MUSCLE FIBRE TYPES AND THEIR RELATION TO MEAT QUALITY TRAITS IN PIGS*

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The authors have been studying various characteristics of muscle fibres and their relationship to the meat quality parameters for many years. However, the conclusions drawn by researchers often differ. A higher proportion of glycolytic IIB fibres in pig muscles is usually related to paler meat with lower water holding capacity. On the other hand the relationship between muscle fibres and meat texture parameters is not clear. Studies using immunohistochemistry methods that allow a more detailed classification of individual muscle fibre types could bring new findings in this area. It would thus be possible to influence muscle fibre type composition in the muscle to achieve the desired meat quality using various extrinsic and intrinsic factors. The main aim of this review is to summarise current knowledge on the description of muscle fibres typology and the effect of their morphological traits on pork meat quality.

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INTRODUCTION

Meat is primarily composed of skeletal muscle; the heterogeneous tissue consisting of connective and adipose tissue, and a large number of muscle fibres of different types. Muscle fibre is a multinucleate cell with 10–100 μm in diameter and length varying from several millimetres to more than 30 cm (Choi, Kim, 2009). During embryogenesis, the myogenic precursor cells of mesodermal origin differentiate into myoblasts that subsequently differentiate into individual muscle fibres. During myogenesis, muscle fibres develop from two distinct populations. The fibres that arise during the initial stage of myoblast fusion are primary myofibres and serve as a basis for a larger population of smaller secondary fibres (Wigmore, Evans, 2002). These secondary fibres can be observed in pigs around the 54th day of prenatal development (Wigmore, Stickland, 1983). Another population of myoblasts remains undifferentiated and forms so-called satellite cells that are able to divide, fuse and differentiate into new muscle fibres during postnatal growth. Nevertheless, postnatal muscle growth and enlargement mainly result from increased cell size (i.e. muscle hypertrophy). This process is accompanied by the proliferative activity of satellite cells, which are supposed to be important for incorporation of new nuclei into existing muscle fibres (Rehfeldt et al., 2004). Individual types of muscle fibres differ in their molecular, metabolic

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and structural properties, which are the main factors affecting *post-mortem* energy metabolism and thus also the ultimate meat quality (Choi, Kim, 2009).

Classification of muscle fibres

The morphological properties of muscle fibres can be described using various histochemical methods. Although basic staining methods, such as hematoxylin and eosin staining, do not allow to distinguish individual muscle fibre types, they can be applied to stain specific tissue areas for subsequent histochemical or immunohistochemical (IHC) analyses (Peinado et al., 2004; Francisco et al. 2011). They can also be used to determine other morphology traits such as total number of fibres in the muscle or fibre density.

In order to distinguish muscle fibre types to red (type I) and white (type II), the histochemical method using Sudan dyes (e.g. Sudan Black B, Oil Red O) has been widely used. Most existing histochemical methods for distinguishing different types of fibres are based on differences in the enzyme activity and chemical composition of fibres (Dux et al., 1981). The Sudan stains are able to distinguish a muscle fibre type according to the amount and composition of lipids (Karlsson et al., 1999; Culling, 2013; Prats et al., 2013).

Three types of muscle fibres (red, white, and intermediate) were distinguished by Gauthier (1969) on the basis of histochemical reaction for enzymes of aerobic oxidative capacity, using the succinate dehydrogenase (SDH). This method is based on differences in these enzyme activities and reflect mitochondrial content (high, intermediate, low) of individual fibre types (Klont et al., 1998).

According to Brooke, Kaiser (1970), histochemical method of fibre typing is based upon myofibrillar actomyosin adenosine triphosphatase (ATPase) activity in an acidic or alkaline environment and correlates with contractile properties of individual muscle fibres (Pette, Staron, 2000). More detailed study using this method led to the description of muscle fibre types I, IIA, IIB, and minor group IIC. Type I fibres are red with slow contraction, have more myoglobin, mitochondria and lipids, they are surrounded by extensive capillaries and contain less glycogen. Their metabolism is oxidative and they are most resistant to fatigue. Type IIB fibres (white) have completely opposite traits. They are fast-twitch, with less mitochondria, lower content of lipids, blood vessels and glycogen and thus, fatigue quickly. Type IIA fibres are the transition between the types I and IIB. They have intermediate numbers of mitochondria and blood-carrying myoglobin, and their oxidative potential improves their resistance to fatigue (Choi, Kim, 2009). Type IIC fibres are considered as transitional to types I and II and can be observed in newborns, bodybuilders, and during muscle recovery (Pette, Staron, 1990; Karlsson et al., 1999). As a complementary reaction, the PAS (periodic acid-Schiff) method for detecting tissue polysaccharides (e.g. glycogen contained in muscle fibres) was used in the study of Brooke, Kaiser (1970). This histochemical staining method is able to detect the metabolic features of the predominant type of muscle fibre.

