Some recent advances in muscle biology and its regulation by nutrition: consequences for bovine meat quality

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Summary

Quality is nowadays one of the important social and economic challenges for producers. Beef quality traits (tenderness and flavour) depend on various muscle characteristics that are also related to the potential of muscle growth but, despite considerable progress, the relative importance of these characteristics is only partially known. The new scientific orientations towards transcriptome and proteome analysis have opened up new possibilities for discovering molecular predictors (i.e. new highly–regulated genes or molecular polymorphisms) that control muscle growth and meat quality traits. One of the major genes already known is the myostatin gene; when it is mutated or deleted, this gene induces muscle hypertrophy and modifications to the muscle characteristics by molecular mechanisms that that are currently under study. In addition changes in nutrition affect muscle biology, and hence muscle growth and characteristics. Undernutrition during foetal life impedes muscle differentiation and changes energy metabolism in a way that is detrimental for postnatal growth. By contrast, overfeeding of veal calves induces dysregulation of glucose metabolism. In growing cattle, compensatory growth and grass–feeding on pasture also induce a plasticity of muscle characteristics. The underlying mechanisms in all these situations are thought to involve molecular regulation by nutrients and/ or hormones (e.g. insulin, thyroid hormones). Research is currently being carried out to identify those mechanisms.

Keywords: growth, cattle, meat quality, fibre type, collagen, metabolism

Introduction

Muscle biology is complex due to the different biological functions of muscles. Firstly, skeletal muscle plays an important role in maintaining the skeleton and in allowing movements such as changing posture or engaging in various physical activities. Secondly, muscle is involved in deposition of proteins, especially in growing individuals. Thirdly, it has a role in the protection of individuals against any drop in body temperature via shivering or non–shivering thermogenesis (for review, see Hocquette *et al.* 1998). In addition, muscle metabolism may play a role in the pathogenesis of metabolic disorders (obesity and diabetes in humans) and in the transformation of muscles to meat in farm animals (for reviews, see Corthright *et al.* 1997 and Geay *et al.* 2001). Research was therefore conducted to determine the basic mechanisms of muscle biology which (i) control growth, body composition and health of humans and animals, (ii) optimize the performance of athletes or of race–horses, and (iii) optimize the muscle characteristics involved in meat quality. This latter aspect is of prime importance since quality is nowadays an important social and economic challenge for beef producers and retailers (for review, see Tarrant 1998).

This review aims to demonstrate how the recent advances in the understanding of muscle physiology may contribute to a better knowledge of the biological mechanisms involved in the determination of meat quality traits in cattle. The first part of this review will deal with the relationships between muscle characteristics and meat quality traits. The second part will address the development of muscle tissue during foetal life and its control by nutrition. The third part of the paper will describe how breeding factors affect meat quality traits in the various types of bovines commercialized for meat production in France.

Relationships between muscle characteristics and meat quality traits

Variability in meat quality, especially in tenderness, depends in part on differences in the biological characteristics of skeletal muscles at slaughter. These are the subject of active research (for reviews, see Tarrant 1998; Picard *et al.* 2000; Geay *et al.* 2001).

The first objective of such studies is to determine what are the most important muscle characteristics related to meat quality. It is now generally accepted that muscle fibre characteristics, muscle glycogen content (which determine the ultimate pH of the meat), collagen content and solubility, and the activities of proteases and of their inhibitors during aging are the most important physiological parameters that determine meat tenderness. Content and composition of intramuscular fat contribute to the determination of flavour as well as the changes (lipolysis, oxidation, etc) occurring during aging of the meat.

However, these general relationships are more complex. Indeed, in some studies, collagen–rich skeletal muscles are clearly shown to be tough but, in others only a slight relationship between collagen content and meat tenderness has been reported. Furthermore, collagen solubility is determined by several parameters of the connective tissue including the types of collagen (the two major isoforms being types I and III) and other non–collagenic molecules (e.g. proteoglycans). Although tough muscles are rich in type III collagen, other authors showed opposite results or even no effect of type III collagen content on texture (for review, see Bailey and Light 1989). In addition, the *M. semitendinosus* (ST) contains more decorin than a tender muscle, the *Psoas major* (Pedersen *et al.* 2001). These results suggest that proteoglycans should be studied together with collagen to understand which molecules control the solubility of the extracellular matrix.

