LIPIDS AND MEAT QUALITY - LIPOLYSIS - OXIDATION AND FLAVOUR

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ABSTRACT

This paper is an overview of the role of intramuscular lipids in meat flavour. The first part is devoted to the composition of intramuscular and its main factors of variation. The second and the third parts deal with the lipid degradation through lipolysis and oxidation in muscles. The four is devoted to the interaction between lipid oxidation and Maillard reaction with emphasis on typical cooked meat aroma and warmed-over -flavour.

Phospholipids are the main substrates of both lipolysis and oxidation in muscle. Very little is known about lipolysis in skeletal muscles and the relationship between lipolysis and oxidation is not yet clearly established. Even if many potential mechanisms of lipid oxidation in muscle cells have been described, their relative contribution to oxidation processes in meat in not yet assigned. Lipids primarily interfere in Maillard reaction through their oxidation breakdown products which quench the formation of heterocyclic compounds, mainly sulfur containing heterocyclic compounds. The overall aroma of cooked meat results in a subtle equilibrium between the products from lipid oxidation and Maillard reaction.

The lacks in the present knowledge are underlined in the conclusion.

INTRODUCTION

Intramuscular lipids are involved in many quality traits of meat and meat products such as nutritional value (energy, fatty acid and cholesterol supply), sensory attributes (tenderness, juiciness, colour and flavour) and technological properties (shelf-life, ...). Many papers have been devoted to nutritional implications of meat consumption in human heath (Rogowski, 1980 ; Hermus & Albers, 1986 ; Gandemer, 1992) so this aspect is not developed in the present paper. Among sensory attributes, the one mainly related to intramuscular lipids is flavour. Lipids contribute to the development of positive flavour but also to its deterioration (Gray et al., 1996). Despite numerous studies, the contribution of lipids in the processes of flavour development and deterioration is not completely understood (Spanier et al., 1988). The post-mortem changes in lipids during meat and meat products processing largely conditioned the development and the deterioration of flavour of meat or muscle food and affect the self-live of meat products.

Lipid breakdown begins immediately after the death involving both lipolysis and oxidation which contribute to flavour degradation (Pearson et al., 1977). However lipids can also contribute to the formation of desirable flavour compounds during cooking because they interfere in Maillard reaction (Mottram & Edwards, 1983, Whitfield, 1992).

This paper deals with the present knowledge on intramuscular lipid in muscle and their implications in the development and deterioration of flavour through lipolysis, oxidation and Maillard reaction.

INTRAMUSCULAR LIPIDS

Intramuscular lipids designate both lipids of intramuscular adipose tissue and muscular fibres. The intramuscular adipose tissue is formed of cells located along the fibres and in the interfacicular area Cassens & Cooper, 1971). The fat cells are isolated or in clusters. They contain almost exclusively triacylglycerols. The lipids of the fibres consist in both cytosolic droplets of triacylglycerols and in membrane lipids, phospholipids and cholesterol. The amount of triacylglycerols in the fibres varies from one muscle to another but it accounts only for a small part of total intramuscular triacylglycerols which are mainly located in fat cells.

Triacylglycerol content varies from 0.2% to more than 5%. It depends on many factors. The most important ones are anatomical location, breed, age and sex (Pearson et al., 1977). Recently, it has been postulated that triacylglycerol content of muscle is under genetic control. Janss et al. (1994) detected a major recessive gene, named IMF affecting the intramuscular triacylglycerol content in the pig. The double carrier of the high-IMF allele have a Longissimus dorsi with 3.9% intramuscular lipids while the same muscle in the non-carriers or single carriers contained only 1.8%. This high-IMF allele was evidence in Meishan pigs segregating in a pure population at the frequency of 0.5. The possible presence of this allele in industrial breed is under investigations. The main interest of this discovery is to offer the opportunity to create genotypes with intramuscular lipids close to 4-5% within a breed by

segregating the high-IMF allele in only two generations. A level of 4-5% intramuscular fat was often reported as the level required to improve significantly the eating quality of fresh pork meat (Gandemer et al., 1991 , Touraille et al., 1989). Creating high-IMF genotype will permit to evaluate the effect of a higher intramuscular fat on eating quality of fresh and processed meat avoiding any interference with other parameters (age, breed or genotype) as it is the case in many studies. Besides the genetic factor, the second most important factor of the variability of intramuscular triacylglycerol content is the anatomical location of muscles in the pig (Leseigneur-Meynier & Gandemer, 1991), the cattle (O' Keefe et al., 1968) and the chicken (Kim & Gandemer, 1987). Others factors such as rearing conditions, age, sex, dietary regimen affect intramuscular lipid content but in a lesser extend because intensification of animal production leads to a standardisation of the rearing conditions in many countries.

Despite intramuscular deposition of lipids is important for meat flavour, very little is known on the development of intramuscular adipose tissue. Compared to the extramuscular adipose tissues, the intramuscular one develops latter. As fat cells of others adipose tissues, intramuscular fat cells probably have a perivascular origin (Nnodin, 1987). The first intramuscular fat cells appear in the new-born. They develop at slow rate because they have a lower capacity for de novo fatty acid synthesis (Mourot et al., 1995) and for taking fatty acids from circulating triacylglycerols via lipoprotein lipase activity (Henry, 1977). Consequently, these adipose cell were smaller in size than those of other adipose tissues (Hausser et al., 1997). The distribution of fat cells within muscle remain largely unknown.