The combination of SDH staining and myosin ATPase activity was used by Ashmore, Doerr (1971) to determine the muscle fibres. Three types of muscle fibres were determined as follows: βR – ATPase acido-stabile and oxidative; αR – acido-labile and oxidative; and αW – acido-labile and glycolytic (Klont et al., 1998).

In addition to the ATPase staining method, the technique of NADH-TR (nicotinamide adenine dinucleotide tetrazolium reductase) was performed by Peter et al. (1972) to distinguish different types of muscle fibres. Based on the contraction speed and metabolism capacities, three major fibre types have been classified into SO (slow-twitch oxidative fibre), FOG (fast-twitch oxidative-glycolytic fibre), FG (fast-twitch glycolytic fibre).

According to Larzul et al. (1997), myofibres can be classified as oxidative types I, IIA, and moderately oxidative (IIBr) or not oxidative (IIBw) types of IIB as a result of SDH and ATPase staining. According to Ashmore, Doerr (1971), types IIA and IIBr fibres correspond with αR fibres whereas I and IIBw fibre types correspond with βR and αW types, respectively.

However, these classification systems appear to be incompatible for comparison of individual fibre types. Additional procedures for fibre classification based on IHC or immunofluorescence analysis allow improved staining and thus more precise and detailed classification of muscle fibres. The molecular basis of this typology resides in polymorphism of the myosin heavy chains (MyHC) – the most abundant protein expressed in skeletal muscle, comprising about 35% of the protein pool (Lefaucheur, 2010). Each isoform is encoded by a single gene (Weiss et al., 1999).

Skeletal muscles of different mammalian species contain four major MyHC: I, IIa, IIx and IIb. Despite the presence of the *MyHC-IIb* gene (*MYH4*) in all mammals, the type IIb MyHC isoform was originally found only in small mammals such as mouse, rat or rabbit, and reported to be unexpressed in skeletal muscles of large mammals (Lefaucheur, 2010). However, more recent studies demonstrated that the IIb MyHC isoform was highly expressed in glycolytic muscles of pigs and llamas (Graziotti et al., 2001; Chang et al., 2003).

To distinguish pure and hybrid (co-expression of two or more MyHC isoforms) types of muscle fibres, IHC methods use the specificity of monoclonal antibodies against individual MyHC isoforms (Kim et al., 2014). Muscle fibre classification using IHC methods appears

Table 1. Muscle fibre area composition in the *longissimus dorsi* muscle of pigs depending on the classification method

Nomenclature/ staining method	Author	Muscle fibre type (%)					
Peter et al., 1972	Maltin et al., 1997	**SO** 4.65–15.3		**FOG** 20.3–39.6		**FG** 53.7–73.6	
Ashmore, Doerr, 1971	Candek-Potokar et al., 1999	**βR** 10.4–11.9		**αR** 9.9–10.5		**αW** 77.7–79.7	
Brooke, Kaiser, 1970	Ruusunen, Puolanne, 2004	**I** 6.5–13.0		**IIA** 3.2–17.3		**IIB** 69.7–90.3	
	Ryu et al., 2008	**I** 5.4–7.5		**IIA** 5.6–7.1		**IIB** 85.1–88.2	
Larzul et al., 1997 ATPase/SDH	Larzul et al., 1997	**I** 6.5		**IIA** 3.5	**IIBr** 7.5		**IIBw** 82.5
IHC	Chang et al., 2003	**I** 10.6–15.4		**IIa** 3.5–6.2	**IIx** 28.7–35.5		**IIb** 48.6–54.4
	Fazarinc et al., 2013	**I** 10.8–17.0		**IIa** 11.5–26.3	**IIx/b** 15.7–31.0		**IIb** 25.7–62.0
	Kim et al., 2014	**I** 8.6–14.5	**IIA** 5.7–9.4	**IIAX** 1.7–5.5	**IIX** 17.2–21.8	**IIXB** 2.9–11.9	**IIB** 54.7–62.8

