

EXPRESSION OF MYOSIN HEAVY CHAIN ISOFORMS IN LONGISSIMUS MUSCLE OF DOMESTIC AND WILD PIG

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Summary: The expression of myosin heavy chain (MyHC) isoforms in the myofibers of domestic and wild pig was studied to characterize muscle tissue differences related to species domestication and selection. Muscle samples were obtained from longissimus muscle of five two years old wild and domestic Large White pigs. Four different MyHC isoforms (MyHC-I, MyHC-IIa, MyHC-IIb, MyHC-IIx) were determined in the myofibers of both, domestic and wild pig, and allowed the distinction of I, IIa, IIx/b and IIb myofiber types. Oxidative types I and IIa and type IIx/b myofibers were notably more abundant in longissimus muscle of wild than domestic pig. On the contrary, the number of glycolytic IIb myofibers prevailed in domestic pig. The cross sectional areas (CSA) of different MyHC myofiber types were 2 to 3 times smaller in wild than in domestic pig. In wild pig, CSA was more homogeneous between myofiber types with no difference between CSA of types I, IIx/b and IIb myofibers, whereas IIx/b and IIb myofibers exhibited greater CSA in domestic pigs. Type IIa myofibers were the smallest ones in both, domestic and wild pig. The presence of MyHC-IIb isoform was clearly established in the myofibers of wild pigs denoting that its expression is not just the result of the intensive selection for growth efficiency and muscularity. On the other hand, it is evident that domestication and breeding goals in pigs resulted in the hypertrophy of all myofiber types, in particular of those in which MyHC-IIb isoform is expressed.

Key words: myosin heavy chains; myofiber; immunohistochemistry; domestic pig; wild pig

Introduction

Skeletal muscles of mammals are composed of heterogeneous myofibers, in which distinct sets of structural proteins and metabolic enzymes are expressed. Such heterogeneity of skeletal muscles is related to the diversity of myofibrillar proteins, in particular myosin heavy chains (MyHC). In mammalian skeletal muscles up to 9 MyHC isoforms have been identified, each encoded by a distinct MyHC gene (1). Some of them are expressed transitorily during development or only in some functionally specialized muscles (2).

In the adult mammalian locomotor skeletal muscles four MyHC isoforms have been described: one slow (MyHC-I) and three fast isoforms (MyHC-IIa, MyHC-IIx and MyHC-IIb). Studies on isolated myofibers in rodents showed that the maximal shortening velocity increased in the following pattern: I<IIa<IIx<IIb (3). Slow twitch type I myofibers consisting of predominantly of MyHC-I isoform exhibit a sustained, tonic contractile motor activity, whereas type II myofibers consisting of fast MyHC isoforms are recruited by acute motor neuron activity (4). The activities of metabolic enzymes generally match the energetic demands of each MyHC. Type I myofibers have greater oxidative capacity to support sustained contraction, type IIb myofibers are predominantly glycolytic and use

glycogen for short bursts of activity, whereas Ila and IIX myofibers are intermediate to I and IIb myofibers (1). In agreement with a predominant oxidative metabolism, type I and Ila myofibers contain also a lot of myoglobin, mitochondria, and phospholipids, contrary to glycolytic IIb myofibers (5).

The expression of the fast MyHC isoforms seems to be species specific. In fast-twitch myofibers of small mammals (rodents and lagomorphs) all three fast MyHC isoforms (-IIa, -IIb, -IIX) are expressed (6). On the contrary, only two isoforms (-IIa and -IIX) were demonstrated in the locomotor skeletal muscles of humans (7, 8), some large animals like cats (9), dogs (10), cattle (11), goats (12), horses (13) and bear (14).

With the exception of lama, the domestic pig is the only large mammal in which all three fast MyHC isoforms (-IIa, -IIX, -IIb) have been demonstrated up to now. The MyHC-IIb positive myofibers are numerous especially in the so called white muscles in the peripheral region of the muscle fasciculi (15, 16). The reasons for the high expression of MyHC-IIb isoform in domestic pig muscles are not known. Domestic pig is a meat producing species, which has been intensively selected for growth rate and muscularity. Thus, it has been suggested that high MyHC-IIb isoform expression is related to genetic improvement and breeding conditions (17). Several studies compared muscle characteristics of wild and domestic pig, which demonstrated a large increase in the size of the myofibers and a switch in myofiber type composition towards the fast-twitch glycolytic character in the modern breeds of domestic pig (18, 19). Most of these studies were based on the histochemical classification of myofibers according to the myosin ATPase reaction and metabolic enzyme activities such as succinate dehydrogenase (SDH) and α -glycerophosphate dehydrogenase (α -GPDH) activities. However, the staining pattern of the myosin ATPase is ambiguous due to its pH sensibility and can lead to the misclassification of the myofiber types (20). Furthermore, hardly any evidence is available about the immunohistochemical expression of MyHC isoforms in muscles of wild pig. Therefore, the main objective of this study was to examine the myofiber profiles based on the expression of MyHC isoforms in the muscle of adult sows of the Large White breed as compared to wild pig in order to improve the understanding of the effect of genetic progress in pig breeding on myofiber type

