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Review article

Effect of nutritional factors on biochemical, structural and metabolic characteristics of muscles in ruminants, consequences on dietetic value and sensorial qualities of meat

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Abstract — Ruminant meat is an important source of nutrients and is also of high sensory value. However, the importance and nature of these characteristics depend on ruminant nutrition. The first part of this review is focused on biochemical and dietetic value of this meat. It offers a panel of quantitative and qualitative contributions, especially through its fatty acids characteristics. Since saturated and trans-monounsaturated fatty acids are considered as harmful to human health, their amount in muscles can be reduced by increasing the proportions of dietary polyunsaturated fatty acids (PUFA) absorbed by the animals. On the contrary, some fatty acids (n-6 and n-3 PUFA, conjugated linoleic acid) specifically incorporated in muscle tissues would play a favourable role in the prevention or reduction of major diseases in human (cancers, atherosclerosis, obesity) and therefore be recommended. The second part of this review treats different aspects of the sensorial qualities of meat. Skeletal muscle structure and its biochemical components influence muscle transformation to meat and sensorial qualities including tenderness, colour, flavour and juiciness. This paper shows how nutrition can influence, in ruminants, metabolic activity as well as muscle structure and composition, and thereby affect meat quality.

muscle / meat / ruminant / nutrition / dietetic value / sensorial quality

Résumé — **Nutrition des ruminants et qualités de leurs viandes.** Les viandes des ruminants sont une source importante de nutriments pour l'alimentation humaine et leurs qualités sensorielles sont très appréciées. L'importance et la nature de ces particularités dépendent toutefois de la nutrition des ruminants. La première partie de cette revue bibliographique est consacrée à la composition

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chimique et à la valeur diététique de ces viandes. Celles-ci offrent un éventail d'apports quantitatifs et qualitatifs, notamment sous forme d'acides gras. Si les acides gras saturés et monoinsaturés trans sont à proscrire pour le consommateur, il est toutefois possible de réduire leur teneur dans la viande en augmentant la proportion des acides gras polyinsaturés (AGPI) absorbés par les ruminants. En revanche d'autres acides gras (AGPI n-6 et n-3, acide linoléique conjugué) incorporés spécifiquement dans les muscles pourraient jouer un rôle très favorable sur la santé humaine comme agents préventifs ou curatifs de pathologies majeures chez l'homme (cancers, athérosclérose, obésité) et être ainsi recommandés. La seconde partie de cette revue est centrée sur l'analyse des qualités organoleptiques des viandes. La structure du muscle squelettique et ses composants biochimiques influent sur la transformation du muscle en viande et conditionnent ainsi les qualités sensorielles de cette dernière : tendreté, couleur, flaveur et jutosité. L'article montre comment la nutrition du ruminant, influençant l'activité métabolique, la structure et la composition des muscles, va donc affecter ces qualités sensorielles.

muscle / viande / nutrition des ruminants / qualité sensorielle / qualité diététique

1. INTRODUCTION

With 31 kg carcass equivalent (CE) per person and per year in 1998 [103], the consumption of meat from ruminants (5 kg (CE) for sheep and goat meat and 26 kg (CE) for beef) represents less than one third of total meat consumption in France. Beef meat consumption was the highest at the beginning of the 1980s (33 kg per person and per year) but, unlike sheep meat consumption, has been decreasing by 1.5–2% per year. This decrease has also been observed in Europe and the USA. It is explained, at least in part, by the severe competition with white meats, the price of which is relatively low. However, it is also explained by consumers behaviour. They are concerned by health factors, due largely to statements from the medical profession that beef meat may contain too much saturated fat (SFA) and transmonounsaturated (MUFA) fatty acids, which can be major risks for the development of coronary heart disease.

The decrease in meat consumption is also due to media events (boycotts of veal meat, illicit trading and use of hormones, "mad cow" crisis…) and to the recent economic transformations (industrialisation, intensification of agriculture and urbanisation) which have all increased the distance between producers and consumers and have created a new type of consumer less informed of product definition, quality, and origin. These difficulties increase the dissatisfaction of the consumer, which is especially true in the case of red bovine and ovine meat.

Quality is therefore now an important social and economic challenge which is amplified by the saturation of food markets due to the high efficiency of modern agriculture. This is the reason why food quality was put at the top of the research agenda many years ago all over the world, and especially in France by INRA. The ultimate objectives of this research is to control the biological characteristics of muscles, intramuscular fat and carcass adipose tissues, which determine dietetic and organoleptic meat quality traits. These tissue characteristics depend on many breeding factors including nutrition, the physiological state and genetic type of the animal, as well as on rearing systems (grass-fed or grain-fed animals, grazing system or feed lot).

The aim of this review is to analyse the various nutritional possibilities that control muscle characteristics in ruminants. Success will require the production of consistent and predictable high quality meat to ensure consumer satisfaction. This means high quality organoleptic traits and also the presence within meat of healthy and easily assimilated nutrients for both young and old

people. The first part of this review will focus on the biochemical composition, nutritional value and sanitary traits of ruminant meats. The second part will focus on the structural and metabolic characteristics of muscles, which determine meat organoleptic quality in ruminants. In these two parts we will describe the possibilities of controlling the organoleptic and dietetic quality of meat by nutritional means.

2. BIOCHEMICAL COMPOSITION AND DIETETIC VALUE OF RUMINANT MEATS

2.1. Biochemical composition

Meat represents, above all, an important source of proteins (17 to 22% fresh tissue), rich in essential amino acids (55.2 g for 16 g N) [27]. These proteins, slightly deficient in sulfur amino acids, are rich in lysine (9.1 g for 16 g N).

Meat from ruminant animals, especially from bovines, is also an important source of heminic iron (about 2 to 5 mg·100 mg^{-1} fresh tissue according to the type of muscle, which is respectively 3 to 4 times higher than that in meat from pork and chicken) (Tab. I), which is 5 to 6 times more absorbed than the non-heminic iron from plants. Zinc is also abundant in bovine meat (3 to 11 mg·100 g^{-1} according to cuts) [14]. Finally, meat from ruminant animals is an important source of vitamins of the B group: B1, B2, B6, B12 and niacin [29] especially vitamins B6 (0.3 to 0.4 mg·100 mg^{-1} in the bovine; 0.15 to 0.25 mg·100 g^{-1} in the lamb) and B12 (1.5 to 2.5 mg·100 g^{-1}) virtually absent in plants but synthesised by microorganisms of the digestive tract of ruminants (Tab. II).

Although the chemical composition of muscles is relatively constant (about 75% of water, 19 to 25% of proteins, and 1–2% of minerals and carbohydrates), the chemical composition of meats is highly variable, especially for lipids. Indeed, their lipid content (in comparison with that in cooked products) depends on the choice of the butchery pieces which have relative proportions of intermuscular and subcutaneous adipose tissues incorporated in the cuts [14]. For example, the proportion of lipids varies from 2.5% (veal escalope) to 17.3% (grilled lamb cutlet) with intermediary values of 3.6% (grilled rumpsteak or boiled shin with vegetables) and 11.8% (grilled steak cut from the ribs) (Tab. II). However, in order to express these values according to

Table I. Comparison of cooked meats composition from beef, pork and chicken (from Favier et al. [29]).

	Beef (faux filet roasted)	Porc (filet roasted)	Chicken (meat and skin roasted)
Energy (kJ·100 g^{-1})	700	667	678
Proteins (g·100 g^{-1})	28.1	28.8	56.4
Lipids (g·100 g^{-1})	6.0	4.8	6.2
Cholesterol (g·100 g^{-1})	0.06	0.07	0.09
Fatty acids saturated/unsaturated	0.86	0.61	0.43
Iron (mg·100 g^{-1})	3.0	1.5	1.3
Niacin (mg·100 g^{-1})	4.5	4.7	7.7
Vit. E (mg·100 g^{-1})	0.3	0.1	0.2
Vit. B6 (mg·100 g^{-1})	0.4	0.4	0.4
Vit. B12 (mg·100 g^{-1})	2.0	0.6	0.3
Folates (mg·100 g^{-1})	15.0	6.0	8.0

nutritional needs, it is important that the contribution of bovine meat to total intake of lipids by the consumer does not exceed 5% [19]. In addition, bovine meat is also characterised by a high ratio of proteins to lipids which can reach, according to the cooked cut, values between 12 and 2. These values are much higher than in other foods, still rich in proteins, such as eggs (1.20), cheese (cantal: 0.75) and some fatty fishes (mackerel: 0.80).