Nevertheless, despite some ambiguous data, attempts have been made to evaluate the respective contributions of the muscle characteristics to the overall quality. A recent study indicates that only one fourth to one third of the variability in tenderness or flavour is related to the variability of various muscle characteristics (Renand *et al.* 2001). This low level of prediction may be explained by many factors: (i) measurement errors with respect to both muscle and meat quality traits; (ii) gaps in the knowledge of the major biological mechanisms that determine the various quality traits.

The second objective of the research on determinants of meat quality is to identify the most important muscle characteristics that may be considered as quality predictors. Such predictors could be used either to predict the ability of a young animal to produce meat of good quality when it is older, or to include these predictors in selection programs. Special attention has been focused on proteins that determine muscle fibre types (such as myosin heavy chain isoforms [MHC]) because variability in meat quality is related to the properties of muscle fibres (for review, see Klont *et al.* 1998). It is therefore important to define rapid and reliable methods for classifying fibre types. Consequently a great deal of research has been carried out to compare (Picard *et al.* 1998) and to improve (Picard *et al.* 1994a) the available methods for fibre type classification. Recently, genetic variants of fatty acid binding protein (FABP) were discussed as a new predictor of intramuscular fat content in pigs (Gerbens *et al.* 2000). However, FABP protein content or mRNA level do not seem to be good predictors of bovine intramuscular fat content (Brandstetter *et al.* 1998a; for review, see Hocquette *et al.* 1998).

During the last few decades, new research orientations have appeared in the search for molecular predictors of meat quality, i.e. highly regulated genes in muscular tissues, or genes with polymorphism associated with variation in quality traits. Indeed, the deciphering of an increasing number of complete genomes concomitantly with the development of new molecular techniques (the DNA chip technology) has opened the way to an almost exhaustive analysis of gene expression in various physiological conditions. Scientists are now able to conduct what is called transcriptome and proteome analysis, i.e. analyses of the expression of genes at the mRNA and protein levels, respectively. Given these new possibilities scientists can work with a high number of known genes involved in one specific biological function of interest, or discover new molecular predictors, i.e. genes that have not been previously sequenced or with unknown sequences. Whatever the type of strategy, this approach will be used in many laboratories, as it is in INRA, with the aim of identifying the major genes that control muscle growth and meat quality (Sudre *et al.* 2000).

Ontogenesis of muscle characteristics during foetal life

Quantitatively, the potential for muscle growth depends on the number of muscle fibres. Qualitatively, meat properties are related to muscle characteristics as discussed previously. Growth *in utero* plays a very important role in these processes and depends on many factors including nutrient supply, and thus maternal and foetal nutrition. However, a better knowledge of the different steps of muscle differentiation in cattle is first required. Current research in our group is thus being conducted with this goal in mind.

The ontogenesis of collagen, the major component of intramuscular connective tissue has been studied during the foetal life. In foetal and adult skeletal muscle, seven collagen types have been detected, types I, III, IV, V, VI, XII and XIV (Listrat *et al.* 2000). The most important changes in collagen content occur during the two first trimesters of gestation. They are mainly explained by changes in type I collagen content. Absolute quantities of types I and III increase up to a maximum reached at 180–230 days post–conception (p.c.) then decrease up to 260 days p.c. As in the adult muscle, foetal perimysium is mainly composed of type I collagen, with traces of type III, whereas foetal endomysium contains mainly type IV collagen, with small amounts of types I and III. The other collagen types are also present**:** type V and VI in the peri– and endomysium, with type XII and XIX exclusively expressed in the perimysium. Although total collagen content is higher at 260 days p.c. than during post–natal life, the differences between muscle types are the same as those in adult muscles. To summarize, at the end of foetal life skeletal muscle has already acquired its postnatal structure (Listrat *et al.* 2000).