composition. We focused on longissimus muscle, which is a typical fast-twitch glycolytic muscle. This muscle is of particular interest, because it is used as an indicator of muscular development in breeding programs for pigs. Moreover, a condition related to low meat quality also known as pale, soft and exudative (PSE) meat occurs mainly in muscles with predominantly glycolytic metabolism.

Materials and methods

Muscle samples

Muscle samples were obtained from five two years old sows of Large White breed (carcass weight between 185 and 200 kg) and approximately two years old sows of wild pig (carcass weight between 46 and 60 kg). All five wild pigs were shot in the same season on the basis of the regular annual bag. Approximately one cubic centimetre of muscle samples were taken from the central part of the longissimus muscle (at the level of the last rib) within 24 hour *post-mortem* in both wild and domestic pigs. Samples were frozen in liquid nitrogen and stored at -80°C . Transverse serial cryosections (10 μm) of muscle tissue were cut with Leica CM 1800 cryostat at -17°C , mounted on APES-covered slides and air-dried.

Enzyme-immunohistochemistry

To show MyHC isoforms expression, four monoclonal antibodies specific for MyHC isoforms were used: NLC-MHCs (Novocastra laboratories, Newcastle on Tyne, UK) reactive with slow-twitch MyHC-I, antibody SC-71 specific for MyHC-IIa of rat, BF-F3 specific MyHC-IIb of rat and BF-35 specific for all MyHC isoforms except -IIX of rat. SC-71, BF-F3 and BF-35 antibodies were purchased from The Developmental Studies Hybridoma Bank, University of Iowa. Serial muscle cryosections were incubated with primary antibody in a humidified box overnight at 4°C . The binding of the primary antibody was detected with the peroxidase-conjugated secondary antibody and visualised by Dako REALTMDAB+Chromogen (Köbenhavn, Denmark). To determine the metabolic profile of the myofibers, activity of the mitochondrial oxidative enzyme succinate dehydrogenase (SDH) was histochemically

demonstrated according to Nachlas et al. (21). The sections were counterstained with hematoxylin, dehydrated and mounted with Synthetic Mountant (Shandon, USA).

Analysis of serial cryosections

Nikon Microphot FXA microscope (Nikon Instruments Europe B.V., Badhoevedorp, The Netherlands) and Lucia-G image analysing system (Laboratory Imaging Ltd., Prague, Czech Republic) were used to analyse the serial sections processed for immuno- and enzyme-histochemical staining. Approximately 400-500 myofibers in five randomly selected fascicles were analysed per each muscle in order to determine the pattern of MyHC expression. The selected fascicles were the same for all antibodies on serial sections. The average proportions of myofiber types were determined according to the MyHC isoform expression and cross-sectional areas (CSA) of myofiber types were established. When measuring the CSA, the attention was paid to the delimitation of myofibers on the borders of endomysium.

Data analysis

Data were submitted to one-way analysis of variance (MIXED procedure by SAS Inc., Cary, NC, USA) including fixed effect of pig genotype (wild, domestic) or myofiber type. Means were compared using Tukey's test.