In general, the amount and the nature of lipids stored in muscle mainly depends on feed conditions, and on digestion, intestinal absorption, hepatic metabolism and lipid transport systems to muscle. In the weaned ruminant, a high proportion of dietary unsaturated fatty acids (FA) is hydrogenated in the rumen, leading to intramuscular FA that are far less unsaturated in bovines and ovines than those in pigs and poultry (Tab. I) [43]. Consequently, muscle FA in bovine and lamb are composed of 50% saturated FA (SFA) and 50% unsaturated FA, the most abundant FA being oleic acid [14]. If external adipose tissues of ruminants are effectively rich in SFA, the intramuscular adipose tissue contains a significant proportion of polyunsaturated FA (PUFA), especially in lean animals [19] (Tab. II). Indeed, phospholipids in muscle membranes (0.5 to 1% of muscle weight) are very rich in PUFA (45–55%), whatever the animal species. On the contrary, intramuscular triglycerides contain only 2–3% PUFA in bovine but 7–15% in the pig and 20–25% in the chicken, especially in fatty animals [34].

2.2. Meat lipids: dietetic aspects

Previous observations have reported values for the ratio of PUFA to saturated FA

Table II. Nutritional values (per 100 g of cooked meat) of various types of ruminant meats (from C.I.V. [14]).

	Beef			Lamb	
	I	II	III	IV	IV
Energy (kg)	485	625	849	727	1 042
Proteins (g)	21	23	24	23	23
Lipids (g)	3.6	6.4	11.8	8.9	17.3
Cholesterol (mg)	35	33	45	70	90
Fatty acids: composition (%)[a]					
Saturated	44	49	50	50	48
Monounsaturated	40	44	41	38	41
Polyunsaturated	9	3	5	10	10
Iron (mg)	2.9	1.9	2.6	2.0	5.3
Zinc (mg)	4.2	3.3	5.4	2.9	2.5
Vitamins					
B1 (mg)	0.10	0.04	0.09	0.13	0.10
PP (mg)	7.30	5.90	6.20	7.20	7.60
B5 (mg)	1.47	0.34	1.37	0.83	0.70
B6 (mg)	0.56	0.29	0.42	0.34	0.36
B12 (µg)	1.50	0.54	1.40	1.60	1.70
E (mg)	0.44	0.20	0.58	0.18	0.11

[a] Per 100 g of raw meat.
I: Grilled rumpsteak; II: roasted faux filet; III: grilled steak cut from the ribs; IV: roasted leg; V: grilled rib cut.

of lipids from bovine or lamb meats between 0.11 and 0.15, which are lower than the recommended values for man (0.45) [122].

PUFA of the n-3 family (C18:3n-3 and its derivates) and of the n-6 family (C18:2n-6 and its derivates) are synthesised only by plants. No metabolic conversion between n-3 PUFA and n-6 PUFA is possible. These fatty acids have to be provided by the diet. Linoleic acid (C18:2n-6) is essential for growth and reproduction. Linolenic acid (C18:3n-3) is essential for brain and retina functions. Moreover, n-3 PUFA exert a positive influence in the prevention of cardiovascular diseases [18]. A too high value of the ratio of n-6 PUFA to n-3 PUFA is associated to an increased risk of atherosclerosis or coronary diseases. Generally, the recommended average value for the ratio of n-6 PUFA to n-3 PUFA for human nutrition is 2 [85]. In this aspect, ruminant meat (bovine, ovine) is superior to pork, since its values for the ratio of n-6 PUFA to n-3 PUFA are comprised between 1 to 2 versus 7 for pork [123]. This is due to the fact that linolenic acid, (C18:3n-3) abundant in fresh forrages (> 50% total fatty acids) [4], is stored in significant amounts in ruminant tissues [24]. Although an important proportion of linolenic acid is converted to its saturated counterpart (C18:0) by ruminant biohydrogenation, small but significant amounts escape ruminant metabolism [4, 6] and are subsequently absorbed by the small intestine [122]. Therefore, it is possible to induce a modification of the fatty acid composition of tissue lipids by feeding treatment, as we will describe in the next chapter.

Rumen bacteria can produce specifically conjugated linoleic acid (CLA). These fatty acids are generated by trans-isomerisation reactions catalysed by bacterial enzymes during the biohydrogenation processes of plant linoleic (C18:2n-6) and linolenic (C18:3n-3) acids (Fig. 1). Although these fatty acids are minor in lipids (Tab. III) of milk products (5.5 $mg \cdot g^{-1}$ total lipids) and meat (2.9 to 4.3 $mg \cdot g^{-1}$ total lipids) from ruminants [16], they are subject to increasing interest owing to their important properties in the prevention or the therapeutic treatment of several cancers (breast, prostate, skin...). These properties have been demonstrated by using CLA mixtures in different rodents or in different normal or cancerous cell lines [50, 88]. In other respects, CLA have been shown to have protecting effects

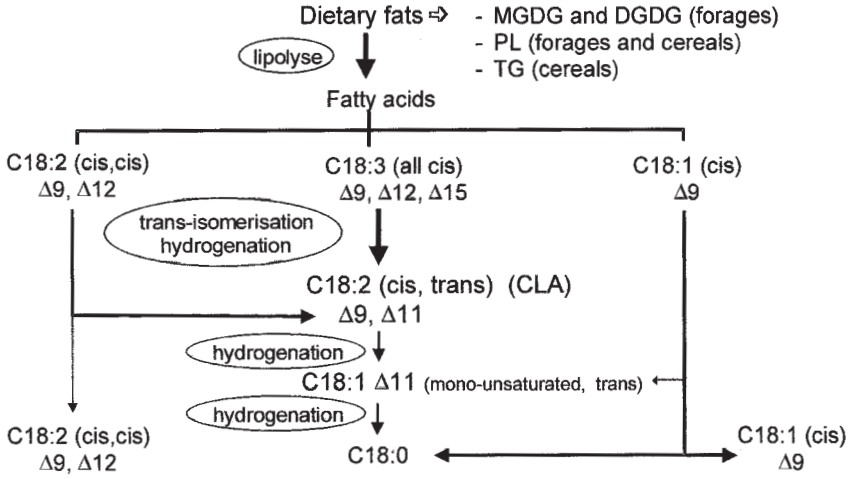

Figure 1. Lipolysis and biohydrogenation of dietary fatty acids by bacteria of the rumen. MGDG: monoglycerides; DGDG: diglycerides; PL: phospholipids; TG: triglycerides.

Table III. CLA content in animal products (meats, milk) and vegetable oils (from Chin et al. [16]).

Origin	CLA ($mg \cdot g^{-1}$ lipids)	cis 9, trans 11 (%)
Meat		
Beef	2.9–4.3	79
Mutton	5.6	92
Chicken	0.9	84
Porc	0.6	82
Salmon	0.3	ND
Milk		
Dairy cow	5.5	92
Vegetable oils		
Sunflower	0.4	38
Olive	0.2	47

against cardiovascular diseases (hypolipemic effect in rabbits) and to reduce adiposity in rodents as well as in pigs [88]. A very recent study confirmed the properties of CLA to limiting the extent of body fat stores in man [113]. From a quantitative point of view, the principal types of CLA produced by rumen microorganisms are Δ9 cis-Δ11 trans as well as Δ10 trans-Δ12 cis [40] and Δ7 trans-Δ9 cis [129] and to a lesser extent, their trans-trans isomers Δ9-Δ11 and Δ10–Δ12 [40]. The minor forms are represented by cis-trans isomers in positions 7–9, 8–10, 11–13, and 12–14 and by trans-trans isomers in positions 8-10 and 11–13 [40]. The detailed analysis of fatty acids in animal tissues additionally shows the presence of higher counterparts of CLA, but their therapeutic properties are still unknown.

Bacterial biohydrogenation of dietary PUFA in the rumen also leads to the production of trans isomers of oleic acid (C18:1n-9 cis). These fatty acids are not favourable for human health. Indeed, these fatty acids are considered to be aggravating factors of cardiovascular risks for the same reasons as their homologous fatty acids generated by the food industry (for production of margarines) by catalytic biohydrogenation of plant PUFA. Trans-isomers of oleic acid represent about 15% of the total isomers (cis plus trans) of oleic acid, which corresponds to 6% of total fatty acids in muscle lipids [8]. Daily uptake of trans-isomers of oleic acid has been estimated at 0.8–1.8 g per person in countries of the European Union [121].