ATPase = adenosine triphosphatase, SDH = succinate dehydrogenase, IHC = immunohistochemistry

to be a suitable method, especially for the assessment of fibres in the pig muscle. The *musculus longissimus dorsi*, which is used in a number of studies as a reference muscle, has very high proportion of glycolytic fibres, which constitute as much as 90% of the total fibre surface (Ruusunen, Puolanne, 2004; Choe et al., 2008). On the other hand, low amounts of type I and IIA fibres do not influence the quality parameters of pork meat. Pig muscles contain all four types of MyHC isoforms (Realini et al., 2013; Kim et al., 2014), whereas MyHC-IIb expression in cattle was described only in the extraocular muscles (Toniolo et al., 2005), and in the *semitendinosus* and *longissimus dorsi* muscles of the Blonde d'Aquitaine breed (Picard, Cassar-Malek, 2009). Kim et al. (2014) classified a total of six fibre types, including four pure types (I, IIA, IIX, IIB) and two hybrid types (IIAX and IIXB) according to the expression of MyHC isoforms in the pigs' *longissimus dorsi* muscle. The distribution of individual fibre types in *longissimus dorsi* muscle of pigs according to various classification methods is shown in Table 1. The main advantages of IHC methods are the identification of hybrid fibres and distinguishing of immature and regenerating myofibres from adult ones. In addition, these methods also provide more accurate results in *post-mortem* samples with reduced ATPase enzyme activity, which is crucial for some above-mentioned classification techniques (Pette, Staron, 2000).

Muscle fibres and pork quality

Meat quality parameters are most often associated with the properties of muscle fibres, such as the total number of fibres, cross-section area of fibres and fibre type composition (% of area or number) in muscle (Ruusunen, Puolanne, 1997; Choe et al., 2008; Joo et al., 2013; Choi, Oh, 2016).

The decisive qualitative factor of meat that affects consumers' purchase decision is its colour (Su et al., 2013). The differences in the colour of meat are due to a different myoglobin content. Higher concentrations of myoglobin and, therefore, reddish colour have muscles with higher levels of red fibres of type I and IIA (Listrat et al., 2016). For instance, a high proportion of fibre types I and IIA is found in the muscles *masseter, trapezius*, *triceps brachii*, *infraspinatus*, in the red part of the *semitendinosus* muscle, and *psoas major*. On the contrary, the higher proportion of IIB fibres is in the muscles *longissimus dorsi*, *gluteus medius, biceps femoris*, *quadriceps femoris,* and *semimembranosus* (Horak, 1988; Karlsson et al., 1999; Kirchofer et al., 2002; Ruusunen, Puolanne, 2004; Bee et al., 2007; Realini et al., 2013). Generally, the deep muscles involved in maintaining the body position are more oxidative and contain more fibres of type I. On the other hand, the muscles placed more on the surface, used for fast movements, contain more fibres of type IIB (Joo et al., 2013). Realini et al. (2013) observed a significantly lighter (L^*) and less red (a^*) colour of the *longissimus dorsi* muscle and the light part of the *semitendinosus* muscle compared to the *masseter* and the dark part of the *semitendinosus* muscle, which contain a higher proportion of type I fibres. Also Chang et al. (2003) observed darker and redder colour of the *psoas major* muscle compared to the *longissimus dorsi* muscle where they found higher proportion of MyHC IIB fibres.

During meat storage, myoglobin can be oxidized into metmyoglobin, which produces a brown, unattractive colour (Listrat et al., 2016). Faster colour change during storage affects the muscles with the

predominance of red – oxidative fibres due to faster oxygen consumption (Joo et al, 2013). These fibres, compared to fibres of type IIB, also contain more blood capillaries, of which the higher density also causes a darker colour of the meat (Su et al., 2013). The darker colour of pork meat in connection with the higher proportion of type I fibres, i.e. the negative correlation between the lightness of meat and the presence of type I fibres, was determined by Ryu, Kim (2005), Kim et al. (2014) or by Lee et al. (2016). Kim et al. (2014) also observed hybrid fibres of type IIAX and IIXB. Between meat lightness and concentration of IIAX fibres they observed significant negative correlations, the same like in the case of type I and IIA fibres. For IIXB fibres, this correlation was positive. Ryu, Kim (2005) and Lee et al. (2016) classified muscle fibres using the method of Brooke, Kaiser (1970) and established a positive correlation between the presence of type IIB fibres and the meat lightness. Meat colour can be affected not only by the fibres concentration but also their size. Kim et al. (2013a) found that pigs with a higher proportion of large type IIB fibres had a lighter colour compared to animals with a higher proportion of small or normal sized fibres.

