MUSCLE FIBRE TYPE AND MEAT QUALITY

R. E. KLONT, G. EIKELENBOOM & L. BROCKS.

Institute for Animal Science and Health (ID-DLO), P.O. Box 65, Lelystad, The Netherlands.

ABSTRACT

Muscle morphology and fibre type composition are briefly reviewed in relation to colour stability and tenderness in beef, and water holding capacity, colour and eating quality in pork. A large inter-muscle and inter-animal variation exists in meat quality, which is often related to metabolic and contractile properties as determined by their muscle fibre type distribution. Characteristics of different muscles may be modified in living animals by environmental conditions and genetic selection. Selection experiments based on biochemical and histochemical characteristics determined in biopsies or otherwise, and study of correlated selection responses, may lead to the development and applications of (new) muscle traits in future breeding programmes.

INTRODUCTION

There is a large individual variation in meat quality both within and between animals of the same breed, sex and environment, which is not well understood (Lawrie, 1985). This variation is likely to be caused by differences in various known and unknown intrinsic (genetic) and extrinsic (environmental) factors, which interact and determine the outcome of metabolic processes in the peri- and postmortem period.

Muscle fibre type composition, fibre areas and the capillary density of specific muscles are important factors influencing many of the peri- and postmortal bio-chemical processes and thereby meat quality. A characteristic of skeletal muscle is its diversity, consisting of different kinds of fibres which moreover, vary within themselves (Pette and Staron, 1990). There are marked differences in fibre type composition of different muscles, both within and between animals, which may influence meat quality and depend on factors such as body location, age, weight, and breed (Cassens and Cooper, 1971; Essén-Gustavsson, 1995).

The purpose of this paper is to briefly review the relationship between muscle fibre type composition, structure and meat quality characteristics in various meat animals, as they are influenced by certain genetic and environmental factors. It will focus on relationships with quality aspects as colour stability and tenderness in beef, and water holding capacity, colour and eating quality in pork. Also, the effect of genetic selection in pig breeding on fibre type characteristics will be discussed as well as the possibilities for future breeding strategies to modify muscle metabolic and structural characteristics with the aim of influencing meat production and its quality.

MUSCLE FIBRE TYPING

Histochemical characterization

During the last 40 years, there have been extensive studies on muscle fibre types both on the cellular and molecular level (Cassens and Cooper, 1971; Pette and Sharon, 1990). The different methods which have been used for classification of muscle fibres, have resulted in a wide spectrum of different nomenclature. Muscle fibres can be classified according to their metabolic, contractile and colour properties. For clarity, some commonly used methods are briefly mentioned here. Terms in the review will be used as they were used in the original publications.

Gauthier (1969) used a method of fibre typing based on histochemical reactions of aerobic oxidative capacity, using the reference enzyme succinate dehydrogenase (SDH). Three major fibre types were distinguished: red, intermediate and white. Basically this method reflects differences in mitochondrial content.

Another frequently used and reliable method for histochemical classification of muscle fibres is based on the difference in sensitivity of ATPase activity after exposure to either high or low pH. The conditions of this pH pre-incubation must be defined for each species. The following types can be delineated on the basis of myofibrillar ATPase (mATPase) activity after pre-incubation: I, IIA, and IIB (IIC) (Brooke and Kaiser, 1970).

Ashmore and Doerr (1971) combined the oxidative SDH staining with ATPase activity leading to three types of fibres: βR, ATPase acido-stabile and oxidative; αR, acido-labile and oxidative; αW, ATPase acido-labile and glycolytic. Combination of

the histochemical stains for the oxidative enzyme NADH tetrazolium reductase and ATPase, resulted in three major fibre types: slow-twitch oxidative (SO), fast-twitch oxidative glycolytic (FOG) and fast-twitch glycolytic (FG) (Peter et al., 1972).

The classification systems based on stains for enzymes involved in oxidative metabolism (Peter et al., 1972) and mATPase activity (Brooke and Kaiser, 1970) appear to be incompatible. The SO fibres correspond to type I, but FG and FOG fibres do not fully match fibre types IIA, IIB or IIC (Pette and Staron, 1990). Essén-Gustavsson and Lindholm (1984) classified various pig muscles according to ATPase (I, IIA and IIB) and NADH tetrazolium reductase. They found that 15-20 % of type IIB fibres in M. longissimus stained medium for NADH-tetrazolium reductase. Similar results have been found by Fernandez et al. (1995) who used ATPase and SDH staining methods and showed that 7% of the type IIB fibres in longissimus lumborum muscle stained positively for SDH and would thus be classified as αR fibre types in Ashmore and Doerr's classification.