Trans isomers of oleic acid are mainly represented in muscles of steers by trans vaccenic acid (C18:1-Δ11 trans; 66% of total trans isomers of oleic acid) and to a lesser extent by trans isomers Δ13 (10%), trans Δ9 (8%), trans Δ12 (7%) trans Δ15 (4%) and trans Δ16 (5%) [8].

Finally, although meat contains significant amounts of cholesterol (50–100 $mg \cdot 100\ g^{-1}$), it is less rich in cholesterol than offals and eggs (Tab. I). Moreover, it is important to state that in man more than half of the amount of cholesterol is synthesised in the liver and in the small intestine [27] and, therefore, food products provide less than half of the amount of cholesterol.

3. EFFECTS OF RUMINANT FEEDING ON THE NUTRITIONAL VALUE OF MEATS

Ruminant meats, especially bovine meats, are criticised for the nutritional value of their lipids and saturated fatty acids which are considered to be too abundant. Therefore, we are devoting this chapter to the available means which limit the extent of these negative nutrients.

For example, fresh grass given to Holstein-Friesian steers out to pasture gives a higher proportion of n-3 PUFA in adipose tissues (×2.4 for C18:3n-3; ×1.3 for C18:4n-3; ×3.5 for C20:5n-3; ×1.8 for C22:5n-3) than a hay- and cereal- based diet [82]. This preferential incorporation of linolenic acid (C18:3n-3) and its counterparts (C20:4n-3; C20:5n-3; C22:5n-3 and C22:6n-3, also important in human nutrition) has also been reported

by [23] in steers given a grass-based diet, compared to a cereal-based diet. This n-3 PUFA incorporation is parallel to that of C18:0 and to the detriment of C18:1 and, to a lesser extent, to that of C18:2n-6 [102]. Conversely, cereal-based diets lead to higher amounts of n-6 PUFA such as C18:2n-6 in fat stores of steers [23]. Neutral lipids (mainly triglycerides) of muscles mainly incorporate PUFA as C18:2n-6 and C18:3n-3. Polar lipids (phospholipids) are less selective and incorporate not only C18:2n-6 and C18:3n-3, but also their counterparts (C20:3; C20:4; C22:5) [56].

Addition of fish oil to the diet of steers composed of wheat straw (30%), corn seeds (30%), and lupin seeds (20%) leads to a preferential incorporation of long n-3 PUFA (C20:5 and C22:6) not sensible to rumen biohydrogenation. The use of the same fish oil previously protected against rumen degradation by coating with formaldehyde–treated casein favours the high incorporation of C20:5n-3 (15 vs. 2% of total FA) and C22:6n-3 (4 vs. 2%) into muscle phospholipids. However, it does not modify the proportion of these fatty acids in triglycerides of intramuscular or external adipose tissues [2]. Similar results have been obtained with fish meal enriched diets. These results showed that preferential incorporation of C20:5n-3 and of C22:6n-3 in lipids of *Longissimus thoracis* was to the detriment of n-6 PUFA, especially of C20:4n-6 [65].

In the same way, oleaginous seeds, rich in PUFA, added to the diet of steers, modify differently the FA composition of lipids in muscles and in adipose tissues. Thus, the addition of rapeseed (7, 14 or 24% of diet DM) to a cereal- and wheat straw-based diet reduces the level of C16:0 to the benefit of C18 FA [31]. However, intramuscular lipids contain more C18:1 and C18:2n-6 than lipids of adipose tissues. Addition of this kind of seed highly increases the concentration of vitamine E in body fat stores (from 4.5 to 14.9 $\mu g \cdot g^{-1}$ tissue). This antioxidant contributes to the stability of FA against peroxidation (doubling of lag time in the induction of peroxidation) [31].

The addition of rumen protected fats induces a high modification of the FA composition of lipids in growing bovines. Thus, cotton or canola seeds, rich in C18:2n-6, protected by tanning proteins with formaldehyde, significantly increase the level of C18:2n-6 of neutral lipids in adipose tissues ($\times 6$ with cotton seed; $\times 2.5$ with canola seed), to the detriment of C18:1 (cotton seed) or C16:0 (canola seed). In the same way, C18:2n-6 is incorporated preferentially in muscle lipids, especially phospholipids of membranes rich in choline groups [104].

CLA production by ruminants is mainly regulated by the type of rations, more or less rich in n-3 and n-6 PUFA [24]. Thus, grass-based diets (rich in C18:3n-3), increase CLA production compared to hay-based diets. This production of CLA is higher with young grass in the spring than with old grass in the autumn [57]. In other respects, CLA production was markedly increased in animals fed rations containing oleaginous seeds (rich in C18:2n-6 or C18:3n-3) or their equivalent in vegetable oils not protected against rumen fermentation [57, 58]. Addition of fish oil in diets highly increases ($\times 6$) CLA production (mainly as C18:2 $\Delta 9$ cis-$\Delta 11$ trans) [15]. Many aspects of CLA production need to be specified more. They mainly concern the relationships existing between the source and concentration of PUFA, the chemical nature of neosynthesised CLA produced in the rumen, the liver, the adipose tissues or in the mammary gland and finally their partition between different tissues.

Increasing levels of food intake favours body fat deposition as well as intramuscular lipids [36]. However, when food intake is increased after a period of food restriction, this leads to a compensating growth. This can significantly reduce intramuscular lipids with a concomitant increase in external adipose tissues as noted in Belgian Blue bulls,

a late maturing breed of cattle [47]. This leaner meat corresponds better to food recommendations for man. However, a reduction in intramuscular lipids and an increase in lipid deposition in other adipose tissues depend on the physiological status of the animal, such as the degree of intramuscular fat stores compared to other fat stores at the time when the refeeding was started [35].

It is noteworthy that the genotype of cattle strongly influences the amount and fatty acid composition of stored lipids. Thus, compared to lipids of Brahman steers, those of Hereford steers have a higher proportion of saturated FA (38.8 vs. 34.5% total FA) but lower proportions of monounsaturated (53.4 vs. 59.5%) and polyunsaturated (1.8 vs. 2.4%) FA with both groups of steers being given the same diets. Hereford steers have 5% more FA in fat stores than Brahman steers [48]. The same differences have been reported for intramuscular lipids and cholesterol [110]. Differences in the amount and composition of intramuscular lipids have been reported between Galloway, Holstein, and Belgian Blue breeds [83] and between Holstein and Black Japanese breeds [130]. Therefore, the effect of diet or of the level of energetic food supplies on tissue lipid deposition can be amplified by the animal breed.

4. STRUCTURAL AND METABOLIC CHARACTERISTICS OF MUSCLE TISSUE AND SENSORY PROPERTIES OF MEAT

4.1. Characteristics of muscle

Striated muscle is made up of fibre bundles surrounded by a connective tissue network (Fig. 2). Collagen, the main protein of this tissue, accounts for 2 to 15% of the dry matter content, depending on the muscle. Other cells, quantitatively less important, such as intramuscular adipocytes, are localised in the connective network.

The connective network has three levels of organisation: epimysium, perimysium and endomysium from the outer part to the inner part of the muscle. The epimysium is the connective external envelope of the muscle; the perimysium surrounds each myofibre bundle and connects the bundles and the endomysium is a thin layer of the extracellular matrix which surrounds the sarcolemma of each myofibre. Collagen is, in fact, a family of proteins of at least 21 isoforms. Seven of them have been identified in the skeletal muscle [60], with types I, III and IV being the most abundant [68]. The respective proportions of these three collagen types depend on muscle, animal age, genetic background and also location in the

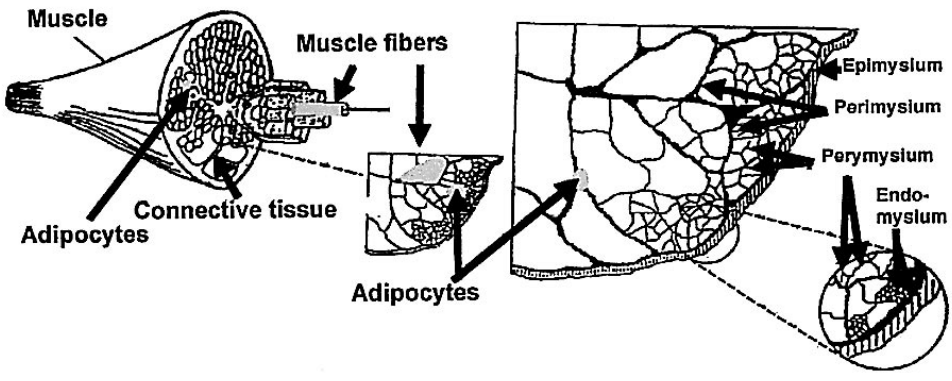

Figure 2. Muscle structure.