Phospholipid content varies from 0.5% to 1.0 % of wet weight whatever total lipid content of muscles. Phospholipid fraction is mainly composed of phosphatidyl choline (PC) and phosphatidyl ethanol amine (PE) which account for 45-60% and 20-30% respectively. The relative proportions of cardiolipin and phosphatidyl inositol (PI) are 2-10% and 4-10% respectively (Gandemer, 1990 and 1989 ; Leseigneur-Meynier & Gandemer, 1991 ; Alasnier et al., 1996 ; Kim & Gandemer, 1987) (Table 1). Muscle phospholipids contain also a small amount of sphingomyelin and phosphatidyl serine (less than 2%). Phospholipid content and composition are related to metabolic type of muscle. Oxidative muscles contain more phospholipids (0.5% versus 1.0%) and a higher proportion of cardiolipin and PE than glycolitic ones. These results are mainly explain by the higher mitochondria content of oxidative muscles as compared to glycolytic ones. First, oxidative muscles are mainly formed of oxidative fibres which contain more mitochondria and consequently more phospholipids per g of muscle than glycolytic ones (Cassens & Cooper, 1971). Secondly, mitochondria are the only organelles which contain an appreciable amount of cardiolipin located in the inner membrane (>20%, Fleischer & Rouser, 1965) and they exhibit a higher proportion of PE as compared to sarcoplasmic reticulum and sarcolemma (Jain, 1988). Phospholipid content of muscles are slightly or not affected by breed (Wood & Lister, 1973), rearing conditions (Gandemer et al., 1990 ; Gandemer & Kim, 1993), age (Link et al., 1970 ; Girard et al., 1983) or diet (Girard et al., 1983).

Fatty acid compositions of triacylglycerols and phospholipids and their factors of variation have been extensively studied. Triacylglycerols and phospholipids have a very different pattern in fatty acid composition which probably explain a large part of the difference in their contribution to the development and the deterioration of flavour.

The animal species is the main factor of variation of fatty acid composition of triacylglycerols, especially in polyunsatured fatty acid (PUFA) proportion which accounts for 2-3% in the cattle, 7-15% in the pig, 20%-25% in the chicken and more than 30% in the rabbit. PUFA are mainly composed in C18 PUFA, namely linoleic acid and a small proportion of linolenic acid. Anatomical localisation of muscle only slightly affects fatty acid composition of triacylglycerols in the cattle, rabbit and chicken (2 à 3%, 28 à 32% and 24 à 26% respectively) but it greatly affects that of triacylglycerols in the pig (7 à 15%) (Leseigneur-Meynier & Gandemer, 1991). In the pig and chicken, fatty acid composition of triacylglycerols reflects that of the dietary lipids (Girard et al., 1983 ; Marion, 1965).

Fatty acid composition of phospholipids is characterised by a high proportion of polyunsaturated fatty acids (PUFA)(45-55%). These PUFA are linoleic acid (14-30%) and long chain PUFA such as arachidonic acid (8-14%) and 22C fatty acids such as 22:4 n-6, 22:5 n-3 and 22:6 n-3 (Gandemer, 1997a and b) (Tables 1). The proportion of total PUFA in muscle phospholipids shows only small variation according to many factors (animal species, breed, dietary fat composition, sex, ...), because phospholipids are membrane components and large variations in fatty acid composition of phospholipids alter membrane properties. Consequently, fatty acid composition of phospholipids are strictly controlled by complex enzymatic systems involved in fatty acid desaturation and elongation and in their subsequent esterification in phospholipids. Conversely, we observed small differences in the relative proportions of PUFA of n-3 and n-6 series in phospholipids. In monogastric animals, the ratio n-3 PUFA/n-6 PUFA depends on dietary supply of linoleic and linolenic fatty acids which are the precursors of long chain PUFA. In contrast, large differences in fatty acid composi-

tion are observed according to the phospholipid classes. Thus, proportion of PUFA as well as type of PUFA are completely different from one phospholipid class to another. Thus cardiolipin and PE are the most unsaturated classes. However, PUFA are represented by linoleic acid in cardiolipin while PE contain a large amount of long chain PUFA. PC contain about 30% of PUFA formed by a large amount of linoleic and a low proportion of arachidonic acid (Alasnier & Gandemer, 1998).

Table 1. Content and fatty acid composition of triacylglycerols and phospholipids of muscles in the farm animals.

Species	Beef (1)		Pork (2)		Chicken (3)		Turkey (4)		Rabbit (5)	
Metabolic type	Glycolitic	Oxidative	Glycolitic	Oxidative	Glycolitic	Oxidative	Glycolitic	Oxidative	Glycolitic	Oxidative
Muscle	Longissimus dorsi	Diaphragma	Longissimus dorsi	Masseter	Pectoralis	Sartorius	Pectoralis	Sartorius	Psoas major	Semi-membranosus
Triacylglycerols										
Content (g/100 g)	2.1	4.1	1.0	0.9	0.6	1.5	0.9	2.0	0.5	3.5
Fatty acid composition (%)										
18:2 n-6	1.6	2.5	7.2	8.2	17.9	16.9	24.6	24.2	21.2	18.8
18:3 n-3	0.4	0.5	0.7	1.0	1.2	1.1	5.1	5.3	3.7	3.3
Phospholipids										
Content (g/100 g)	0.7	1.1	0.5	0.9	0.5	0.9	0.5	0.9	0.7	0.9
Fatty acid composition (%)										
18:2 n-6	13.8	20.1	22.9	24.7	14.8	21.8	18.1	23.5	25.5	14.3
Long chain n-6	11.6	11.2	8.3	8.5	20.3	19.5	15.8	18.8	15.6	18.5
Long chain n-3	6.2	4.4	1.1	1.9	5.0	5.1	7.5	5.8	2.8	3.7

(1) Gandemer et al., unpublished data ; (2) Leseigneur-Meynier et Gandemer (1991) ; (3) Kim et Gandemer. (1987) , (4) Genot et al. (1996) ; (5) Alsnier et al. (1996)

LIPOLYSIS

Lipolysis is one of one of the main causes of lipid degradation in meat. It only occurs in fresh meat during ageing or during process involving raw meat such as dry sausage or dry cured ham production. Lipolysis is due to specific enzymes, lipase's and phospholipases.

