de novo* fatty acid synthesis and, consequently, show greater relative incorporation of the strictly essential dietary fatty acid C18:2n-6 into their tissues.

Genetic Variability

Breed differences: Breeds or genetic types with a low concentration of total lipid in muscle, in which phospholipids are in high proportion, present higher proportions of PUFA in total lipid [14]. Also, leaner breed are notable in having high muscle lipid (marbling fat) content relative to subcutaneous fat compared with other

breeds [44]. Evidences showed breed significant source of variation for both the thioesterase, stearoyl-CoA desaturase and elongase indices in the *longissimus* muscle of pigs and of cattle [45,46].

Breed differences reported for beef meat are often confounded by differences in fatness. Several authors made corrections for the effect of fatness by including it as a covariate in the statistical analyses or compared breeds at similar carcass fat levels, and still found significant differences in individual fatty acid concentrations between breeds, as well as in the triacylglycerols and in the phospholipids fraction [12]. Specific breed differences in the n-6/ n-3 ratio and in the levels of longer chain fatty acids C20:5n-3 and C22:6n-3 that probably could not be attributed to differences in the fat level, have also been reported in cattle [47].

Implication of major genes: Some major genes may also be implicated in genetic variability on fat content and fatty acid composition [12]. In pig, only minor effect of the stress susceptibility genotype on the subcutaneous and intramuscular fatty acid profiles were found by Piedrafita et al. [48] and De Smet et al. [12] while Hartmann et al. [49] reported a significantly higher P/S ratio in muscle and adipose tissue for stress-susceptible pigs compared to normal pigs. But, the genotype effect in this case might take into consideration a confound effect of fat content variations [12], since relatively small differences in fatty acid composition were found between pigs with and without the RN- allele. Polymorphisms in the H-FABP gene have also been associated with variability in intramuscular fat content, largely independent of back fat thickness [50,51]. In a QTL mapping study, Pérez-Enciso et al. [52] pointed out that, the metabolism and (or) deposition rate of C18:2n-6 in pig, is under control of a QTL situated on chromosome 4. Also in cattle, the Belgian Blue beef breed is well known for its extreme carcass leanness and the accompanying high P/S ratio in the intramuscular fat, due to the high selection effort on conformation and to the associated high frequency of double-muscled animals caused by a mutation in the myostatin gene. The intramuscular fatty acid composition was examined in the three myostatin genotypes (double-muscling, *mh/mh*; heterozygous, *mh/+*; normal, *+/+*) by Raes et al. [53]. Results suggested a markedly higher P/S ratio as well as higher proportions of LA (C18:2n-6), α-LNA (C18:3n-3), EPA (C20:5n-3) and Docosapentaenoic acid (DPA, C22:5n-3), for the double-muscled animals compared with the normal and heterozygous ones.

Quantitative genetic variations: Within-breed, quantitative genetic variations in the proportion of the major FA in backfat and intramuscular fat were reported in several studies. Sellier [54] and Cameron & Enser [11] cited a high heritability of the intramuscular lipid content (h² around 0.50 and 0.53 respectively) and of subcutaneous fat firmness traits related to FA composition in pig. Average heritabilities for the major intramuscular fatty acids are estimated between 0.25 and 0.50, except for C18:0 and C18:3n-3 with values of 0.73 and 0.62 respectively [11,12]. Similarly, heritability ranging between 0.24 and 0.73 for C18:2n-6 was found for intramuscular FA by Cameron and Enser [11].

On the other hand, negative correlations between C16:0, C18:0 and C18:1 proportions and carcass lean weight were found, at genetic and phenotypic level, whereas the proportion of C18:2n-6 showed opposite correlations for the inner layer for IMF [55,11].

Reports of genetic parameters for fatty acid composition traits in other species are scarce. Heritability estimates for individual fatty acids and their summations, desaturation and elongation indices, melting point and marbling were reported to be low to moderate (0.14–0.33), in adipose tissue samples (subcutaneous and muscle) of crossbred cattle (Hereford dams × seven sire breeds) [56]. Genetic correlations between fatty acid composition and carcass traits were found not significant, allowing the authors to conclude that simultaneous improvement in carcass and meat quality traits is feasible.

Sex factor: Studies showed a higher IMF content, higher proportions of total SFA and MUFA as well as lower proportions of total n-6 PUFA in intramuscular fat of barrows compared to gilts [45]. Huang & Horrobin [57] studied the effect of sex on the distribution of long-chain n-3 and n-6 fatty acids in essential fatty acid-deficient rats fed C18:2n-6 concentrate and/or C20:5n-3 and C22:6n-3-rich fish oil, and observed a greater incorporation of the sum of total long-chain essential fatty acids (EFA; C20:4n-6, C20:5n-3 and C22:6n-3) in females than in males.

Castration of piglets was also associated with increased fat deposition in pig [58,59,60] and reduces the efficiency of conversion of feed into meat.

In cattle, residual sex effects independent of fat content seem to exist for fatty acid composition, and some authors linked them with possible effects of sex hormones on the enzyme systems such as Δ9-desaturase that may interfere in MUFA metabolism [12,59,60].

Conclusion

Trends in healthy eating, in modern societies, have created a demand for leaner meat in respect with healthy eating guidelines. This evolution in a decline of the fat content may adversely affect eating quality and further meat processing. Thus, a dilemma would be dealt with between eating quality indices and human health aspects in evolution of meat production, e.g. the desire to reduce PUFA content of intramuscular fat, from a technological perspective, should be balanced by the need to increase ratios of polyunsaturated/ saturated fatty acids (P/ S) and n-6/ n-3 PUFA. One would raise a question: What is the point in tropical areas and emerging country?

In any of the cases, there is a huge interest in reflecting on ways to control the fat content and composition in meat (and other animal products), to improve its nutritional and eating quality indices.

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