More recently immuno-histochemical studies have become available, which use poly-, and monoclonal antibodies raised against myosin preparations from muscles with a predominance of either fast or slow fibre types (Schiaffino et al.,1986, 1989; Gorza, 1990). Immuno-histochemically three fast fibre subtypes can be defined: IIA, IIX, and IIB. The acid stability of type IIX fibres is similar to type IIB and the aerobic capacity intermediate between type IIB and type IIA fibres. Part of the above mentioned incompatibility between classification systems may be explained by this subtype.

Biochemical characteristics

The variation in muscle oxidative, glycolytic and/or contractile properties can also be assessed by biochemical techniques, since the concentration, activities and/or ratios of different enzymes used for contraction and energy metabolism differ in the various types of muscle (Kiesling and Hanson, 1983; Pette and Staron, 1990). Briand et al. (1981) used ATPase, glycolytic and mitochondrial enzyme activities to classify 12 different sheep muscles into three metabolic types. Similar studies have been carried out in various muscles from beef cattle (Talmant and Monin, 1986) and pigs (Laborde et al., 1985; Monin et al., 1987).

Isolation of different heavy and light chain myosin isoforms by electrophoretic techniques is another way of muscle typing. Four different single myosin heavy chain (MHC) isoforms have been identified in ATPase based fibre types: MHCI in type I, MHCIIa in type IIA, MHCIIb in type IIB and MHCIId(x) in type IID(X) (Hämäläinen and Pette, 1995). Muscle fibres can contain either one type of MHC or various combinations of different types (Rivero et al., 1996; Rosser et al., 1996). This creates a large spectrum of different fibre types, which in combination with different myosin light chains leads to a diversity of fibre types far beyond that can be histochemically identified.

Muscle morphology and variation

An important point when analysing muscle fibre type composition of a muscle and its relation to meat quality, are the structural differences associated with different fibre types and the variation in fibre types within muscles. Most research shows an inverse relationship between fibre diameter and the oxidative capacity of muscle fibres. Type I are the smallest, type IIB fibres have the largest diameter, and IIA fibre have an intermediate size (Cassens and Cooper, 1971; Rosser et al., 1992). Moreover, type I and IIA fibres have a greater lipid and myoglobin content and more capillaries per fibre than type IIB fibres (Essén-Gustavsson et al., 1992). The combination of fibre type, size and capillarisation is important in relation to the perimortal muscle metabolism and meat quality (Cassens et al. 1976; Henckel, 1995). Capillary density is an important factor that should be focussed on in future research, since the function of muscles antemortem, depend to a large extent on the oxygen supply and the potential to remove waste products such as lactate. Assessment of capillary density does give estimates of the upper capacity for blood flow (Saltin and Gollnick, 1985).

Variation of fibre type distribution within muscles is of importance when studying fibre type composition in relation to meat quality. Muscles involved in posture are more oxidative than those involved in movements (Totland and Kryvi, 1991; Henckel, 1995). In pigs, it has been demonstrated that the deepest muscles of the limbs generally have the highest percentage of slow oxidative type I fibres, while the superficial muscles have the highest percentage of glycolytic (type IIB) fibres (Armstrong et al., 1987). Brandstetter et al. (1997) found similar results for beef semitendinosus muscle by analysing metabolic enzymes and MHC isoforms. Moreover, deep IIB fibres are more oxidative and have a smaller diameters than superficially situated type IIB fibres (Rosser et al., 1992). Variation in meat quality traits within muscles (Lundström and Malmfors, 1985) in addition to the inter-muscle differences in fibre type composition suggest that representative sampling procedures should be considered in future studies designed to study relationships between these two aspects.

BEEF QUALITY

Colour stability

There are considerable differences between species in colour stability. Atkinson and Folett (1973) found in their study on the colour stability of lamb, beef and pork, that oxygen consumption was inversely related to the rate of discolouration in various species. Beef, with the lowest oxygen consumption rate and lamb with the highest oxygen consumption rate, had the best and worst colour stability, respectively. Hood et al. (1980) concluded that muscle type is the major factor controlling the rate of discolouration of beef muscle on exposure to oxygen, accounting for almost half of the variances in colour stability. The longissimus muscle was found to be very stable and the psoas major unstable.