Lipases: Numerous studies have been devoted to lipases in adipose tissue and to a lesser extend, in heart and skeletal muscles . The muscles contain two important lipase systems, lipoprotein lipase (LPL) and hormono-sensitive lipase (HSL)(Oscai et al., 1990). The former acting at the capillary endothelium is responsible of the degradation of lipoprotein triacylglycerols and permit fatty acid uptake by the cell. The latter located in the cytosol of the fat cell hydrolyses triacylglycerols and diacylglycerols permitting fatty acid mobilisation. A monoacylglycerol lipase ends the process hydrolysing the monoacylglycerols. In vivo, the rate-limiting step of the hydrolysis is catalysed by the HSL which hydrolyses triacylglycerols slower than diacylglycerols and monoacylglycerols (1:10:4). The activity of the monoacylglycerol lipase is higher than that of HSL (Belfrage et al., 1984). These observations explain why monoacyl and diacylglycerols do not accumulate in tissues. Muscles also contain an acid lipase located in the lysosomes but its activity is low (Motilva et al., 1993b).

Very little is known on the post-mortem activity of these enzymes in muscles. Recently, Motilva et al.(1993b) have given evidence of activities of at least free lipases in pig muscles, acid, neutral and basic lipases which are probably, lysosomal, hormono-sensible and lipoprotein lipases. These enzymes remains active, post-mortem, up to 15 months in dry-cured ham). Oxidative

muscles have higher neutral and acid lipase activities than glycolytic ones in pigs (Hernandez et al., 1998) and muscles from heavy pigs have a higher neutral lipase activity than those of light pigs (Toldra et al., 1996).

From most of the studies on post-mortem lipolysis in muscles, it is difficult to conclude if triacylglycerol lipolysis is a specific or a non-specific process for at least two reasons. First, free fatty acids extracted from muscles are originate from both triacylglycerols of fat cells and, triacylglycerols and phospholipids of fibres. Second, the hydrolysis of triacylglycerols which is initiated by LPL and HSL is generally complete because of the high activity of monoacylglycerol lipases. A recent study from our laboratory supports the hypothesis of a specific hydrolysis of triacylglycerols containing polyunsaturated fatty acids. We have observed in subcutaneous adipose tissue of Corsican pigs that the free fatty acids contained a larger amount of linoleic acid than triacylglycerols (14% *versus* 8%) and lipolysis affected mainly the triacylglycerols containing linoleic acid such as palmitoyl-oleyl-linoleyl-glycerol (Coutron & Gandemer, 1998). This results could be explained by the liquid state of this triacylglycerol while the most of the triacylglycerols of pig fat are solid at the temperature of dry-cured ham processing (Davenel et al., 1998).

Phospholipases : Many studies deals with the activities of phospholipases in mammalian heart because of role of these enzymes in ischemia. Studies devote to the enzymes in skeletal muscles were limited. Hydrolysis of fatty acids of phospholipides involves phospholipases A (A1 and A2) and lysophospholipases. These enzymes are involved in the turnover of phospholipids and fatty acid metabolism. Recent results of our laboratory indicate that phospholipases are active *post-mortem* in Rabbit muscles (Alasnier, 1996). The main activities are related to basic phospholipases A (maximum activity at pH 8-9) which are probably membrane-bound enzymes. These enzymes are more active in oxidative muscles than in glycolytic ones. The activity of lysophospolipases is far higher than that of phospholipases in muscles. This result explains why the amount of lysophospholipids is always very low in the muscles. Even if phospholipase activities are obviously very low after the death because of the pH and temperature decreases in muscle cells, these enzymes remain active. This hypothesis is supported by the fact that long chain PUFA proportion increase in free fatty fraction for at least 6 months in dry-cured hams giving evidence of phospholipid hydrolysis.

The phospholipases would be specific neither for phospholipid classes nor for the length and the unsaturation of fatty acid chains because several authors haven't observed significant changes in the fatty acid composition of both free fatty acid fraction and phospholipids during ham processing (Buscailhon et al., 1994 ; Flores et al., 1987).

Time-course of lipolysis in muscles - Relative contribution of phospholipids and triacylglycerols to free fatty acid fraction.

Free fatty acid amount is always low in muscles immediately after the death but it increases slowly during meat storage at 4°C to reach about 1% in 5-7 days (Currie & Wolfe, 1977 ; Sklan et al., 1983 ; Valin et al., 1975). In dry-cured processing that intramuscular lipids are subjected to an intensive lipolysis (Flores et al., 1985 ; Motilva et al., 1993b et 1994 ; Buscailhon et al., 1994). Fast during the first six months of processing, the rate of lipolysis is slow from 6 months to the end of the process (12 - 24 months). At the end of the process, free fatty acids account for 8 to 20% of total lipids in muscles and adipose tissue according to the length of the process, the technology and the raw matter (Motilva et al., 1994 ; Buscailhon et al., 1994c ; Coutron-Gambotti et al., 1998 ; Coutron- Gambotti & Gandemer, 1998). Oxidative muscles contains more free fatty acids than glycolytic one in both chicken and rabbit (Sklan et al., 1983 ; Alasnier, 1996).