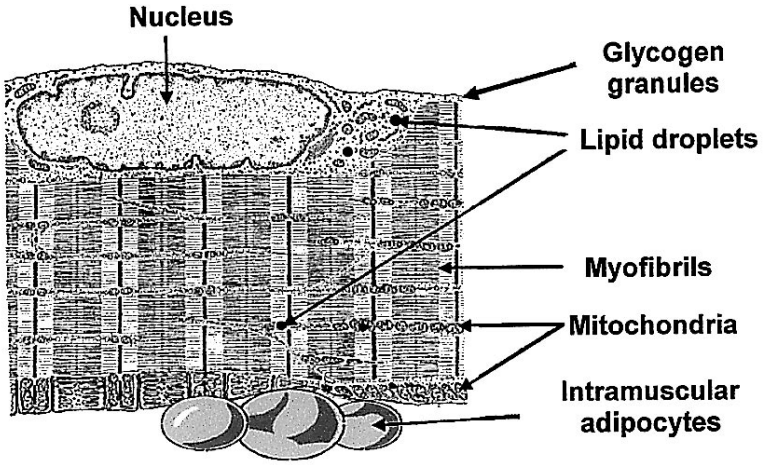

Figure 3. Schematic presentation of skeletal muscle fibre.

muscle. Indeed, the perimysium contains types I and III mainly, whereas the endomysium contains types I, III and IV [60]. The common characteristics of all collagens is the presence of one or several helicoidal domains due to the α-helix organisation of these peptide chains. This helicoidal structure is stabilised by intra-and inter-molecular bonds. The main intra-molecular bonds are disulfide and hydrogen bonds whereas covalent crosslinks such as pyridinoline and deoxypyridinoline are involved in inter-molecular bonds.

Muscle fibres are long, plurinucleus cells containing the contractile proteins, the enzymes for the storage and utilisation of energy (carbohydrates and lipids) and the proteolytic enzymes involved in the in vivo protein metabolism but also in the degradation of proteins during meat ageing (Fig. 3). The contractile properties of myofibres are dependent on the type of myosin heavy chains, main contractile protein, whose at least 10 isoforms have been identified [37]. The metabolic activity of myofibres is due to the respective activities of the enzymes of the different pathways of utilisation of the energy nutrients (glucose, fatty acids, lactate). Two main metabolic pathways have been distinguished: the anaerobic glycolytic and the aerobic oxidative ones. The first pathway leads either to the formation of lactate from glycogen and glucose degradation or to the storage of glucose by synthesis of glycogen. In the second pathway, glucose and lipids are oxidised in mitochondria. In addition triglycerides are stored partly in myofibres but mainly in adipocytes [46]. Three main myofibre types, which have an influence on meat quality, have been identified according to their contractile and metabolic activities: slow-twitch red oxidative (type I or SO), fast-twitch red oxidative and glycolytic (type IIA or FOG) and fast-twitch white glycolytic (type IIB or FG).

4.2. Muscle to meat conversion

After animal death, muscle is submitted to complex enzymatic (endogenous proteases) and physico-chemical (pH decrease, osmotic pressure increase) processes (Fig. 4) whose mechanisms are not completely elucidated [87].

When the blood circulation stops after animal slaughtering, muscle metabolism is

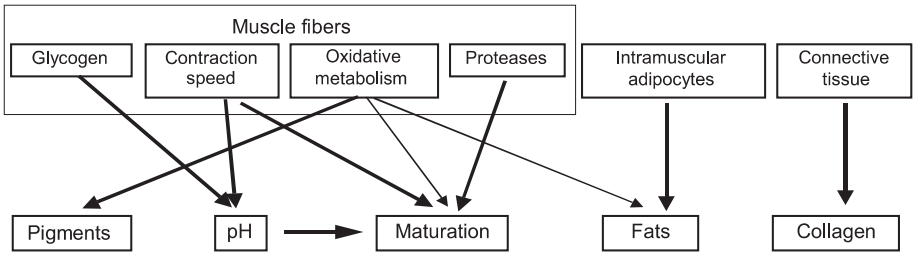

Figure 4. Relationships between muscle structure, metabolism and biochemical characteristics (adapted from Touraille [111] and Hocquette et al. [45]).

dramatically modified. In anoxia conditions, acidification of muscle is provoked by the conversion of glycogen into lactic acid. Then, pH decreases from 7.0–7.2 to 5.4–5.8. This decrease favours meat storage due to the slowering of microflora development. However, it induces a lower water holding capacity as pH approaches the muscle protein isoelectric point [111]. The post-mortem pH fall rate depends on the contraction rate of the myofibres. As a consequence, it strongly varies from one muscle to the other. Meat quality is much dependent on the respective kinetics of muscle pH and temperature falls. A fast pH fall associated to slow chilling can induce pale, soft and exudative meat. This phenomenon is, however, seldomly observed in bovine meat. In contrast, a slow falling pH associated to fast chilling can provoke cold-shortening inducing toughening of meat after cooking. An ultimate pH value, depending on the amount of available energy stores (glycogen content), influences meat quality. Glycogen content depends on the nutritional status of the animal in particular on the former exchanges of energy substrates between the liver, adipose tissue and muscles when it leaves the farm to go to the abattoir [46]. It also depends on the level of physical exercise and stress conditions of the animal during the period of time between the farm and slaughter. In beef as in pork, ultimate pH is muscle dependent: slow-twitch red muscles, with lower glycogen contents, exhibit higher ultimate pH than fast-twitch white muscles [109]. Ultimate pH also depends on the buffering capacity of muscle which increases when glycolytic metabolism increases [78].

Moreover, from animal death and during storage, biochemical and structural changes occur in meat. Myofibrillar proteins are hydrolysed by endogenous proteases (calcium dependent neutral protease or calpains, lysozomal proteases or cathepsins and proteasome). Release of calcium ions in the cytosol, pH fall and increase in osmotic pressure influence the activity of the different proteolytic systems and the susceptibility of the substrates. The importance of proteolysis depends on the duration and temperature of meat storage [86]. Post-mortem proteolysis is also dependent on muscle type which influences the contents and activities of proteases as well as the susceptibility of myofibrillar proteins to hydrolysis. During storage of meat, other modifications occur: oxidation of intramuscular lipids and myoglobin, pigmentation of meat (Fig. 4).

4.3. Sensory properties of meat

Colour, flavour and texture (juiciness and tenderness) of meat are dependent not only on the structural and metabolic characteristics of muscle at slaughter but also on their modifications during rigor mortis and ageing.

4.3.1. Colour

It represents together with the amount of visible fat (marbling), shape and structure, the first characteristics the consumer takes into account to judge meat quality. Colour depends on the content and the chemical state of myoglobin, the principal pigment in meat. This protein is bound to the external membrane of the mitochondria and sarcoplasmic reticulum [52]. Muscle structure also influences meat colour as it more or less absorbs or reflects light and allows oxygen to penetrate [97]. Myoglobin, whose in vivo function is storage and transport of oxygen, has a higher concentration in oxydative red muscle.

According to the oxidation state of haeme iron and to the presence and nature of the compounds (mainly oxygen) bound to the myoglobin molecule, different myoglobin (Mb) forms can be found. Inside the muscle, due to the absence of oxygen, myoglobin is reduced (Fe^{2+}) and exhibits a purple colour characteristic of deoximyoglobin. In contrast, at the surface of meat, myoglobin in contact with air is oxygenated and exhibits a bright red colour. However, prolonged storage in the presence of air induces oxidation of the pigment (Fe^{3+}) and formation of brown metmyoglobin (MMb), unacceptable for the consumer.