Similar results have been observed by Klont et al. (1998) for longissimus and psoas major muscles from veal calves differing in their preslaughter blood haemoglobin content. Colour was found to be stable and independent of haemoglobin content in the blood for the veal longissimus muscle. The psoas major muscle was less colour stable with increasing discolouration rates in muscles from calves with higher preslaughter blood haemoglobin concentrations. Both veal muscle types from calves of the low haemoglobin group tended to have more glycolytic muscle fibres compared to muscles from the high haemoglobin groups. Longissimus muscles from veal calves with low preslaughter blood haemoglobin contents also had significantly smaller muscle fibre areas than similar muscles from calves of the high blood haemoglobin groups, which did not result in different shear force measurements.

Factors influencing the rate of discolouration and accumulation of metmyoglobin in beef muscles under aerobic display are (1) the rate of oxygen diffusion and consumption, (2) the autoxidation of the pigment in the presence of oxygen, and (3) the rate of metmyoglobin reducing activity (Faustman and Cassens, 1990). Differences in oxygen consumption rate and myoglobin autoxidation rate, explained better the variation in colour stability between different muscles than the enzymic ferrimyoglobin reduction did (Renerre and Lebas, 1987). A higher proportion of type I muscle fibres will coincide with a higher concentration of mitochondria in muscles. After aerobic exposure of the meat surface, intact mitochondria might compete with myoglobin for the uptake of oxygen thereby reducing the depth of the bright-red oxymyoglobin layer (Monin and Ouali, 1992).

In practice, considerable inter-animal variation can be observed in colour stability of homologous muscles. Judged from the differences in colour stability between animal species and muscle type, these differences may, at least partly, also be related to variation in rate of oxygen consumption or other metabolic characteristics associated with their fibre type distribution.

Tenderness

Post mortem tenderisation during the ageing of beef is a variable process depending on a number of biological, as well as external factors. Of all these factors, muscle type plays a major role (Dransfield et al., 1980-81). As reviewed by Ouali (1990), the ageing rate is faster in fast twitch white muscles than in slow twitch red muscles. Three different mechanisms were suggested to explain these differences in ageing rate between different muscle types: (1) levels of proteases and inhibitors, (2) sensitivity of muscle proteins to proteolysis and (3) osmotic pressure (Ouali, 1990; Monin and Ouali, 1992). Most emphasis in recent years has been on the first aspect. The evidence suggests that calpains are primarily involved in post mortem proteolysis of myofibrillar and associated proteins (Koohmaraie, 1996).

Ouali (1990) showed that slow twitch red muscles, which exhibit the lowest ageing rate have the highest calpain content and suggested that the expression of these proteinases is muscle dependent. The same author concluded that, in order to better understand the complex process of meat ageing, studying biological and biochemical factors associated with ageing in muscles of different contractile and metabolic types might constitute a good model (Ouali, 1991).

Davis et al. (1979) found an increased tenderness with larger sarcomere lengths. Similar results were found for lamb muscles by Ceña et al. (1992) who also showed that oxidative fibres in unrestrained muscles had a more intense shortening than glycolytic fibres. Smulders et al. (1990), however, found that tenderness was completely independent of sarcomere length in rapidly glycolysing postmortem muscles. The nature of the actin/myosin cross-bridge interaction during the first 72 hours of postmortem tenderization is another major factor influencing meat tenderness according to Goll et al. (1997). This interaction will also depend on muscle fibre type and future research on this subject might further explain contradictory results in literature about the relationship between sarcomere shortening en meat tenderness.

PORK QUALITY

Water holding capacity and colour

Water holding capacity and colour are major quality characteristics for fresh pork, with pale, soft and exudative (PSE) and dark, firm and dry (DFD) being the extreme types of meat (Lawrie, 1985). In PSE meat denaturation of muscle proteins and a decrease in the electrostatic repulsion between myofilaments are caused by a combination of low pH and high muscle temperature soon after slaughter. Colour and water holding capacity of meat are related to the extent of protein denaturation and lateral shrinkage of the myofibrils and the subsequent increase in light scattering properties (Bendall and Wismer-Pedersen, 1962; Offer, 1991).