The relative contribution of triacylglycerol and phospholipid hydrolysis to free fatty acids is an important question because hydrolysis of tryacylglycerol release only PUFA with 18 carbons and 2 or 3 double bounds while that of phospholipids releases long chain PUFA with 4, 5 or 6 double bounds which are very sensitive to oxidation. The relative contributions of triacylglycerol and phospholipid hydrolysis to free fatty acids were generally estimated by the comparison of the fatty acid composition of free fatty acid fraction with these of triacylglycerols and phospholipids. Hydrolysis of both triacylglycerols and phospholipids contributes to free fatty acid generation and the relative contributions of these lipids depend on animal species, lipid content and composition of raw matter and process. Phospholipids are the main substrates of lipolysis in fresh meat and dry-cured hams (Figure 1) (Sklan et al., 1983 ; Currie & Wolfe, 1977 ; Motilva et al., 1994 ; Buscailhon et al., 1994 ; Coutron-Gambotti et al., 1998). This conclusion is supports by the fact that free fatty acid contain a large amount of long chain polyunsaturated fatty acids which come unambiguously from phospholipids (Sklan et al., 1983 ; Currie & Wolfe, 1977 ; Buscailhon et al., 1994c ; Coutron-Gambotti et al., 1998). However, triacylglycerols provide also free fatty acids. The con-

tribution of triacylglycerols to lipolysis appears to be related to the lipid content of the muscles. So it is low in Bayonne ham while it is more important in Iberian and Corsican hams which contain a higher amount of triacylglycerols than Bayonne hams (5-8 versus 2 g/100 f of fresh meat). Similarly, after 7 days of refrigerated storage of rabbit muscles, the relative contribution of triacylglycerols was similar to that of phospholipids in oxidative muscles while it was lower than that of phospholipids in glycolytic ones (3:2). This is explained by the higher triacylglycerol content of oxidative muscles (Alasnier, 1996).

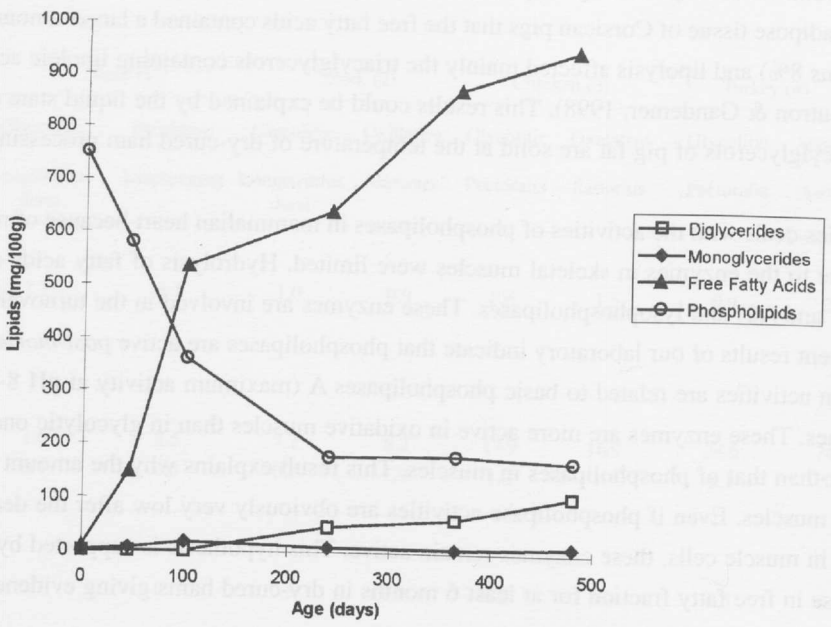

Figure 1. Changes in lipid composition of Serrano dry-cured ham during processing

The relationship between lipolysis and flavour remain unclear. Lipolysis is generally considered as a factor promoting lipid oxidation (Nawar, 1996). However the mechanisms by which lipolysis could promote oxidation remain unknown. Several hypothesis can be put forward. The first one is related to the presence in muscle cells of enzymes such lipoxygenases and cycloxygenases which oxidise free fatty acid such as arachidonic acid. The second one is supported by the fact that low level of phospholipid hydrolysis cause a substantial disorder in the membrane which could promote oxidation of phospholipids by oxygen radicals or iron because of the greater opportunity to penetrate the membrane. However, recent results suggest that lipolysis don't always promote phospholipid oxidation. In dry-cured ham, free fatty acid amount reaches 10-15% of muscle lipids at the end of the process and they contain a high proportion of long chain polyunsaturated fatty which do not significantly vary during the process (Buscailhon et al., 1984). These results suggest that the hydrolysis of phospholipids during processing could prevent their long chain PUFA from oxidation. The mechanism remains unknown.

LIPIDS OXIDATION

Lipid oxidation is one of the main causes of deterioration in the quality of meat during storage and processing. Detailed discussions on lipid oxidation in meat can be found in several recent reviews (Asghar et al., 1988 ; Kanner, 1994 ; Gray et al., 1996). Beside some well-assessed facts, several aspects of lipid oxidation remain confusing.