Results

Using monoclonal antibodies specific to MyHC isoforms, we could demonstrate the presence of four different MyHC isoforms (Figure 1). Thus slow myofibers (type I) were reactive with NLC-MHCs antibody, and all myofibers that remained unstained were presumed to be fast type II myofibers. A certain number of type II myofibers reacted with the SC-71 antibody specific to MyHC-IIa isoform of rat. In both, domestic and wild pigs, this antibody labelled the myofibers with different staining intensities. According to Lefaucheur et al. (17), the SC-71 antibody recognizes both MyHC-IIa and MyHC-IIx in pig; however the affinity of SC-71 is higher for MyHC-IIa. Consequently strongly stained fibres were classified as type IIa myofibers, and moderately

stained ones as myofibers with prevailing MyHC-IIx isoform. Myofibers which reacted with both NLC-MHCs and SC-71 antibodies were hybrid type I/IIa myofibers, however their number was inferior to 0.5% and were thus excluded from the morphometric analysis. Antibody BF-35, which recognises all MyHC isoforms of rat, except MyHC-IIx, reacted strongly only with type I and type IIa myofibers. Indeed, it seems that BF-35 recognizes all MyHC isoforms, except MyHC-IIx and -IIb in pig skeletal muscle, likely with a higher background in domestic pig (Figure 1). The same myofibers reacted moderately or strongly with the antibody BF-F3, which is specific to MyHC-IIb isoform in pig muscles. Therefore, BF-35 negative myofibers can be divided into two subgroups: pure IIb myofibers (strongly stained with BF-F3) and hybrid IIx/b myofibers (weakly stained with BF-F3). According to the SDH staining the myofibers of wild and domestic pigs also showed different enzyme activity. Type I and IIa myofibers were intensively stained (highly oxidative) in both wild and domestic pig, whereas IIx/b myofibers were weakly stained and IIb myofibers totally negative.

The percentage (%) of oxidative type I and type IIa myofibers was significantly higher in longissimus muscle of wild than domestic pig (Table 1), whereas the proportion of glycolytic IIb fibers was higher in domestic pigs. In regard to the size of myofibers (Table 1), CSA of all myofiber types was 2 to 3 times smaller in wild than domestic pig. The CSA of myofiber types was more homogeneous in wild than domestic pigs. The myofiber hypertrophy of domestic pigs affected more type II than type I myofibers, above all the type IIb myofibers, which had the biggest CSA. Myofibers IIa were the smallest in both, domestic and wild pig.

Discussion

Distinctive differences in myofiber type composition of longissimus muscle between wild and domestic pig of modern breed have been mentioned by many authors. In a study performed by Rede et al. (22) wild pig had higher proportion of type I myofibers than domestic pig. Similar results were presented by Essén-Gustavsson and Lindholm (23), showing that muscles of wild boar had much higher oxidative metabolism than those of Landrace pigs. Szenkuti and Schlegel (24)