4.3.2. Tenderness

It is the most important sensory property of bovine meat. It corresponds to the ease of mastication during meat consumption [111]. However, due to a large variability, it is the least controlled sensory attribute of meat. Tenderness depends both on connective tissue and myofibre properties.

Connective tissue is relatively stable post mortem and is not influenced by technological treatments such as electrical stimulation, chilling conditions and ageing. Not only its content but also its thermal stability contribute to meat toughness. The type and content of intermolecular crosslinks, the diameter of the collagen fibres and the isoforms of the collagen molecules influence the thermal stability of connective tissue.

After slaughter, the myofibrillar structure is dramatically modified depending on the treatment of the carcass and muscles and also on the physicochemical and enzymatic characteristics of myofibres. Immediately after slaughter, the metabolism of the cells continues in anaerobic conditions. To maintain homeostasis, the cell progressively consumes the creatine phosphate and glycogen stores. Cytosolic calcium is pumped by the sarcoplasmic reticulum, until the energy level becomes too low. Then calcium is released in the cytosol which favours muscle contraction. In addition, ATP content becomes too low to allow the dissociation of the actin-myosin bond induced by the contraction. A non-reversible actomyosin complex is then formed, inducing meat toughening; this is the so-called “rigor mortis” phase [59]. However, in parallel to pH decrease, osmotic pressure increases and reaches its maximum value after complete onset of rigor mortis [86]. This increase in osmotic pressure contributes to the alteration of myofibrillar integrity and to the dissociation of contractile proteins. Osmotic pressure varies according to muscles [119]. A higher osmolarity is observed in fast-twitch muscles. Immediately after slaughter, proteolysis of myofibrillar proteins and associated proteins occurs. Inter- (desmin and vinculin) and intra-(titin, nebulin, troponin T) myofibrillar proteins, maintaining the integrity of the structure, are degraded. Then, ruptures in the sarcomere structure occur and tenderisation of meat proceeds [51]. Although several proteolytic systems have been described in the literature (calpaines, proteasome, cathepsines), calpains (μ and m), Ca^{2+}-dependent enzymes seem to play a major role [54]. These enzymes specifically degrade certain inter-and intramyofibrillar cytoskeleton proteins such as desmin, nebulin and partly connectin, at the I band and Z disk locations of the sarcomere.

However, a specific inhibitor of calpains, calpastatin, regulates their proteolytic activity. Indeed, it has been shown that the enzyme/inhibitor ratio influences the tenderisation rate [87]. The μ–calpain/calpastatin ratio, increasing when ATPase activity increases, is equal to 1/4, 1/2.5 and 1/1.5 for beef, lamb and pork respectively [54] which can partly explain the lower tenderisation rate in beef.

The initiation of rupture and destabilisation of the myofibrillar structure by calpains could be followed by proteolysis of partially degraded proteins by the 20S proteasome. This proteasome may be formed by the dissociation of the 26S proteasome induced by the depletion of ATP stores [99]. Cathepsins B, H and L may attack the actomyosin complex, but they must previously be released from lysosomes whose membranes are damaged by pH decrease [51].

Meat ageing rate is positively correlated to ATPase activity, which defines the contraction rate of muscle [86]. Indeed, fast-twitch glycolytic muscles have a faster ageing rate than slow-twitch oxidative red muscles. However, other authors consider that meat tenderisation during ageing is not due to proteolysis but essentially depends on the dissociation of myofibrillar structures induced by the increase in cytosolic calcium after slaughter [108].

Dransfield has developed a mathematical model predicting the changes in calpain activities and, as a consequence, tenderness [21]. From the post-mortem kinetics of temperature and pH falls, this model allows to determine the changes in the activities of calpains and calpastatin and to predict the variation in tenderness. Using this model, Morton et al. [79] suggested that, in beef, tenderisation rate is directly dependent on the initial activity of calpastatin, on the autolysis of μ-calpain and on the pH fall rate. In lamb, tenderness depends on the initial content of calpastatin and on the pH decline profile which determine the in situ activity of μ-calpain and as a consequence the tenderisation rate.

4.3.3. Meat flavour

It is the result of the excitation of two physiological senses: taste and smell. However, other sensations such as astringency, juiciness, and mouthfeel can also play a role [26]. Smell is induced by volatile low molecular weight chemical compounds which stimulate the epithelial receptors of the nose. Taste is generally produced by water soluble compounds of higher molecular weights. Finally, there are compounds (glutamic acid, monosodic glutamate and inosinic acid), which are not particularly flavourful, but which enhance the action of other flavourful substances on taste and smell.

Raw meat does not exhibit any flavour, except blood taste, and contains few aromatic compounds. It is only during cooking of meat that a typical flavour is produced. This flavour is strongly dependent on the cooking conditions (type, duration and temperature). Aromatic compounds responsible for cooked meat flavour are produced by two main reactions induced by the high temperature thermal treatment: Maillard reactions between amino acids and reducing sugars on the one hand, and degradation of lipids on the other hand. These reactions generate a very large number (higher than 1000) of volatile compounds from water and lipid soluble precursors. Heterocycles, especially nitrogenous (pyrazins, pyridines) and sulphur (thiazoles, thiophens and sulfides) heterocycles, generate a typical meat flavour. Among water soluble flavour precursors, cystein, thiamin and ribose from nucleotides, play a major role.

Degradation of lipids, triglycerides and phospholipids, leads to a large range of aliphatic compounds (saturated and non-saturated aliphatic chains, alcohols, aldehydes, ketones, acids and esters) as well as cyclic compounds such as furanes, lactones and cyclic ketones. Some of these compounds exhibit intense odours and could be at the origin of flavour differences between

animal species. Moreover, some branched fatty acids, such as 4-methyloctanoic and 4-methylnonanoic acids, are associated with the characteristic flavour of mutton, which can be at the origin of the rejection of this meat by some consumers. It is noteworthy that, if lipids of meat are indispensable substances for the development of lamb flavour, specific beef flavour would not be due to lipids but to compounds resulting from Maillard reactions [94]. However, Grosch et al. [39] cited by Farmer [25], suggested that a branched aldehyde (12-methyltridecanal) derived from plasmalogen phospholipids could be important for the development of beef flavour.

Moreover, it has been shown that the products derived from the oxidation of lipids (aldehyde and carbonyle compounds) can react with intermediate products of the Maillard reactions. Thus, compounds such as thiazoles, pyridines and pyrazines can also be formed and contribute to the flavour of meat.

4.3.4. Juiciness

It is related to the more or less dryness characteristic of meat during mastication [111]. According to Winger and Hagyard [120], there are two components of juiciness. The first one corresponds to the sensation of water released during the first bites, induced by the rapid release of fluid from meat. The second one, more sustained, is due to the influence of lipids on the secretion of saliva. Juiciness not only depends on the characteristics of meat, but also on physiological factors tightly linked to the consumer. This is the reason why its evaluation is complex and very subjective. Structure and the water binding capacity of meat influence juiciness [120]. According to these authors, the water binding capacity can be measured using various methods but it does not give a satisfactory evaluation of juiciness. This sensory attribute varies with the type of muscle and the intramuscular lipid content. However, when a series of 10 muscles of various lipid contents were compared, a relation was obtained between lipid content and juiciness only in the case of one muscle: the *Semitendinosus* [11]. The influence of lipids on juiciness is thus not clear [120].

5. EFFECT OF RUMINANT FEEDING ON MEAT SENSORIAL QUALITIES

The modification of the diet composition and the level of feeding can change the muscle characteristics at slaughter and can then influence the different sensorial qualities of meat.

5.1. Colour

As discussed previously, the pigmentation in meat is due to the relative amounts of myoglobin and its oxidation state and to the muscle structure. The feeding conditions of ruminants can modify these parameters.

5.1.1. Diet composition

Pigment concentration increases in parallel with chronological age and can be modified by diet composition, especially in young animals in anaemic conditions, such as veal calves [95] in which the meat is very pale and the growth rate reduced [7, 44]. This could be due to a reduction in the oxidative metabolism enzyme activity (depending on the iron contribution), in spite of an increase in glucose utilisation by the muscles and an increase in anaerobic glycolysis [45]. In older cattle, a more pronounced pigmentation and a more intense colour have been observed with a grass diet, compared to a grain-finishing diet. But these differences could also be due to the different levels of physical activity and to the different feeding levels between these production systems [114] and, to a lesser extent to the feedstuffs used (grass vs. concentrates).