Studies on bovine foetuses have specified the chronology of the contractile and metabolic differentiation of muscle fibres (Picard *et al.* 1994b; Gagnière *et al.* 1999a and 1999b; for review, see Picard *et al.* 2000). As in other species, bovine myogenesis involves at least two generations of cells. These generations are distinguishable by their size and by the expression of the different MHC revealed by specific antibodies. Myoblasts from the primary and secondary generations proliferate during the first two thirds of foetal life until 180 days p.c. on average. The total number of fibres is fixed from this stage on. The first generation of myoblasts is completely differentiated from the end of the second trimester. It corresponds to slow fibres that will be converted mainly into type I fibres after birth. The second generation achieves its differentiation at the end of foetal life and will give rise mainly to fast fibres after birth but also slow fibres depending on the muscle type (Gagnière *et al.* 2000). These results and those for collagen ontogenesis described previously suggest the existence of close relationships between the differentiation of the connective tissue and that of the first generation of muscle cells. The contractile and metabolic differentiations begin from 180 days p.c., and so during the last third of foetal life the developmental MHC are progressively substituted by the adult isoforms (Gagnière *et al.* 1999a). In addition, the activities of various different metabolic enzymes increase (Gagnière *et al.* 1999b). In the heart, the induction of enzyme activity occurs at various stages of cardiac development, indicating different steps in the differentiation process. These changes suggest a switch in energy substrate preference from glucose to fatty acids with a concomitant change in certain hormonal sensitivities (Hocquette *et al.* 2000). Compared to other mammals, bovine muscle is very mature at birth from the point of view of its contractile and metabolic properties (Gagnière *et al.* 1999a, 1999b; for review, see Picard *et al.* 2000).

Recent studies indicate that differentiation of muscle fibres is under the control of genetic or nutritional factors. For instance, studies on the myogenesis of pig muscle have suggested that the primary myofibres are those most related to the genotype (Stickland *et al.* 2000). A study on bovine muscle confirms that notion: at 100 days p.c. the ST muscle from Holstein foetuses contain a higher proportion of primary fibres than ST from Belgian Blue foetuses (Deveaux *et al.* 2001). This suggests a genetic control for this characteristic. On the other hand, secondary fibres are susceptible to maternal nutritional manipulations. Pregnant sows that are undernourished (60% of *ad libitum* feeding during gestation) produce offspring with fewer secondary myofibres in their muscles whereas primary myofibre number appears not to be influenced (Dwyer and Stickland 1991). Studies in the pig and sheep indicate that the first half of gestation is particularly critical with regard to nutritional influences on the determination of fibre number. All these results suggest that a high nutritional level either increases or prolongs myoblast proliferation. In nutritionally–advantaged foetuses, the total nuclear content of muscles, including the population of satellite cells, is also increased with consequences for postnatal muscle fibre hypertrophy (Stickland *et al.* 2000). The foetus is necessarily dependent on maternal food intake and on the transfer of nutrients across the placenta. Any disturbance in this pathway leading to limitation of substrate supply for the foetus can modify early foetal development with possible long–term effects. Changes in the hormonal status are thought to be mediators of this nutritional adaptation since many of the putative endocrine regulators of cell differentiation and nutrient partitioning (hormones, growth factors) are highly sensitive to nutrition. All these observations have led to the concept of 'Nutritional programming' which has been demonstrated convincingly in a range of mammals in the fields of both medical and animal science (for review, see Hocquette *et al.* 2001).

Control of muscle characteristics

In addition to the improvement of growth, the objectives of research programs are also to control the biological characteristics of tissues (muscles, fat depots) that determine dietetic value (see review by Geay *et al.* 2001), and organoleptic meat quality traits that will be discussed here. These tissue characteristics are in part genetically determined. The greatest differences, however, are between milk–fed calves raised for veal production and weaned growing cattle raised for red meat production. We believe these differences relate more to the divergent nutritional regimens for the two classes of animal than to age.

Regulation of metabolism by nutrition in veal calves

Despite a 16% decrease between 1990 and 1998, France is still the largest producer in Europe of veal, followed by the Netherlands and Italy, and the nutrition of veal calves is the subject of active research to optimize their growth. In pre–ruminants, the balance between dietary carbohydrates and fats affects a number of processes in nutrient absorption and metabolism.

The coagulation of milk caseins in the abomasum of the calf results in the retention of dietary proteins and triglycerides in an insoluble clot for several hours.