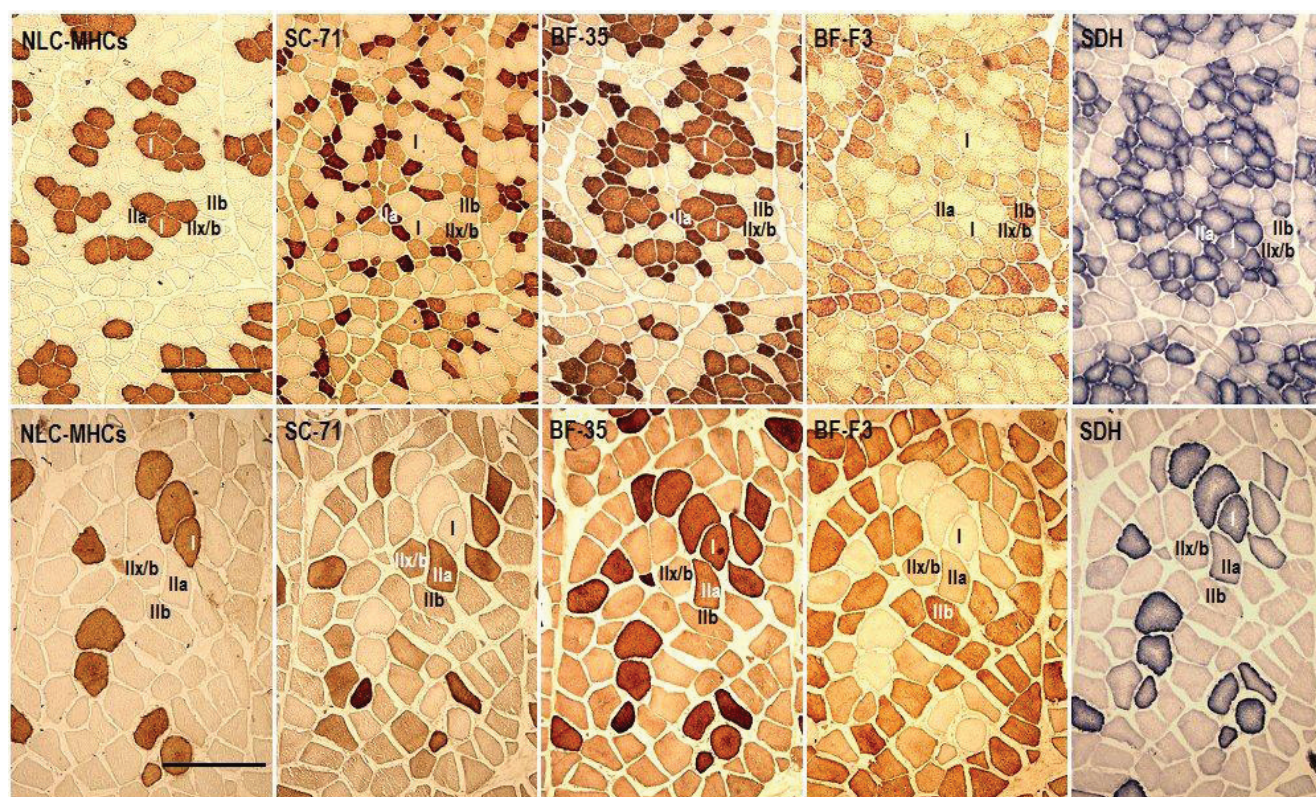


Figure 1: Antibodies reactivity and SDH activity in wild (upper row) and domestic pig (lower row). Bar = 250 μ m

Table 1: The proportion and cross sectional area (CSA) of myofiber types (based on MyHC isoforms) in the longissimus muscle of domestic and wild pigs

Item		Myofiber type			
		I	IIa	IIx/b	IIb
Proportion, %	Wild	17.0 a,y ±1.4	26.3 b,y ±1.3	31.0 b,y ±2.1	25.7 b,x ±0.8
	Domestic	10.8 a,x ±0.5	11.5 a,x ±0.5	15.7 a,x ±1.1	62.0 b,y ±1.8
CSA, μ m ²	Wild	5140 b,x ±272	3183 a,x ±191	4854 b,x ±218	5238 b,x ±1048
	Domestic	11638 b,y ±471	9231 a,y ±557	14244 c,y ±570	14827 c,y ±521

Data (mean±s.e.) measured in 2 years old wild (n=5) and domestic (n=5) pigs/sows.

Different letters (a-c) denote significant ($P<0.05$) differences between myofiber types.

Different letters (x-y) denote significant ($P<0.05$) differences between wild and domestic pigs.

suggested that myofiber composition is genetically determined by showing that despite intensive physical exercise domestic pigs exhibit higher proportion of glycolytic myofibers compared to wild pigs kept in a pen with restricted physical activity. The majority of these studies were based on myosin ATP-ase and metabolic enzyme histochemistry. Recent studies showed that the resolution of commonly used histochemical techniques is not sufficient to characterize adequately myofiber diversity. A better approach is offered by immunohistochemical techniques, although they are also limited by the antibody specificity (25).

The comparison of myosin heavy chain composition of different skeletal muscles in Large White and Meishan pigs clearly indicates that proportion of the different MyHC isoforms differ drastically between pig breeds and that breed affects mostly the MyHC IIx:IIb ratio in white muscles (26). According to muscle tissue properties wild pigs resemble Meishan pigs, which exhibit lower growth rate, poorer feed efficiency and lower meat content than conventional pig breeds (27). Wild pigs are physically highly active animals. Comparisons between wild and domestic pigs showed that they exhibit more oxidative and less glycolytic muscle metabolism and therefore a higher capacity to use lipids as an energetic substrate. Because oxidative metabolism decreases in the rank order I, IIa, IIx, IIb (17) these metabolic changes are consistent with the shift of MyHC profile toward a faster type in the domestic pig muscle. It may be noted, that domestic pigs included in the present study had somewhat higher percentage of slow-twitch oxidative type I and fast-twitch oxidative type IIa myofibers than reported in some other studies (19). This could be due to the breed used or because older pigs (approx. 2 years old) were used in our study. As demonstrated for some species, with aging the muscles become slower and more fatigue resistant as an adaptation to increasing body mass (14). The results of our immunohistochemical analysis are also in accordance with the studies in which the expression of MyHC isoforms in the longissimus muscle of different modern pig breeds or crossbreeds was quantified using a real time PCR at the mRNA level (26, 28, 29), or enzyme-linked immunosorbent assay on the protein level (28). A co-expression of IIx and IIb MyHC isoforms in pig muscles was also described by some other authors and was ascribed to the fine tuning of the

expression of the IIx and IIb genes and its effect on myofiber plasticity (17).