Substrates of lipid oxidation : Phospholipids are the primary substrates of lipid oxidation in muscle food with triacylglycerols playing a minor role (Igene & Pearson, 1979 ; Wilson et al., 1976 ; Gandemer, 1990). The extent of phospholipid degradation in meat depends on storage length and temperature, cooking method, temperature and length (Gandemer et al., 1983, 1985), animal species (Wilson et al., 1976), metabolic type of muscle (Gandemer & Kim, 1993 ; Ngah et al., 1993). The high sensitivity of phospholipids to oxidation have primarily two causes. Firstly, phospholipids contain long chain PUFA which are very sensitive to oxidation. Secondly, phospholipids are membrane components in close contact with catalysts of lipid oxidation loca-

ted in the aqueous phase of the muscular cell. Within phospholipid fraction of muscles, phosphatidyl-ethanolamine is the most sensitive phospholipid class to oxidation because it contains a large part of long chain PUFA of muscles (Gandemer, 1989, Keller & Kinsella, 1973). To illustrate this point, changes in phospholipids during cooking of chicken carcasses are presented (Table 2). Thus, total phospholipid content was slightly reduced in breast glycolytic muscles whereas it decreased markedly in drumstick muscles which are more oxidative muscles. Within phospholipid classes, a large amount of PE was destroyed during cooking (-40-45%) whereas only a small amount of PC disappeared (0-22%). Cooking also induced a partial oxidation of PUFA in phospholipids. The percentage of PUFA destroyed during cooking was higher in oxidative muscles (thigh and drumstick) compared to glycolytic ones (breast). It increased with the number of double bounds of fatty acid backbone. Thus, looses were low (0-20%) for linoleic acid whereas they reached 30-50% for 22 C PUFA with 5 to 6 double bounds.

Table 2. Effect of roasting on losses of phospholipids fatty acids in chicken muscles

Muscles	Pectoral major		Drumstick	
Metabolic type	Glycolytic		more oxidative	
	(1)	(2)	(1)	(2)
Phospholipids (mg/100g)				
Total phospholipids	465	-5	801	278
PC	293	29	399	88
PE	119	-48	282	-129
Polyunsaturated Fatty acids (PUFA) (mg/100 g)				
Total PUFA	122	-20	197	-87
n-6	110	-20	188	-78
18:2	48	0	92	-28
20:4	48	-16	78	-39
22:4 + 22:5	10	-5	15	-9
n-3	12	-7	15	-9
18:3	0	0	1	-1
22:5 + 22:6	12	-8	14	-8

PC = phosphatidyl-choline, PE = phosphatidyl-ethanolamine
(1) PE, PC of polyunsaturated fatty acids gras of phospholipids in mg/100 g fresh muscle.
(2) cooking losses in PE, PC or polyunsaturated fatty acids of phospholipids in mg/100 g fresh muscle.

Mechanism of lipid oxidation : The overall mechanism of fatty acid oxidation is generally a free radicals process including initiation step, propagation step and termination (Frankel, 1984). initiation process take place by loss of a hydrogen radical to form an alkyl radical ($L^{\bullet}$) This radical react with oxygen to form peroxyl radical ($LOO^{\bullet}$)which abstract a hydrogen to fatty acid and form hydroperoxides (LOOH), the fondamental primary products of autoxidation. Since it was established that there is a spin barrier which prevents the direct addition of air oxygen in triplet ground state to singlet state unsaturated fatty acids, the key question of fatty acid oxidation in meat concerns the molecules which could abstract hydrogen from unsaturated fatty acids to form primary alkyl radicals ($L^{\bullet}$). A large number of potential initiators and propagators of lipid oxidation in muscle food, have been described including chemicals such as hydroxyl radical ($OH^{\bullet}$), perferryl and ferryl radical, di-iron-oxygen bridged radical and porphirin cation radical ($P\text{-}Fe^{4+} = O$) (Kanner, 1994 ; Gutteridge, 1984 ; Asghar et al., 1988) or enzyme systems such as lipoxygenases and cycloxygenanses and enzymic systems dependent on NAD(P)H, ADP-Fe^{3+} and O_2 (Rhee and Ziprin, 1987; Lin et Hultin, 1976 ; Kanner et al., 1986). The relative contribution of these possible catalysts of lipid oxidation in muscles remain confusing. Only the pivotal role of the iron in both enzymic and non enzymic peroxidation is well established (Schaich, 1992 ; Kanner,1994). Iron, free and protein bound, heme and non-heme, oxidised or reduced has the ability to oxidise unsaturated fatty acids in meat but the relative contribution of these different forms have not yet been assigned (Gray et al., 1996). The

general mechanisms for metal catalysis of lipid oxidation are well known. Schaich (1992) divided the mechanisms into three types of reactions. A direct initiation which involved three mechanisms :

- higher valence state iron (Fe^{3+}) can abstract hydrogen from unsaturated fatty acid to produce alkyl radical ;
- lower valence state iron (Fe^{2+}) which form metal-oxygen transition complexes producing activated-oxygen species, mainly in non polar solvents. So this mechanism is probably not significant in muscle food ;
- metal autoxidation which produces reactive oxygen species through Haber-Weiss reaction coupled with the Fenton reaction:

$$Fe^{2+} + O_2 \rightarrow Fe^{3+} + O_2^{\bullet -}$$
$$O_2^{\bullet -} + H^+ \rightarrow HO_2^{\bullet -}$$
$$O_2^{\bullet -} / HO_2^{\bullet -} \rightarrow H_2O_2 + O_2$$

Haber-Weiss reactions

$$Fe^{2+} + H_2O_2 \rightarrow OH^{\bullet} + OH^- + Fe^{3+}$$

(Fenton reaction)

The Fenton type reaction is the main reaction involved in hydroxyl radical formation in biological system (Gutteridge, 1984). Both heme and non-heme iron are involved in Fenton type reaction. The $OH^{\bullet}$ is extremely reactive radical which have the ability to abstract hydrogen to unsaturated fatty acids.

The second type of reactions involves an indirect initiation by hypervalent iron complexes. The formation of these iron forms from non-heme iron is questionable because hypervalent complexes requires macromolecular structure and decay of hypervalent states to Fe^{3+} is instantaneous in biological systems. Hypervalent iron complexes have long been recognised as the active forms of heme protein and porphirin compounds. Ferryl iron is formed by numerous enzymes (peroxidases, cytochrome P-450, catalase, and other heme-proteins (myoglobin and hemoglobin). All these heme protein have been shown to directly catalyse lipid oxidation.