This delays the absorption of amino acids and fatty acids and alters the postprandial hormonal status (i.e. insulin plasma concentration), thereby affecting protein metabolism. Studies in humans also indicate that a slow rate of dietary protein digestion as with casein may promote postprandial protein deposition which is not the case with a rapid rate of dietary protein absorption, such as with whey. This remains to be studied in calves (for review, see Hocquette *et al.* 2001).

The second process relates to fatty acid partitioning within the liver, which determines nutrient availability for muscle, and dysregulation of this metabolic pathway may affect growth and health of the calves. Compared to standard milk replacers, diets rich in polyunsaturated fatty acids (soybean oil) or in medium–chain fatty acids (coconut oil) lead to the development of hepatic triglyceride infiltration. For coconut oil, this may be explained by a modification of LCFA partitioning between esterification and oxidation within peroxisomes and mitochondria (for review, see Hocquette and Bauchart 1999).

The third process relates to the dysregulation of glucose metabolism in insulin–sensitive tissues (such as muscles) from intensively milk–fed calves during fattening. There is an age–dependent reduction in the ability of veal calves to handle high amounts of absorbed nutrients, especially glucose. Consequently they develop insulin resistance, especially in the post–prandial state (for review, see Blum and Hammon 1999).

The last process relates to the regulation of energy metabolism by changes in the nature of dietary nutrients, such as at weaning. This regulation may occur through hormonal factors, such as insulin, or nutritional factors such as dietary fat or dietary carbohydrates. For instance, activation of peroxisome proliferator–activated gamma receptors by fatty acids increase the transcription of the lipoprotein lipase gene. Unlike in the rat and in the pig, weaning is characterized in the calf by a decreased dietary supply of carbohydrates and fat due to fermentation of food in the rumen. This induces a small decrease in the expression of glucose transporters and a twofold decrease in lipoprotein lipase expression in adipose tissues (for review, see Hocquette *et al.* 2001) which may be under control by peroxisome proliferator–activated gamma receptors.

Regulation of metabolism by specific nutrients is now a new frontier for nutrition scientists.

Regulation of metabolism and muscle plasticity in growing cattle

A large part (44%) of the bovine red meat production in France comes from culled cows and 31% is from young bulls; steers and heifers contribute 9% and 15% respectively of the total production. The sources of the production in the whole European Union are similar, but British beef production is dominated by steers with a negligible production of bulls. In France, young bulls are fed a diet consisting of mainly corn–silage, hay and a source of protein, and are usually castrated at 9 months of age. They are slaughtered at 15–19 months of age, 600–750 kg liveweight (380–450 kg carcass weight). Liveweights of animals slaughtered at 30–36 months of age are 730–750 kg for steers and 650–700 kg for heifers.

A large part of red meat production in France comes from late–maturing bovine breeds or breeds selecting for muscling. The various factors that affect muscle characteristics, and hence meat quality, are the genotype, sex and age, nutritional level, and the type of diet.

Genotype Double–muscled (DM) cattle display strong muscle hypertrophy (about 20%) and lower fat deposition (–50%) in their carcass. Compared with other breeds with normal musculature, their muscles contain twice the number of fibres (Wegner *et al.* 2000). Their meat is very tender due to a lower collagen content than normal animals (for review, see King and Ménissier 1982), but their meat is less tasty due a lower intramuscular fat content. Their muscles are more glycolytic since they contain a higher proportion of fast glycolytic fibres than bovines with normal muscle mass. DM cattle are also characterized by an enhanced muscle sensitivity to insulin (for review, see Hocquette *et al.* 1998), and by lower levels of triiodothyronine, insulin and glucose plasma concentrations (Hocquette *et al.* 1999), underlining the importance of the metabolic and hormonal status in the control of carcass composition and muscle characteristics. The gene of muscular hypertrophy has been mapped on chromosome 2 (Charlier *et al.* 1995). Using a positional candidate approach, Grobet *et al.* (1997) have demonstrated that a mutation in bovine myostatin gene, that encodes a member of the TGFb superfamily, was responsible for the double–muscling phenotype. Series of mutations or deletions have been identified in the myostatin gene in different DM breeds (Grobet *et al.* 1998).