Colour stability is one of the most important quality attributes contributing to meat shelflife. Meat discoloration is due to pigment oxidation which leads to the formation of the oxidised form, metmyoglobin (MbO_2). Ferrous (Fe^{2+}) iron in heme is oxidised into the ferric form (Fe^{3+}) and releases an electron recovered by oxygen which is transformed to superoxide anion ($O_2^{-\cdot}$) during the pigment autoxidation [93]. Antioxidant defences (lipid and hydrosoluble) exist naturally in muscle cells [96]. Among these defences, superoxide dismutase (SOD), with a manganese ion at its active site in mitochondria and copper and zinc ions at the active sites in the cytoplasm and nucleus, transforms the anions to H_2O_2. The catalase and the glutathione peroxidase safely decompose hydrogen peroxide and fatty acid hydroperoxides. With Se, Mg, Cu, and Zn deficiencies or during the ageing of meat, enzymatic regulation becomes defective. The concentrations of radicals, $O_2^{-\cdot}$ and H_2O_2 increases and they are transformed by the effect of Fe^{2+} to hydroxyl (OH^-) which are able to promote colour degradation and lipid oxidation. Lipid oxidation in fresh meat could also be due to MMb-H_2O_2 and in the cooked meat by Fe^{3+} released by MMb. MMb formation and accumulation of lipid oxidation products are positively correlated [28]. Mb oxidation precedes the muscular lipid oxidation [77] and could play a catalyst role in the process of deterioration of flavour [98]. The free radicals also play a catalyst role in the transformation of Mb in MMb. However, oxidised lipids promote myoglobin oxidation.

The supplementation of the ruminants diet with selenium and more particularly vitamin E can strongly reduce myoglobin oxidation [62, 63] and increase the shelflife of the meat (from 3 to 6 days, according to the dose, the length of the supplementation and the type of muscle). Feeding vitamin E increases the α-tocopherol concentration in cell membranes, especially in mitochondria and microsomes. Vitamin E and selenium (a constituent of glutathione peroxidase) are the main antioxidants in all cells types [70]. They protect membrane phospholipids and cholesterol against oxidation. This resistance to the formation of lipid oxidation products could indirectly increase the shelf-life of meat and prevent its discolouration. α-tocopherol could also stabilise oxymyoglobin via the more intensive reduction of metmyoglobin, regulated by Cytochrome b5 [63]. However, the mechanisms are poorly characterised.

The amount of vitamin E in green roughages is 5 to 10 times higher than in cereals, but it decreases rapidly during tedding (–40%) and much less during dehydration (–12%). Silage is the type of roughage conservation which is the most favourable for vitamin E preservation [93]. INRA advises [49] that the allowances of vitamin E of sheep per kg. However, to obtain a significant preservative effect the dose of α-tocopherol in meat has to be around 0.30–0.35 mg·100 g^{-1} of fresh meat [70]. This needs much higher supplementation: for example, a minimum of 500 mg·d^{-1} during 120 days is necessary for fattening steers [62, 70] which means a minimum of 50 mg·kg^{-1} of feed.

5.1.2. The feeding level before slaughter

It seems to influence the amount of meat pigment in ruminants, and a reduction in allowances increases the oxidative fibre proportion [91, 115]. The colour of the *Semitendinosus* and *Longissimus thoracis* of restricted bulls were darker than those of control bulls at a high feeding level and slaughtered at the same live-weight [115]. The pigmentation and the capillary density of the restricted bulls were also higher. The rib cut colour of steers slaughtered directly from pasture feeding was judged darker than that of control steers fed subsequently a finishing feeding with a high cereal content [67]. The longer was the finishing period,

the brighter red was the colour (0, 33 or 75 days).

The pigment status, which means its oxidation degree, depends on the mitochondrial oxygen consumption after slaughter and the meat pH. Indeed, pH decreases due to the post-mortem glycolysis and the accumulation of lactic acid. A high pH (> 6) leads to a dark, sticky meat characteristic of stressed animals before slaughter, when glycogen reserves are exhausted [97]. Low muscle glycogen levels and a higher incidence of dark-cutters may be induced by subcutaneous epinephrine injections [42]. Muscles in which glycogen reserves are mostly reduced have a low ability to produce lactic acid, their mitochondria activity is not reduced, and oxygen consumption stays at a high level. The dark colour predominates [3]. At the surface of the meat, only a thin layer of myoglobin is the oxygenated bright red colour. Moreover, high pH meat has a high water-binding capacity, associated with greater translucence and less scatter of incident light, allowing greater light penetration and absorption which makes meat appear darker [17].

The frequency of dark-cutting meat can be reduced by improving the management of the animals before slaughter: well fed animals, managed without stress, transported during short times and maintained briefly in conditions avoiding conflict between animals. On the contrary a gradual decrease of pH during 24 h down to an ultimate value of 5.6 leads to a cherry-red meat, preferred by consumers. But a fast decrease of pH leads to a pale colour typical of the excessive fluid or drip loss meat (PSE pork). The most susceptible muscles to producing this type of meat have a high proportion of intermediate fibres and a great ability for anaerobic glycolysis [17].

Consequently a low glycogen level preslaughter or a fast glycogen degradation in the muscle post-slaughter explains the colour degradation of the meat.

5.2. Tenderness

Nutritional conditions can change the fibre type, glycogen level and solubility, muscular energetic reserves, and the activity of the proteolytic systems which determine the tenderness. Among these conditions, effects of feeding level variations, in particular fasting before slaughter, effects of diet composition, and the use of growth promoters (β-adrenergic agonists), will be discussed.

5.2.1. Feeding level before slaughter

Many authors have shown, that the reduction of feeding level before slaughter spoils the sensorial qualities of meat and in particular tenderness [30, 74, 75, 114]. Indeed, ruminant feed restriction leads to a decrease in the amount of white glycolytic fibres and an increase of red oxydoglycolytic fibres and also red and slow fibres [91]. The collagen percentage increases due to the reduction of myofibrillar proteins, and the collagen solubility decreases in growing steers [30] and in cows [75]. Moreover, the reduction in feeding level leads to a decrease in carcass fatness [36] and intra-muscular lipid content [12]. Recently, various studies have shown a strict relationship between tenderness and subcutaneous fat, 6–10 mm of subcutaneous fat protecting the muscle against cold shortening and maintaining the muscular temperature to a level which accelerates the ageing of meat [12]. Moreover the reduction of intra-muscular fat decreases tenderness, even if this fat explains only 3 to 10% of the variation between samples [21]. The intra-muscular fat plays a more favourable role in tenderness when its amount exceeds 6%. This is the case for Black Japanese cattle in which intra-muscular lipid content varies between 8 and 20% of fresh muscle [81]. But these amounts are not compatible with a good acceptability by the European consumer.

Therefore, on the one hand, the increase of the energy level during the finishing

period in ruminants is favourable for the improvement of sensorial qualities of meat. On the other hand, the increase of the protein level leads to a reduction of carcass fatness and muscle lipid content [117] and also of meat tenderness [10] even if this increases daily live-weight gain and muscle gain.

5.2.2. Fasting before slaughter

As seen previously, the suppression of feed 24 to 36 h before slaughter, associated with transport and handling of animals, can have a negative effect on meat colour and preservation. However, meat from these animals becomes tender quickly [116] and their final tenderness is higher [106]. This could be due not only to the increase in the water holding capacity of meat but also to a higher post-mortem proteolysis [112]. The proteolysis could be explained by 2 processes: a reduction in the potential activity of muscular calpastatins before slaughter, and a high pH favourable to the activity of calpaïns. In fasting lambs a reduction of protein synthesis and an increase in protein degradation has been observed [84]. This increase could be due to a reduction in calpastatin activity, without any modification of calpaïn activity [69]. These authors have shown that in lambs before slaughter (60% of maintenance requirements) these processes lead to a significant increase in the myofibrillar fragmentation index – a proteolysis estimator, and in tenderness as measured by Warner-Bratzler shear force. In similar studies, a higher solubility of myofibrillar proteins in dark-cutting muscles has been suggested in relation to a greater activity of calpaïns at a higher pH [106]. However, the shelf-life of these meats is too short, especially in vacuum where their colour is unstable. To allow the animal to reconstitute its energetic reserves, feeding roughages at the slaughter house has been tried, but it did not improve the ultimate post-mortem pH [124]. On the contrary, feeding sugars that are rapidly degradable in the rumen (lactoserum, sorbitol), during the 48 h before slaughter, seems to significantly decrease the frequency of carcasses with high pH [33, 41]. However, it takes a long time for ruminants (10 days for cattle) to recover their glycogen reserves [71] except after a reliability trial [45], so it is preferable to finish the animal with a high feeding level. In studies of lambs [90], heifers [71], and young bulls [115], the beneficial effect of an increase in feeding level on the muscular glycogen level has been demonstrated.