Transition of MyHC isoforms is sequential, yet with a reversal pathway: $I \leftrightarrow IIa \leftrightarrow IIx \leftrightarrow IIb$ (1). It thus seems that breeding programs selecting for rapid, massive muscular growth pushed myofiber type to the right of this equation. Indeed, lower postnatal muscle growth was ascribed to decreased expression of glycolytic fibers in Chinese Meishan as compared to modern Yorkshire breed (31). Moreover, as shown here and in other studies, the MyHC-IIb isoform is the predominant isoform in the longissimus muscle. It contributes to the increased muscle mass which is the main goal of animal breeders (28). On the other hand, better water holding capacity, colour characteristics and tenderness are positively related to the presence of oxidative myofibers and hence the favourable MyHC isoforms would be -I, -IIa and -IIx (5). Overall, the available literature studies show that the prevalence of MyHC-IIb is probably responsible for the increased glycolytic potential of longissimus muscle. Moreover, when the CSA of myofibers increases, the density of capillary network in the endomysium of the same myofibers decreases particularly that of the largest myofibers (in our case type IIb), which makes it difficult to extract the lactate from them. Muscles composed predominantly of IIb myofibers are thus more susceptible to rapid post-mortem glycolysis which is negatively correlated with meat quality, in particular water holding capacity and may contribute to generating PSE meat condition (18, 32).

In conclusion, the present study showed that the expression of MyHC-IIb isoform in the muscles of domestic pig should not be considered as the sole consequence of intensive selection for muscularity and rapid growth. The fastest isoform i.e. MyHC-IIb is evidently expressed in the muscles of wild pigs, although less strongly than in domestic pig. It can also be deduced that due to the domestication and breeding goals, CSA of all myofiber types was considerably increased, in particular of those in which MyHC-IIb is expressed. The manifestation of MyHC isoforms is important for meat characteristics. For this reason the quantification of the expression of MyHC isoforms may represent a novel approach for future breeding programs, in particular in view of the balance between growth performance, muscularity and meat quality.

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IZRAŽENOST ISOFORM TEŽKIH MIOZINSKIH VERIG V NAJDALJŠI MIŠICI (*M. LONGISSIMUS*) PRI DOMAČEM IN DIVJEM PRAŠIČU

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Povzetek: Ugotavljali smo razlike v izraženosti izoform težkih miozinskih verig (MyHC) pri domačem in divjem prašiču kot posledico udomačitve in selekcije prašičev. Vzorce mišičnega tkiva smo odvzeli iz najdaljše hrbtne mišice (LM) petih divjih in petih domačih prašičev (pasma velika bela) starih dve leti. V mišičnih vlaknih obeh, domačega in divjega prašiča, smo imunohistokemično dokazali štiri različne izoforme MyHC (MyHC-I, MyHC-IIa, MyHC-IIb, MyHC-IIx), ki so omogočile razlikovanje tipov I, IIA, IIx/b in IIb. Vlakna tipa I, II in IIx/b so bila oksidativna in številnejša v LM pri divjem prašiču, pri domačem pa so prevladovala mišična vlakna IIb, ki so glikolitična. Prečni preseki vseh tipov mišičnih vlaken so bili dva- do trikrat manjši pri divjem prašiču kot pri domačem. Pri divjem prašiču je bila velikost vlaken različnih tipov tudi bolj izenačena kot pri domačem. Razlik v velikosti med vlakni I, IIx/b in IIb nismo ugotovili, medtem ko so pri domačem prašiču bila vlakna tipa IIx/b in IIb najdebelejša. Vlakna tipa IIA so bila najmanjša pri obeh, domačem in divjem prašiču. Prisotnost MyHC-IIb izoforme pri divjem prašiču dokazuje, da njena prisotnost v mišicah domačega prašiča ni zgolj odraz selekcije na boljši prirast in mesnatost. Razlika med divjim in selekcioniranim domačim prašičem se kaže predvsem v hipertrofiji vseh tipov mišičnih vlaken, posebej tistih z najbolj izraženo izoformo MyHC-IIb.

Ključne besede: težke miozinske verige; mišično vlakno; imunohistokemija; domači prašič; divji prašič