Until now, genetic selection has been directed in favor of higher muscle development. As a general rule, whichever the species and as observed in DM cattle, this type of selection induces an increase in glycolytic muscle energy metabolism and an enhanced sensitivity to insulin (for review, see Hocquette *et al.* 1998). Indeed, the comparison of two lines of Charolais young bulls obtained by divergent selection on growth rate and feed efficiency demonstrated that an increased lean to fat ratio was associated with greater muscle glycolytic metabolism, lower intramuscular fat content (Renand *et al.* 1994), a greater number of fibres, a higher proportion of fast glycolytic fibres and a lower proportion of slow fibres (Duris *et al.* 1999). Furthermore, the Blonde d'Aquitaine breed, in which neither deletion nor mutation in the myostatin gene have been yet identified (Grobet *et al.* 1998), shows similar muscle characteristics to those of DM cattle (Listrat *et al.* 2001); however, unlike DM, selection on growth parameters does not change total collagen content, but slightly increases heat–labile collagen content (Renand *et al.* 1994). In addition, the muscles of animals from sires selected for low muscle weight contain more type XIV collagen than those of animals from sires selected for high muscle weight, both during the foetal life and after birth, with DM foetus being intermediate (Listrat *et al.* 2000).

Whatever the genotype (breeds with or without mutation in the myostatin gene, genetic selection on growth parameters within a breed), muscle hypertrophy is generally associated with a higher glycolytic muscle metabolism and a lower intramuscular fat content. The collagen characteristics, however, may be under genetic control unrelated to muscle hypertrophy.

Sex and age There are many reports showing that bulls are superior to steers in growth rate, feed efficiency and carcass muscle proportion, but there is evidence that meat from bulls is less tender than that of steers. Muscle glycogen depletion leading to dark, firm and dry (DFD) muscle is also a greater problem in bulls than in steers. The frequency of dark–cutting meat can be reduced by improving the welfare and the management of the animals before slaughter: high nutritional level, no stress, short transportation, no conflict between animals. Intramuscular fat is lower in bulls than in steers, resulting in a less tasty meat, particularly because these animals are slaughtered at a younger physiological age than other meat–producing cattle.

The livestock industry worries nowadays about the low level of intramuscular fat in young bulls reducing the acceptability of their meat in terms of taste, flavour, or juiciness, especially in the extremely lean double–muscled Belgian Blue type cattle. Selection of animals for increased protein retention has also induced a reduction in intramuscular fat content. French breeders or beef producers are thus at a serious disadvantage for the export of beef meat to North American and Asian markets. Thus, current research aims to understand the biological mechanisms that may improve intramuscular fat content. *De novo* synthesis of fat in intramuscular adipocytes seems to occur from glucose (and less from acetate, as in bovine adipocytes from other fatty tissues). This suggests that it may be possible to increase fat accumulation within intramuscular adipocytes independently from that in fatty tissues of the carcass, by using glucose only as a fat precursor. For this reason, research is focused on the insulin–sensitive glucose transporters (for review, see Hocquette and Abe 2000) which are considered to control glucose utilization by muscle cells and adipocytes. Consequently they may play an important role in muscle metabolic traits, linked to obesity and diabetes in human subjects, or to meat quality in farm animals.

Nutritional level Steers and heifers often receive a restricted food supply in winter when feed availability is low (average daily growth rate less than 500 g/d), and then they are fed on pasture *ad libitum* in spring when the grass grows again (average daily growth rate 0.8–1.0 kg/d). In this situation the animals increase growth at a higher rate than do previously unrestricted cattle.

Muscle fibres are able to adapt their characteristics in order to optimize protein turnover. The size of the different fibre types is always decreased after a period of energy restriction, whether before or after weaning (Brandstetter *et al.* 1998b ; for review, see Geay *et al.* 2001). This is due to a reduction in muscle DNA and protein contents. These effects disappear after a re–feeding period. Consequently, undernutrition at the beginning of postnatal life has no effect on the quality of meat at the slaughter age (Picard *et al.* 1995). The effect of the energy restriction would, however, depend on whether it occurs before or after weaning. Energy restriction after weaning decreases the proportion of type IIB fibres and increases those of IIA and I fibres (Picard *et al.* 1995). These modifications are accompanied by an increase in the oxidative activity of the muscles (Brandstetter *et al.* 1998b). The effect is more pronounced in bulls than in steers. All these changes in fibre size and types are commonly explained as a consequence of the mild hypothyroidism that occurs during a period of undernutrition (Cassar–Malek *et al*. 2001).