The third type of reactions includes the mechanism of indirect initiation-propagation of lipid oxidation. Both heme and non-heme iron in both ferrous and ferric states can catalyse the decomposition of performed hydroperoxides into peroxyl radicals (LO°, LOO°) which in turn can abstract a hydrogen radical to unsaturated fatty acids:

$$LOOH + Fe^{3+} \rightarrow LOO^{\circ} + H^+ + Fe^{2+}$$

or

$$LOOH + Fe^{2+} \; LO^{\circ} + OH^- + Fe^{3+}$$

Notes that the second reaction involving ferrous state more likely occurs in meat because the pH is acid in meat after slaughter. These decomposition of hydroperoxides increase the rate of lipid oxidation propagation because these radicals abstract hydrogen at a faster rate than initial alkyl radical (L°).

The difficulties to determine what is the main reactions involved in lipid oxidation in meat is related to the complexity of the biological systems (Schaich, 1992). In most of the studies on cells, membranes and tissues, numerous conditions remain not precisely controlled. One critical aspect is that biological systems are always inhomogenous system including at least a hydrophilic aqueous phase and a hydrophobic lipid phase. Initiation of lipid oxidation necessarily occurs in the interior of the membrane where the unsaturated fatty acid are located. So, reactions occurring in aqueous phase where most of the initiators of lipid oxidation are located can initiate lipid oxidation in membranes or lipid droplets of muscle fibres only if the reactive molecules diffuse to the surface of the droplets or the bilayers or into the bilayers. Iron binds to surface sites on membrane protein and to phosphoric acid moieties of phospholipids which can promote lipid oxidation. Very little is known on the reactions which occur in hydrophobic bilayers of membranes or lipid droplets catalysed by solubilised iron. Some evidences have been demonstrated that reactions such as Fenton and other iron-reactions in aprotic medium such as the inner layer of membranes and the core of triacylglycerol droplets does not proceed as they would in water or protic solvents (Schaich, 1992).

Peroxide decomposition and volatile formation : Numerous studies have been devoted to the description of hydroperoxide decomposition which involves a very complicated set of reaction pathways (Frankel, 1984). These reactions have been studied extensively and the attention have been focused on the volatile products because of their impact on flavour. The fragmentation of monohydroperoxides involves carbon-carbon cleavage of alkoxy radical on either side of the alkoxy radical to form a large variety

of volatiles including alkanes, adehydes, alcohols, esters and carboxylic acids (Frankel, 1984). If this mechanism explains the formation a large part of the volatiles found in food system, the origin of several volatiles such as furans, ketones, lactones and aromatic compounds remain uncertain (Frankel, 1984). The nature and the relative proportion of the compounds in the volatile fraction extracted from foods depend on numerous factors among which the fatty acid structure is the primary one because it affects the number and the proportion of hydroperoxide isomers. However the conditions in which peroxides are decomposed strongly affect the composition of volatile fractions. This includes the mechanisms of oxidation (autoxidation, thermo-oxidation, photo-oxidation, ...) and the medium conditions (temperature, pH, presence of iron, ...) (Frankel, 1985 ; Grosch, 1987). Among the numerous volatiles form from unsaturated fatty acid oxidation, the most important aroma compounds are aldehydes and several unsaturated ketones and furan derivatives (Grosch, 1987). They include C3-C10 aldehydes, C5 and C8 unsaturated ketones and pentyl or pentenyl furans. These compounds have a large variety of aroma properties and their odours have been described as oily, tallowy, deep-fried, fresh grass, metals, cucumbers, mushroom, fruity. Notes that volatiles arising from n-3 polyunsaturated fatty acids tend to have low odour threshold values. So, these fatty acids highly sensitive to oxidation could have a larger impact on flavour than n-6 fatty acids, even if they are always present is lower proportions in phospholipids and triacylglycerols of muscles.

LIPID OXIDATION AND MAILLARD REACTION

During many years, lot of studies were focused on the role of phospholipids in oxidation and these molecules were mainly considered as precursors of off-flavour through lipid oxidation. In contrast, Maillard reaction were recognised as the most important route to formation of many of the volatile compounds involved in positive flavour of cooked meat and the contribution of lipids was negligible (MacLeod & Seyyedain-Ardebill, 1981 ; Hornstein & Crowe, 1960). So the Maillard reaction between amino acids and reducing sugars form various heterocyclic compounds which are recognised to largely contribute to the overall aroma of cooked meat. They included O-, N- and S- heterocyclics such as furans, furanones, pyrazines, oxazoles, thiazolins, thiophenes and cyclic polysulfides (Bailey, 1982). Heterocyclics containing sulfur have been reported as key aroma compounds in cooked meat and H_2S is an important reactant in the formations of these heterocyclic compounds. H2S primarily comes from the Stecker degradation of sulfur containing amino-acids (cysteine, cystine, methionine). Most of these compounds are produced at low concentration but they have very low odour thresholds (MacLeod, G. & M. Seyyedain-Ardebilli, 1981). More recently, Mottram & Edwards (1983) have postulated that phospholipids are required to get cooked meat aroma. Since many studies have been undertaken to understand the mechanisms involving phospholipids in meat aroma compound formation. The course of both lipid oxidation and Maillard reaction is modified by the reactants, intermediates and products of the other reaction (Whitfield, 1992). Because the Maillard reaction and phospholipid oxidation are very complex processes, most of the studies dealing with the interactions between these two types of reactions have been conducted on model system. Mottran and co-workers have developped a meat like model system made of amino acid (mainly cysteine or methionine) and ribose in a phosphate buffer in which they added various phospholipid moieties or phospholipids

Whitfield, 1992 ; Farmer, 1994). From these studies, it was concluded that :

In the model system containing only cysteine and ribose, the main volatiles formed were furans and sulfur heterocyclic compounds. The overall aroma of the system was unpleasant with strong sulfurous and burnt odours.