Much early work has been done on the relationship between muscle fibre type distribution and stress-susceptibility (PSS) and PSE in pigs, reviewed by Swatland (1984). One problem in evaluating these results is that the accuracy of fibre typing is rather poor by present standards, as methods for fibre typing have been considerably improved since than. The other problem is that in many breeds at that time the halothane gene was present, which may have caused considerable individual variation both in quality aspects and muscle fibre type. More recent work has shown that muscles from halothane positive pigs have an increased number of glycogen depleted type IIA and IIB-fibres at slaughter, larger mean fibre areas and a lower capillary density than non-carriers (Essén-Gustavsson et al., 1992; Fiedler et al., 1993).

Glycolytic type IIA and IIB fibres in rest have a higher glycogen concentration and are metabolically better equipped for anaerobic glycogen utilization than type I fibres. In general, glycolysis and onset of rigor mortis are faster in white than in red muscles. However, variation in temperature conditions due to the muscle location in the carcass, may hide this relationship in practice (Monin and Ouali, 1992). Ultimate pH is positively related to oxidative capacity and the area of slow oxidative fibres (Maltin et al., 1997). Due to the non-linear relationship between glycogen content and ultimate pH (Fernandez and Tornberg, 1991), the latter is also more variable in muscles with a higher oxidative capacity. This is also true for the occurrence of DFD meat. Nevertheless, most studies dealing with meat quality aspects seem to focus on the LD muscle, which has a high glycolytic capacity. Variation in meat quality is also related to heterogeneity in glycogen depletion between different fibre types. Karlsson et al. (1993) showed that pigs free of the halothane gene had low glycogen levels in type I and IIA fibres of the M. Longissimus dorsi, while a greater variation in glycogen content existed in type IIB fibres. Moreover, muscle samples with more than 30% depleted IIB fibres tended to have meat with more DFD characteristics. Fernandez et al. (1994) showed that preslaughter agonistic behaviour between pigs primarily resulted in glycogen depletion of fast-twitch muscle fibres. Fasting-induced glycogen depletion was shown to be both muscle-type and fibre-type-dependent (Wittmann et al., 1994). The extent of glycogen depletion after 24 hours fasting is higher in semispinalis than in longissimus muscles. Within semispinalis muscles the oxidative βR-fibres were almost depleted after 24 hours fasting, while in longissimus muscles only fast twitch fibres showed a significant decrease in glycogen. These results show that variation in meat quality is not only caused by a variation in muscle fibre type composition, but also by its interaction with preslaughter stress conditions. This is of interest for future research.

Eating quality

There have been numerous studies comparing sensory characteristics of different pigs breeds. The intramuscular fat (IMF) content is an important factor that influences sensory quality. However, the observed beneficial effects depend on the breed studied (Fjelkner-Modig and Tornberg, 1986; Cameron et al., 1990). Lipids are mainly stored in type I and some IIA fibres (Essén-Gustavsson et al., 1994). However, Henckel et al. (1997) found that the IMF content was positively correlated with the frequency of type IIB fibres. Essén-Gustavsson and Fjelkner-Modig (1985) concluded that meat tenderness is related to the metabolic muscle profile. Hampshire pigs were shown to have a higher oxidative capacity, and greater storage of both triglycerides and glycogen compared to Yorkshire pigs, with Swedish Landrace pigs having intermediate values. Ruusunen and Puolanne (1997) found similar results including a higher capillary density for the Hampshire breed and stated that the variation in muscle fibre composition in pigs within breeds was larger than the average variation between breeds. Larzul et al. (1997) did not find any relationship between IMF content and fibre type numerical percentages at a commercial slaughter weight of purebred Large White pigs and suggested that both traits can be manipulated separately.

Maltin et al. (1997) recently compared LD muscle fibre characteristics of pigs from eight different breeding populations in relation to the variation in eating quality. They found that the fibre diameter of fast twitch oxidative glycolytic fibres significantly contributed to the variation in instrumentally determined meat tenderness. Karlsson et al. (1993) found a negative correlation between the proportion of fast twitch (type IIB) fibres and shear force value in the LD muscles from halothane gene free Yorkshire pigs fed on a low protein diet.

Effects of selection in pig breeding

Muscle fibre type composition and structure is genetically defined and can to some extent be influenced by environmental factors, such as physical activity and housing systems (Petersen et al., 1997; Stecchini et al., 1990), nutrition (Karlsson et al., 1994), climatic circumstances (Herpin and Lefaucheur, 1992), and administration of specific growth promoting agents (Oksbjerg et al., 1994; Rehfeldt and Ender; 1993; Solomon et al., 1994).