Re–feeding after a restriction period results in a superior growth rate, termed compensatory growth, a phenomenon of particular interest to our research group in our studies of the effect of the nutritional level on the plasticity of the muscle characteristics. In a first study conducted with young Montbéliard bulls and steers, we induced compensatory growth by feeding the animals a restricted diet from 9 to 12 months of age followed by *ad libitum* feeding from 12 to 16 months of age. The animals were compared to control subjects undergoing continuous growth during the same periods. Metabolic enzyme capacity was primarily affected after compensation (Brandstetter *et al.* 1998b). Oxidative isocitrate dehydrogenase activity was lower in compensated than in continuously growing bulls, but this effect was not observed in steers or for glycolytic lactate dehydrogenase activity. The muscles of bulls also presented a higher proportion of type IIB fibres at the expense of type I fibres, suggesting an orientation towards glycolytic metabolism. Moreover, the content and/or the solubility of collagen was increased in the muscles of steers (Damergi *et al.* 1998) suggesting collagen neosynthesis. Recently, another similar experiment was conducted with Montbéliards steers only. In this experiment, associated with the compensatory growth, the characteristics of the oxidative muscle *Triceps brachii* were distinctly modified at 16 months. The oxidative metabolism was enhanced as shown by an increase in mitochondrial enzyme activity. This was coincidental with an elevation in circulating thyroid hormone levels and in the potential to produce T3 as shown by increased 5'deiodinase activity in the liver (Cassar–Malek *et al.* 2001). In addition, the amount of total and soluble collagen as well as the mean fibre area were increased in experimental animals compared to control subjects.

To summarize, nutritionally induced compensatory growth is closely related to a plasticity of muscle characteristics, probably via endocrine mechanisms. Interestingly, oxidative muscles appear to be more sensitive to variation in nutritional level. Further work is needed to understand better these mechanisms. Because the activity of satellite cells (adult myoblasts) is a requisite for muscle growth and hypertrophy, we are also studying how these cells may be activated under nutritional and hormonal manipulation. In particular, our *in vitro* data indicate that the restoration of insulin and T3 levels during re–feeding could contribute to fibre hypertrophy by increasing satellite cell fusion with existing fibres during compensatory growth (Cassar–Malek *et al.* 1999). The molecular mechanisms involved in the changes of collagen characteristics during compensatory growth are also unknown. They may imply a modification of the cross–links of the collagen fibres and/or a regulation of the expression of the different collagen types. In any case the plasticity of collagen in muscle tissues is well established (Bailey and Light 1989; McCormick 1994). However, energy restriction generally has a greater effect on early–maturing breeds such as Holstein, than on late–maturing breeds such as Hereford, Charolais, Angus or Simmental. During rapid growth, the expansion of the collagen matrix could occur by degradation of the proteoglycans, assuming that these compounds play a significant role in stabilizing the collagen fibres. Indeed, proteoglycans have a higher metabolic turnover than the collagen (Bailey and Light 1989).

Nature of the diet Among the factors affecting muscle characteristics the effect of diet has often been described (for review, see Geay *et al.* 2001), but its effect has seldom been studied independently of the energy level or independently of other factors that may affect muscle physiology (ambient temperature, housing, etc).