5.2.3. Compensatory growth

When ruminants receive a high feeding level after a restriction period, their growth rate is higher than that of non-restricted controls. This “compensatory growth” is often used to economically fatten cattle on grass after a winter period, or indoors with concentrate after a restricted summer period on grass. Several studies have shown the improvement of tenderness due to this type of management [1, 100, 125]. This can be explained partly by an increase in soluble collagen content [68]. This improvement could also be due to an increase in type III collagen content [60]. This collagen could play a role in tenderness by reducing the thickness of Type I collagen fibres. Some in vitro studies have shown that type III collagen can control the diameter of type I collagen fibres by covering their surface [92]. The improvement of the tenderness could also be related to the increase of the proportion of fast ageing muscular glycolytic fibres, at the expense of the proportion of slow fibres [91]. Lastly, the tenderness improvement could be related to the increase in intra-muscular lipid content, but this depends on the physiological status of the animal during the finishing period (cf. effects of feeding level).

5.2.4. Variations of diet composition

In ruminants, variations in diet composition allow some modifications in digestive processes, which regulate the nature

and the proportion of absorbed nutrients and thereby affect meat tenderness. Various studies of this effect have compared meat from animals fed with roughages or with cereals [126]. Some studies conclude that meat from roughages is less tender, but generally the feeding level effect has been confounded with the strict effect of the diet composition. Sometimes the physical activity associated with the feeding of roughages can modify muscle characteristics [45] as is especially the case in grazing systems. The differences in tenderness can be explained by differences in growth rate, fatness or age. To avoid the last two effects, meat from steers fed the 2 previous types of diets have been compared to animals being slaughtered at various ages and with various fatnesses [66]. The meat tenderness of the two types of animals, after correction by taking into account these 2 factors, were not significantly different. These results confirm those of other authors [13, 32, 67]. However, when hay-finished bulls were compared to grass silage-finished bulls, at the same amount of energy intake, hay-finished bulls had lower growth rates and carcass fatness degrees [61]. But the muscles studied (*Semitendinosus* and *Longissimus thoracis)* in the former contained a higher amount and concentration of soluble collagen and type III collagen than the latter. The *Semitendinosus* muscle of hay-finishing bulls also had a lower oxydative activity and the muscle was judged more tender by a taste panel. However, no significant effect of diet composition was observed with the *Longissimus thoracis*, but this muscle has a very low level of collagen and is especially tender. So the diet composition could in some cases modify meat tenderness, but more research is needed to verify this observation.

In the previous chapter it was stated that an increase in free Ca^{2+} concentration in muscle cells can activate the calpaïns, especially μ-calpaïn, post-mortem. Many attempts have been made to elevate muscle calcium concentrations through dietary calcium supplementation and/or infusion of a calcium chloride solution to live animals [107]. Swanek et al. [107], explained that because blood calcium homeostasis is regulated very closely (8 to 12 $mg \cdot dL^{-1}$ in cattle), these attempts have resulted in limited success. However, the oral administration of vitamin D at high concentrations (5, 10, 20 or 30×10^2 UI) or injections of 1 α-hydroxyvitamin D3 (500 to 700 μg) in dairy cows, some days prepartum, increases serum calcium concentration from 1.8 to 2.4 $mg \cdot dL^{-1}$ 3 to 8 days after injection. Previous research has demonstrated that vitamin D increases plasma calcium concentration by stimulating intestinal calcium absorption [80]. Moreover, vitamin D could stimulate the calcium mobilisation and the influx of calcium in skeletal muscle cells through the activation of calcium channels. Swanek et al. [107] have increased the calcium concentration of the *Longissimus thoracis* by as much as 50% by supplementing the diet of steers with 7.5×10^6 IU Vit. D during the 10 days before slaughter. The calcium concentration was about 21 $\mu g \cdot g^{-1}$ of tissue. According to the authors [107], who based themselves on the results of others researchers [38], this should be sufficient to activate μ-calpaïn and m-calpaïn and subsequently improve meat tenderness. But further experiments are needed, which should associate measurements of protease activities with meat tenderness.

In other experiments designed to improve tenderness, daily intramuscular injections of vitamin E were tried on lambs [64], from 5 days after birth and for 25 days. The quantity and concentration of soluble collagen in the *Semitendinosus* muscle studied increased with the injected vitamin E and it became significant from 1000 $IU \cdot d^{-1}$. At the same time, the amount of hydroxylysil pyridinolin decreased significantly from 1000 $IU \cdot d^{-1}$, but this protein is characteristic of the intensity of the intermolecular links and thus partly a characteristic of collagenic toughness. Antemortem treatment of animals with vitamin E should decrease the basic toughness of their muscles.

5.2.5. β-adrenergic agonists (clenbuterol, cimaterol, zilpaterol...)

These molecules have been used for fifteen years to promote the growth rate of meat animals [73, 118]. Their oral administration from 0.05 to 0.20 mg per day and per kg live-weight to cattle and sheep, effectively induces a significant enlargement of muscle mass and reduction of fatty tissues and offals. Considering the very great number of physiological functions controlled by these molecules, it can be suggested that the mechanisms set in action are various. They can include direct action on protein synthesis and proteolysis via specific receptors, stimulation of blood flux for the benefit of muscles, effect on hormone production (insulin, thyroid hormones, etc.) and direct action on the nervous system which controls food intake [73]. The intake of these β-adrenergic agonists also produces a modification of biological characteristics of muscles: in particular, a decrease in collagen content and an increase in its solubility, a reduction of the calpaïn/calpastatin ratio, a slowing down of the tenderness rate of meat, and an increase in tenderness (Geay et al. unpublished data). When the delivery of these molecules was stopped 7 days before slaughter, no residue was observed, but this did not modify the effect of these molecules on tenderness. However, their effect is muscle type dependent [9]: the increase in collagen solubility is higher in the muscles in which collagen content is more important. On the contrary, the increase of myofibrillar toughness is higher in muscles that are ordinarily tender.

5.3. Flavour

Meat flavour will be modified by rearing animals using nutritional conditions which change fat content, and composition, or which change compounds involved in the Maillard reaction.

5.3.1. Effect of pH

The appearance of flavour compounds depends on meat pH [25]. Indeed, a decrease in muscle glycogen content in lambs by stress before slaughter prevents the post-mortem decrease in pH, and also induces a higher production rate of compounds produced by fatty acid oxidation, thereby inducing unpleasant flavour during meat cooking [127]. Furthermore, the higher water-holding capacity of dark cutting meat may also favour the development of unpleasant odours [22]. Thus, the nutritional conditions (already indicated in Sects. 4.1 and 4.2) which optimise muscle glycogen content would also optimise meat flavour.

5.3.2. Nature of fatty acids

Fats contribute to flavour by various means including their fatty acid composition, which determines the nature of compounds produced by oxidation during meat cooking. It is noteworthy that SFA, which resist to oxidation at low temperature unlike PUFA, are also degraded at high temperature. In this case, the hydroperoxides generated differ from those generated by auto-oxidation of fats at low temperature. The products of degradation of the former, generated during cooking, give a great number of volatile products, some of which, such as aldehydes, indirectly determine flavour by being involved in the Maillard reaction [94]. Furthermore, in ruminants, fats contribute to meat flavour by solubilising some compounds such as skatole or terpenoïdes already present in grass or generated during the ruminal digestion of chlorophyll, with some of these compounds being volatile during meat cooking. Moreover, some PUFA-rich fats are relatively unstable in raw meat and are sensitive to oxidation at low temperature. Oxidation products from these types of fat induce unpleasant flavours.