When phospholipids, unsaturated fatty acids and/or polar head of phospholipids were added to the model, a large amount of oxidised products of unsaturated fatty acids appeared in the model system and the amounts and the proportions of sulfur heterocyclic compounds have been markedly reduced whereas only small changes have been observed in the proportions of furans. The most likely mechanism of the reduction of sulfur containing heterocyclic volatiles can be reactions between aldehydes from fatty acid oxidation and H_2S reducing the availability this key compound for the formation of sulfur heterocyclics. An other possible mechanism involves the reactions between furfural coming from reducing sugar and amino group of amino acid or polar head of phospholipids such as ethanolamine. The occurrence of the latter reaction was established by the addition of ethanol amine in the model which induced a decrease in furfural amount. Similarly, aldehydes from lipid oxidation can react with NH_3 to form non-volatile Schiff-bases reducing the availabily of NH3 form the synthesis of pyrazines and alkylpyrazynes (Zhang et al., 1994).

The oxidation compounds of unsaturated fatty acids are 1-octen-3-ol, hexanal, pentanol but the relative proportions of these compounds were different compared to those observed when unsaturated fatty acid was heated alone. This result support the hypothesis of an interference of Maillard reaction products in fatty acid oxidation.

In model system, few specific components seems to arise from Maillard reaction/lipid oxidation interactions. This results in

model system corroborates the results obtained on meat products. Of more than 1000 coupounds identified in volatile extracts of various cooked meat, only a maximum of 32 compounds could be derived from Maillard reaction/lipid oxidation interactions (23 in beef, 5 in mutton and none in pork) (MacLeod & Seyyedain-Ardebill, 1981). They are compounds with an alkyl substituents with chain length equal or greater than 4 carbons.

The interference of lipids in Maillard reaction can be summarised as proposed in figure 2 (Meynier & Gandemer, 1994). Lipids interact in Maillard reaction both by the amino group of polar head of phospholipids and some of the oxidative breakdown products of fatty acids such as aldehydes. So lipids contribute to meat aroma improvement both by reducing the amount of the sulfur containing compounds and by providing volatiles such as carbonyls or alcohols. It seems that the benefit effect of phospholipids on meat aroma is primarily related to the quenching of the formation of Maillard reaction products, mainly sulfur-containing volatiles because the interferences of lipids in Maillard reaction don't generate specific volatiles in a significant amount. Notes that the quenching is more pronounced when the meat contains a high proportion of polyunsaturated fatty acids such as chicken (MacLeod & Seyyedain-Ardebilli, 1981).

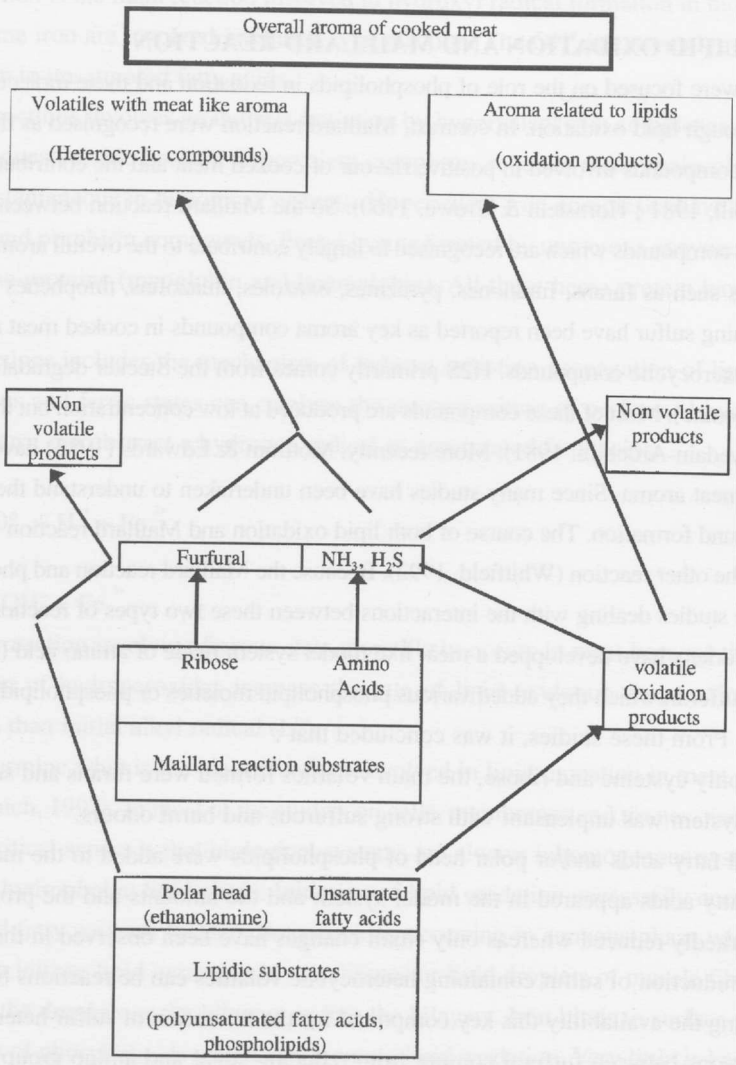

Figure 2. Possible mechanims involving lipids in Maillard reaction

LIPID OXIDATION AND MEAT AROMA

As previously discussed in the present paper, phospholipids are involved in both positive and negative aroma of meat because they oxidise to produces volatiles and they interfere in Maillard reaction. Consequently, the aroma of meat is a subtle equilibrium between lipid oxidation and Maillard reaction (Moody, 1983). The studies on the development of « Warmed-Over-