In an experiment with Salers bulls (Listrat *et al.* 1999), those fed hay had a lower average daily weight gain (–11%) and carcass weight (–7%), and they were leaner (17% less fatty tissue), than bulls fed grass silage at the same level of energy intake; muscle mass, however, was similar. The ST muscle of hay–fed animals had a lower oxidative metabolism but the metabolic properties of *Longissimus thoracis* were not modified, showing that the effect of diet on muscle characteristics differs according to the muscle. In addition, ST muscle from animals fed hay contained similar amounts of total and type I collagen and greater contents of soluble collagen and of type III collagen, than those of animals fed grass silage. In ST muscle, these differences resulted in a more tender meat estimated by a panel of consumers for animals fed on hay (Listrat *et al.* 1999). These results are difficult to explain, but some *in vitro* results show that vitamins and minerals may play a key role in the metabolism of collagen. Compared with corn silage, hay contains higher amounts of manganese and may contain different amounts of vitamins and other minerals. For example, manganese plays an important role in the glycosylation of hydroxylated collagen, but excess or deficiency has a significant effect in extreme nutritional conditions only (Berg 1992).

Body composition and intramuscular fat content result from the balance between energy intake and energy expenditure. This balance may be affected by changes in muscle metabolic activity, and so by movement of the animals. In humans, muscle oxidative capacity may be influenced by overall daily physical activity rather than by intensive regular training. In other words, individuals practising continuous moderate intensity activities have a more oxidative muscle metabolism than sedentary individuals. When extrapolated to ruminants, grazing cattle may have a more oxidative muscle metabolism compared to indoor animals fed the same diet at the same level of energy intake (for review, see Geay *et al.* 2001; Hocquette *et al.* 2001). Indeed, grazing increases oxidative metabolism in oxidative muscles (*Rectus abdominis*), but reduces intramuscular fat content compared to steers fed a maize–rich diet indoors (Jurie *et al.* 2000). This may be due to a higher catabolism of fat by oxidative fibres. However, the respective effects of the diet (grass vs maize) and the activity of the animals in the field need to be determined.

Conclusion

France is the largest producer of beef in the European Union, and has the highest *per capita* consumption though that has decreased by 1.5–2% per year from the beginning of the eighties. This decrease is explained by several factors: (i) the high price compared to white meats; (ii) the inconsistency in its sensory traits; (iii) reduced consumer confidence in product integrity (illegal use of anabolic agents, BSE, foot and mouth disease); (iv) concern for animal welfare; and (v) the behavior of consumers who are more and more concerned for their health (for review, see Geay *et al.* 2001). However, a significant proportion of consumers are ready to buy, at a relatively higher price, certified meat that promises consistent quality with an indication of its origin.

The major challenge facing livestock industries today is thus the production of healthy and high quality meat products. During the last two decades, we have gained substantial knowledge in the regulation of growth processes and ontogenesis of muscle characteristics. This new information enables scientists to consider various nutritional and genetic means to improve growth rate or meat quality traits. In North America, the means that are suggested are, for instance, the use of metabolic modifiers (Dikeman 2000) and genome modifications (Wells 2000). However, among the metabolic modifiers, some are already approved for use such as antibiotics or anabolic steroids (the latter being approved in the US, but not in Europe) or only suggested such as somatotrophin. In Europe, it is much more difficult to gain acceptance by the general public of metabolic modifiers and of biotechnology. Indeed, Europeans consumers are much more concerned about natural feeding of the animals, the reduction of environmental pollution, animal welfare, human heath, etc.

From this review, it appears that the recent advances in muscle biology may be helpful to control tissue characteristics in a way satisfactory for the European consumers. From this new basic knowledge, the selection of young bulls on the basis of quality traits, the promotion of pasture–based systems, or even control of the dam's nutrition during foetal life are 'natural' ways to improve meat quality. Indeed, these strategies do not include any genetic manipulation, nor imply any 'artificial' feeding of the animals. However, many of the differences in both animal performance and meat quality are the consequences of very small, but cumulative, changes in muscle physiology that often fall within the variance of the current biochemical methodology. This is especially the case with meat tenderness and flavour, which both result from the combination of a great number of muscle traits (post–mortem pH, protease activities, collagen and fibre characteristics for tenderness).

From this review, it is also clear that current data may be ambiguous or contradictory, or that some questions are partially or totally unanswered, due to the multi–factorial control of meat quality or due to the inaccuracy of the available methods. Consequently it might be expected that the new technologies available (proteomic analysis, DNA chips) will increase the efficiency of the scientific tools and will provide new concepts in animal science. Again, this must be accomplished without manipulation of the genome, by studying the natural variability of the genome expression under breeding conditions.

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