Results from a large study carried out in The Netherlands investigating the relationships between production and meat quality traits in 7 halothane-gene free Yorkshire populations showed that there were no unfavourable genetic correlations between colour and water holding capacity with carcass leanness and growth rate (De Vries et al., 1994). Increased daily feed intake, however, was associated with a darker colour and higher water holding capacity. It was postulated that this might be due to a variation in energetic needs due to a variation in muscle fibre type distribution, with a higher proportion of oxidative muscle fibres. Henckel et al. (1997) found a negative correlation between feed conversion and the cross sectional area of type I fibres, while a positive correlation existed between muscle gain and both the activity of the oxidative enzyme citrate synthetase and the number of capillaries per fibre.

Intensive selection for lean muscle growth in pigs may have caused a large genetic change in fibre type composition, which resulted in a higher proportion of glycolytic fibres and an increase in the mean fibre diameter in domestic pigs compared to more native breeds (Rahelic and Puac, 1981; Weiler et al., 1995). Petersen et al. (1997) compared the muscle properties of two groups of Danish Landrace pigs known to differ in their growth potential after 20 years of genetic selection for growth performance and carcass traits in one of the groups. The selected pigs reached slaughter weight 25 days earlier than the non-selected pigs, and had a lower pigment content leading to paler and less red meat, which had a lower panel tenderness score. Selection had indeed caused a significantly lower proportion of type I fibres, but did surprisingly not result in a larger mean fibre area. Karlsson et al. (1993) did not find marked changes in muscle fibre composition of different muscles from Swedish Yorkshire pigs selected for lean tissue growth after 2 and 4 generations of selection for increased lean tissue growth rate. Brocks et al. (1998) compared muscle properties from second and fourth generation Large White pigs selected for either lean or fast growth rate. Their results suggested that selection for lean growth generally results in a lower frequency oxidative and more glycolytic fibres in comparison with selection for fast growth, while no selection effects were observed for mean fibre areas. The magnitude of the effects in their study depended on muscle type and the location within a muscle.

Selection possibilities have been suggested on the basis of different muscle properties in order to improve i.e. the oxidative capacity of muscles (Von Lengerkerken et al., 1994; Maltin et al., 1997). Henckel et al. (1997) found significant correlations between histochemical and biochemical muscle traits measured in biopsy samples taken at 65-70 kg live weight and meat quality characteristics after slaughter at 100 kg. They concluded that there were significant correlations between these traits, which might be improved by measuring muscle metabolic profiles closer to the day of slaughter. Larzul et al. (1997) studied phenotypic and genetic correlations of longissimus muscle fibre characteristics in Large White pigs and concluded that these traits have medium heritability and significant genetic correlations with meat quality characteristics. Furthermore their results suggested that it should be possible to include muscle fibre traits in breeding for improved meat quality, while preserving growth performance. In order to use muscle fibre characteristics in a beneficial way for future breeding programmes, further investigations are needed to better understand the physiological mechanisms and to explain the sometimes controversial results found in different selection studies. This also requires more studies defining predictor muscles, optimal sampling locations, and more rapid and less expensive methods of muscle fibre type determination.

CONCLUSIONS

• 1. Considerable variation in meat quality characteristics between various muscles within a carcass exists. This inter-muscle variation is often directly related to the metabolic and contractile properties, as determined by their muscle fibre type distribution.

• 2. There is a large inter-animal variation in meat quality of homologous muscles, which can often be explained insufficiently. Studies directed towards this aspect can undoubtedly benefit from the results obtained on inter-muscle variation in meat quality, fibre type characteristics and their inter-relationships.

• 3. Muscle metabolic and contractile types are adaptable and may be modified in living animals by environmental conditions and by genetic selection. Environmental effects are probably particularly important in cattle, due to the large variation in production methods. In pork, the interactions between preslaughter treatments and both muscle- and fibre types are likely to cause variation in meat quality that deserves more attention in future research.

• 4. Studies have been conducted regarding the effect of breed and genetic selection for production traits, on fibre type composition and pork quality. In general, the current evidence suggests such an influence to exist, although the results are variable.

and often contradictory. Selection experiments based on biochemical and histochemical characteristics determined in biopsies or otherwise and study of the correlated selection responses, may possibly provide better tools to study these relationships. Such experiments may ultimately lead to the development and applications of new muscle traits in future breeding programmes, provided that the associated scientific and practical problems are solved.

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