Flavour» (WOF) in pre-cooked meat gives a good illustration of the delicate equilibrium between lipid oxidation and Maillard reaction products in the aroma of meat during storage. The flavour of cooked meat progressively altered during refrigerated storage of pre-cooked meat. The typical aroma of cooked meat progressively turned to unpleasant aroma named WOF. The degradation of the aroma of pre-cooked meat is attributed to phospholipid oxidation (Pearson et al., 1977). Our results on the changes in volatiles extracted from pre-cooked turkey meat during a 4 week storage at 4°C indicate that phospholipid oxidation is not the only factor involved in flavour degradation. In fact, the quantities of volatile oxidation products are similar at the beginning and at the end of the storage but a dramatic drop was observed in the amount of volatiles coming from Maillard reaction. Consequently, it can be postulated that the decrease in volatiles from Maillard reaction resulted more in a disappearance of the typical aroma of cooked meat than in the appearance of oxidation aroma. This hypothesis is conflicting with that of Farmer (1994) who suggests that the WOF of cooked meat may be attributed to the masking of desirable flavour notes by the increased content of undesirable flavour notes due to lipid oxidation rather than to the degradation of desirable flavour compounds formed through Maillard reaction.

Many factors affect the sensitivity of lipids to oxidation. Regarding phospholipids which are the primary substrates of oxidation in muscles, the control of their sensitivity to oxidation is mainly related to their fatty acid composition and to the amount of natural antioxidant included in the membrane. During the last decades, numerous studies have been devoted to the effect of α - tocopherol on oxidation of membrane phospholipids. Addition of tocopherols in feed improves vitamin E status of muscles and greatly improve oxidative stability of meat. Jensen et al. (1998) have reviewed recent studies in this area. A complementary approach to control lipid membrane oxidation is to change fatty acid composition of phospholipids through dietary fat. In pig and poultry, fatty acid composition of phospholipids depends on dietary fat and feeding highly unsaturated fat increase the unsaturation of phospholipids and their sensitivity to oxidation (Asghar et al., 1988). In turkey meat which is very sensitive to oxidation because of the high unsaturation of their lipids, we have try to control phospholipid oxidation by feeding animals with various fat. Male turkeys with a basal diet containing 6% fat of various origins (tallow, soya or rapeseed oils). As expected, dietary fats affect largely fatty acid composition of muscle phospholipids. Phospholipids of muscles of turkeys fed with "Soya" diet have the highest proportion of n-6 PUFA, these of animals fed with "Rapeseed" diet have the highest proportion of n-3 PUFA whereas these of turkeys fed with "tallow" diet have the lower proportions of PUFA of both n-3 and n-6 series. On liposomes prepared with phospholipids extracted from the breast muscles of turkeys of each group (Kanski et al., 1997), we show that phospholipids from "soya" and "rapeseed" turkey muscles are more sensitive to oxidation than those from "tallow" turkey muscles. The composition of volatiles extracted from muscles of animals of each group shows that it strongly depends on the fatty acid composition of phopholipids. These results are explained by the fact that the structure and the proportion of volatiles arising from fatty acid oxidation is strongly dependent upon the number and the position of the double bounds on the fatty acids (Meynier et al., 1998). It is possible to distinguish volatile fractions of turkey muscles according to the type of dietary fat they fed. This experiment demonstrates phospholipid oxidation and composition of volatile of muscles shoud be controlled by dietary fat. In animal species such as turkey, which is very sensitive to oxidation, a substitution of a part of oil seeds by tallow could improve the oxidative stability of meat. The impact of this change on meat flavour remains to assess.

CONCLUSIONS

It is now demonstrated that phospholipids are the main substrates of both lipolysis and oxidation in muscle food. They can exert a negative effect on flavour because their propensity to both lipolysis and oxidation but phospholipids can also have a benefit impact on flavour through their interference in Maillard reaction. If pathways of phospholipid degradation have been described, too little is know about the regulation of lipolysis and oxidation of phospholipids in muscle to ensure a control of flavour development of meat products. Cooked meat aroma is a subtle balance between the desirable aroma compounds formed through Maillard reaction and the poor odour molecules coming from the oxidative breakdown of PUFA. Further investigations are required to understand the regulation of lipolysis and its relation with oxidation and to describe more precisely the factors involved in oxidation control in muscular cell. The challenge is to get enough oxidation products to obtain desirable flavour of cooked meat but not rancidity.

To my opinion, future researches in meat flavour should be focused on several topics. The first one concerns the changes in the first days of meat ageing. Attention should be paid to the activities of enzymes, mainly lipases and phospholipases and the ones involved

in the oxydo-reduction systems in muscles. Further studies are required to establish the relationship between lipolysis and oxidation and the relative contributions of both pro and anti oxidant substances in oxidation processes. The second challenge is to take into account that muscle is an inhomogeneous food with several compartments in which the enzymic and chemical reactions do not occur at the same rates. This particularly important regarding the processes of lipolysis and oxidation because, i.e. pro-oxidant agents are generally in aqueous phase and fatty acids in hydrophobic environment or lipolysis and oxidation of intramuscular lipids do not occur at the same rate in fat cells located along the fibres and in the fibres. The third one deals with the effect of the structure and the composition of the meat after processing and cooking on the perception of the aroma. This problem includes both the questions of the retention of aroma compounds by the meat during cooking and the release of these aroma compounds in the mouth of the consumer.

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