When ruminants are fed concentrate-rich diets (grains), a high proportion of C18:2n-6

escapes ruminant hydrogenation. Indeed, this fatty acid may be selectively taken up by bacteria fixed to the solid phase of the ruminant content [5]. It is thus protected from hydrogenation and thereby absorbed and deposited in tissues at the expense of SFA. With an increasing duration of feeding on grain-rich diets, the concentration of C18:3n-3 in muscle phospholipids is decreased and that of C18:2n-6 is increased. In addition, it has been shown that meat flavour of grass-fed young bulls is changed when animals are then fed grain-rich diets [55]. The flavour identified as sweet when animals are out to pasture decreases at the expense of the typical flavour of steers. Furthermore, the products of fat degradation (such as aldehydes and cetones) are more apparent in the volatile fraction of meat from grass-fed young bulls than from grain-fed animals [56]. The terpenoids are also less abundant in meat from grain-fed bulls and their contents in meat are associated with various flavours. On the contrary, the increase of C18:2 content from 2 to 20 mg·100 mg^{-1} of total fatty acids in carcass fatty tissues markedly reduces flavour of meat in lambs in favour of an unknown flavour of sweet oil [89]. This result was obtained by feeding animals sunflower seeds protected against ruminal degradation for 6 weeks. The balance between n-6 and n-3 fatty acids in phospholipids would be important for the determination of meat flavour [25].

Furthermore, certain types of pasture can cause off-flavours in lambs. Indeed, rape pasture induces a foreign flavour similar to that of cabbage [72]. White clover pasture leads to a more intense flavour than that of lambs fed ryegrass. However, the composition of volatile products, which determines the flavour of lamb meat, has been studied to a limited extent. Some studies indicate that fats from lambs which have eaten wild white clover have a higher concentration of some volatile products (2,3-octanedione, short-chain fatty acids, medium-chain fatty acids, terpenoïdes) compared to fats of meat from grain-fed lambs. But, the former would have a lower content in γ-dodecalactone [72].

Flavour intensity increases with increasing age and duration of consumption of the diets. On sheep studied at various ages and reared on different pastures, the intensity of the typical flavour of sheep meat was increased with age and was correlated with fat contents of medium and branched-chain fatty acids (C7 to C10) and of 3-methyl indole (skatole) [101, 128].

5.3.3. Auto-oxidation of fats at low temperature

It is a major degradation process which induces meat rancidity and gives rise to compounds which could impair human health (cf. Sect. 2), as is the case for oxidation of cholesterol and especially of PUFA. The oxidative generation of rancidity is a two-step process [93]. In the first step, the lipolysis of phospholipids and triglycerides generates, through the action of various lipases, fatty acids which are sensitive to oxidation [34]. The second step involves the oxidative degradation of fatty acids which needs oxygen to occur and leads to the appearance of free radicals and various molecules (alcanes, cetones, acids, alcohols or aldehydes) which are responsible for the flavour degradation. Phospholipids are the major substrates of lipolysis and oxidation. Through the action of lipases, phospholipids liberate PUFA which are very sensitive to oxidation [34]. The oxidation rate of cholesterol depends, at least in part, on the intracellular concentration of antioxidants (natural or synthetic) and on the unsaturation index of fatty acids. The presence of metal ions, (Fe^{3+}, Cu^{2+}) and oxidation of Mb are important factors which promote the formation of lipid oxidation [25]. As indicated earlier, Mb oxidation occurs before muscle fat oxidation and plays a catalytic role in the process of the oxidative generation of rancidity. Supplementation of animals with vitamin E increases α-tocopherol concentration in cellular membranes, and especially in mitochondria and microsomal membranes, which thereby significantly decreases the

susceptibility of phospholipids to auto-oxidation. Vitamin E acts as an antioxidant by giving a hydrogen atom to a free radical, which gives rise to a stable α-tocopherol radical. Many studies have demonstrated the advantages of such a supplementation to reduce fat rancidity in fresh meat and to increase its duration of conservation.

It is noteworthy that α-tocopherol protects the structural and functional integrity of membranes by decreasing oxidation of their phospholipids. Thus, α-tocopherol reduces water loss of meat by decreasing loss of cytoplasmic water [76].

5.4. Juiciness

This sensorial quality trait has not been studied as much as the others. This may be explained in part by the fact that this trait is less important for beef meat than tenderness and colour, according to consumers. Furthermore, it is a trait difficult to measure instrumentally and it is thus only estimated by sensory test panels which are expensive and time consuming. The methods used to prepare samples (muscle choice, cooking method, temperature, etc.) differ a lot among research groups. The choice of muscles seems especially important. Finally, no study has tried to induce variation of juiciness without modification of the other sensorial quality traits, but, the latter interfere with juiciness [120].

For some authors the nature of the diet does not influence juiciness. Indeed, no significant difference in juiciness has been observed between grass-fed and grain-fed young bulls despite differences in carcass fatness and meat tenderness [114]. Similarly, no significant difference has been observed in juiciness of meats of young bulls fed either an alfalfa silage-diet or a concentrate-diet indoors [66]. However, meat from the *Longissimus thoracis* and *Semitendinosus* muscles of young bulls fattened with hay is more juicy than meat from muscles of young bulls fed grass silage [61].

Although an increase in feeding level was shown to increase muscle fat content and meat tenderness [75], there was no significant differences in juiciness. Similarly, Seideman and Crouse [105] who induced changes in fiber types and diameters by variations in feeding level, did not observe any relationships between fiber characteristics and juiciness. However, Dikeman et al. [20] and Keane et al. [53] pointed out a positive relationship between juiciness (and tenderness) and muscle fat content. In the latter study, the higher fat content was due to higher carcass weight, and not to an increased feeding level. Similarly, an increasing protein intake with a similar energy intake induces an increase in muscle gain, a lower muscle fat content and a slow reduction of meat juiciness [10].

The possibilities to modify meat juiciness by nutritional means are still a matter of debate and some complementary studies are thus necessary before recommending a nutritional strategy to control juiciness.

6. CONCLUSION

Meat from ruminants is a major source of essential nutrients (amino acids, iron, zinc and vitamins from the B group). Due to the diversity of breeding systems and pieces offered in butcheries, meat from ruminants is characterised by great variations in fats, quantitatively and qualitatively. Some of these fats, such as CLA, could be beneficial to human health.

Some saturated (C14:0 and C16:0) and monounsaturated trans fatty acids are not recommended for human consumption and it is possible to reduce their concentrations in meats by increasing the proportions of polyunsaturated fatty acids absorbed by the animals from their diets. To achieve this goal, fatty acids must be protected against hydrogenation in the rumen. Dietary intake by the animals of PUFA from the n-3 series, and especially from the n-6 series, favour

the production of CLA by the rumen bacteria. This point is important since the role of CLA in the prevention of specific cancers and in the treatment of obesity has been demonstrated in animal models and, at least partly, in humans.

Meat, especially from ruminants, remains an attractive type of food, especially because of its sensorial quality traits: colour, tenderness, flavour and juiciness. Many complex mechanisms are involved in the development of the biological and physicochemical determinants of these quality traits. These mechanisms are becoming better known due to progress in scientific research. They concern the metabolic and physicochemical characteristics of muscles at slaughter, and the technological conditions of slaughtering and transformation.

However, muscle characteristics at slaughter depend not only on animal type (breed, sex, age), but also on animal breeding conditions, especially the nature and the level of dietary intake and this is the reason why a high dietary intake is necessary. Proper feeding helps muscle fibres to keep high energetic stores as well as metabolic and contractile properties which favour to a high maturation rate of meat. Furthermore, this increases muscle fat content thereby increasing meat flavour. Meat also becomes red and bright as preferred by consumers. The positive consequences of high dietary intake on tenderness are stronger when animals are subject to compensatory growth after a period of undernutrition.

The nature of the diet may modify tenderness in some cases. In addition, it has greater influences on colour stability and flavour, especially by providing some specific fatty acids, antioxidants (vitamin E) and fat-soluble compounds (terpenoids).

The main effects of breeding conditions on meat quality traits may be cancelled in part or in totality (or at least under-estimated) by uncontrolled conditions of slaughtering or meat transformation which can contribute to the high variation in raw meat quality. However, recent progress in slaughter and storage by the meat industry suggests that breeding factors will become the major causes of inconsistency in meat quality. Research is thus required to obtain better knowledge of the biological mechanisms which control the in vivo elaboration of muscle characteristics, the ultimate objective being to control these mechanisms since they partly determine meat quality traits.

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