There is a higher fibre content of the type IIB in pork meat associated not only with lighter colour but also with a lower water holding capacity (WHC), which is one of the most important quality parameters of pork meat (Su et al., 2013). The WHC is strongly influenced by the rate and extent of decrease in the *post-mortem* pH. A high rate combined with a high muscle temperature causes denaturation of muscle proteins, reduced WHC and increased drip loss and cooking loss of meat (Listrat et al., 2016). Glycolysis metabolism predominates in muscle fibres of type IIB, which contributes to a rapid decrease in pH values in the early *post-mortem* stage. This is especially the problem of pork meat, which, compared to beef or lamb meat, contains a higher proportion of type IIB muscle fibres. Water on the surface of this meat also reflects the light, causing a lighter colour of the meat itself (Joo et al., 2013). Realini et al. (2013) determined lower pH values in the *longissimus dorsi* muscle and the peripheral area of *semitendinosus* muscle compared to the *musculus masseter* and the middle part of the *semitendinosus* muscle, which contains a significantly higher proportion of type I and IIA fibres. Ryu et al. (2006) observed that pigs with a higher proportion of type IIB fibres had a lower pH value and a higher drip loss compared to pigs with a lower proportion of these fibres. Similarly, Lee et al. (2016) stated positive correlation coefficients between the concentration of type IIB fibres and drip loss. They have found a negative correlation between fibres of type I, IIA and drip loss. Kim et al. (2014) found a negative correlation between drip loss and the presence of type I, IIA, IIX, and IIAX fibres. For the fibres of types IIB and IIXB, the correlation was positive. Furthermore, they determined significant negative correlation coefficients between the area of fibres of type I, IIA and IIX and drip loss. Similar results were found for the cooking loss. Kim et al. (2013a) discovered that pigs with higher concentration of large fibres had lighter, tougher and more exudative meat than the groups of pigs with a higher proportion of small- or normal-sized IIB fibres.

Toughness or tenderness is another qualitative parameter of meat. The tenderness of meat depends on the composition of muscle fibres, on the amount and solubility of the connective tissue and the stage of *post-mortem* changes (Joo et al., 2013). Post-mortem aging is faster in muscles with higher concentration of glycolytic (IIB) fibres (Ouali, 1990). However, the influence of muscle fibre traits on meat tenderness is still relatively unclear. Tenderness of meat is negatively affected by the amount of collagen, which increases meat toughness. Muscles with predominance of slow-twitch red fibres of type I contain larger amounts of collagen than the muscles with predominance of white fibres of type IIB (Kovanen et al., 1984), thus a higher content of type I fibres may seem inappropriate for meat tenderness.

The intramuscular fat (IMF) content also affects tenderness and other sensory properties of meat, such as palatability or juiciness (Choi, Kim, 2009). IMF positively correlates with the presence of red fibres of type I in beef meat (Calkins et al., 1981; Choi, Kim, 2009; Hwang et al., 2010). Likewise, Wojtysiak, Poltowicz (2014) observed a higher IMF content, better chewiness and lower shear force (Warner-Bratzler shear force – WBSF) in pigs, which had a higher proportion of type I fibres. Similarly, Realini et al. (2013) observed a higher fat content in the *masseter* muscle, which also contains more fibres of type I and IIA than the *longissimus dorsi* muscle in pigs. On the contrary, Kim et al. (2013b) found a positive correlation between the IMF content and the presence of type IIB fibres in the *longissimus dorsi* muscle in pigs. They determined a negative correlation between WBSF and the concentration of type IIB fibres, however the value was not statistically conclusive. Kim et al. (2014) also did not provide any statistically significant correlation coefficients between muscle fibre composition and WBSF, however the trend was completely opposite in their study. Higher levels of type IIB fibres showed a higher WBSF, on the contrary, a higher percentage of type I fibres showed lower WBSF. These results might be influenced by the IHC classification method, which allows the splitting of fibre types determined by conventional methods such as IIB to type IIX, IIXB and IIB, in this study. Furthermore, the authors evaluated muscle fibres in four groups of meat with abnormal post-mortem changes (meat abnormalities DFD - dark, firm, dry; PSE - pale, soft, exudative; RFN - reddish pink, firm,

nonexudative and RSE - reddish pink, soft, exudative), it also could influenced these results. Kim et al. (2013a) found that pigs with a higher level of large-sized IIB fibres had the highest WBSF and the lowest IMF content. Conversely, according to Larzul et al. (1997) the IMF content positively correlates with the fibre area in pork meat. Moreover, this statement is confirmed by other authors in selected fibre types (Kim et al., 2013b, 2014). Lefaucheur (2010) stated that there is no universal relationship between muscle fibre composition and IMF content in meat and assumes that both these traits are rather independent.

CONCLUSION

The effect of various histochemical characteristics of muscle fibres on the meat qualitative parameters has been confirmed in a number of studies. Nevertheless, the relationship between some quality traits (e.g. textural parameters) and muscle fibre characteristics remains unclear. Further studies on the effect of muscle fibres classified by IHC methods on meat quality could contribute to clarifying these relationships that would subsequently allow us to use various means to influence the composition and structure of muscle fibres to achieve the desired meat quality.

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