Muscle fiber plasticity in farm mammals[1]

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Abstract

Despite intensive research demonstrating the effects of major genes and slaughtering conditions on meat quality, a large variation in meat quality remains in the meat industry. Muscle fiber characteristics are thought to be important factors influencing meat quality; however, identifying a strong correlation between fiber types and meat quality remains to be established. After a brief presentation of recent knowledge underlying conventional fiber typing, this article describes muscle fiber genesis and diversification, as well as some factors regulating these processes. Thereafter, current knowledge about the significance of muscle fiber type in modulating growth performance and meat quality is presented for various species. In addition, this review will cover data showing that muscle fiber type composition is highly variable and can be influenced by many factors. In particular, fiber type can be modified by numerous intrinsic and extrinsic factors, such as muscle type, species, breed, major genes, individual, sex, fetal and postnatal nutrition, ambient temperature, exercise, growth-promoting agents, and transgenes. The relatively high heritability of some histochemical characteristics suggests that selection can be efficiently used to manipulate muscle fiber type composition by including fiber attributes in selection indexes. The correlated responses of growth and meat quality traits to this selection may be useful studies for better understanding the significance of muscle fiber type in determining growth performance and meat quality. Finally, increasing the total number of fibers, a characteristic established before birth in most farm mammals, is a promising way to increase muscle mass without increasing fiber size, which is sometimes speculated to alter meat quality. However, there still is not enough research that definitely demonstrates the deleterious effect of increasing fiber size on meat quality, and more research is also needed to better understand the mechanisms that regulate the total number of fibers.

Key Words: Muscle Fibers, Growth, Meat Quality, Plasticity

Introduction

Meat animals have been aggressively selected for improved growth performance, in particular a rapid accretion of muscle. Evidence suggests this increased capacity to deposit muscle proteins has resulted in altered meat quality characteristics, at least in pigs (reviewed by Sellier, 1997). Providing the meat industry with a consistently high-quality product is becoming an increasingly important objective, yet the precise factors that determine eating quality are not well-identified. Despite the efforts to understand the effects of major genes and slaughtering conditions on meat quality, little progress has been made toward reducing the large variation in meat quality. Muscle characteristics, in particular muscle fiber type composition, have been thought to contribute to variation in eating quality of meat. However, a direct effect of fiber type on meat quality remains unclear. This may be, in part, due to indirect effects of muscle fiber type on meat quality through differences in associated muscle components, such as sarcoplasmic proteins, muscle enzymes, intramuscular fat, and connective tissue. Therefore, the extent to which fiber types specifically explain the residual variation in meat quality, in relation to growth condition, needs to be clarified.

The purpose of this paper is to review the specific role of muscle fiber characteristics in accounting for variation in growth performance and meat quality in farm mammals. After a brief review of recent data underlying conventional myofiber classification, we will review the main steps of muscle fiber genesis and diversification; present the relationships between muscle fiber type composition, growth performance, and meat quality; and review the influence of some intrinsic and extrinsic factors on muscle fiber composition.

Myofiber Classification

Muscle fibers are polynucleated, elongated cells that can be classified according to their contractile and metabolic properties. The contractile type is based on the polymorphism of myosin heavy chains (**MyHC**), which form the major component of the thick filaments and are major determinants of shortening speed. Slow-twitch type I fibers are used to maintain posture, whereas those with fast-twitch characteristics (type II) are specialized in producing movement. Conventionally, differences in sensitivity of the actomyosin-ATPase (**AM-ATPase**) activity to pH preincubation has been used to type fibers by histochemistry (Brooke and Kaiser, 1970; Guth and Samaha, 1970). In pigs, three fiber types can be distinguished after preincubation at pH 4.35: types I, IIA, and IIB (Lefaucheur et al., 1991). The metabolic type can be determined on a serial section by revealing the activity of a mitochondrial enzyme, succinodehydrogenase (**SDH**). This allows distinction between oxidative (red) and nonoxidative (white) fibers (Gauthier, 1969). It is noteworthy that, whereas type I and IIA fibers are always red, type IIB fibers can be either red or white, denoting a heterogeneity within IIB fibers. Approximately 15% of IIB fibers are red in pig longissimus (Essén-Gustavsson and Lindholm, 1984; Larzul et al., 1997). The biochemical characteristics of individual fiber types are presented in Table 1.

More recently, immunocytochemical studies using heterologous monoclonal antibodies raised against different MyHC confirmed the heterogeneity of pig IIB fibers (Lefaucheur and Ecolan, 1998). Most conventional IIB fibers of pig longissimus were recognized by BF-F3 antibody (IIB specific in rat; Schiaffino et al., 1989), whereas all IIB fibers were unstained in the red portion of semitendinosus muscle (**RST**). Conversely, all conventional IIB fibers were labeled with a specific IIA + IIX monoclonal antibody (INRA-S5-7D4) in RST, whereas only a subpopulation of IIB fibers were reactive in longissimus (Lefaucheur and Ecolan, 1998). The heterogeneity of IIB fibers was also demonstrated at a molecular level using specific pig RNA probes with in situ hybridization (Chang and Fernandes, 1997; Lefaucheur et al., 1998). Thus, all IIB fibers are actually IIX fibers in the RST muscle, whereas they are either hybrid IIA/IIX, pure IIX, hybrid IIX/IIB, or pure IIB in pig longissimus. The polymorphism of MyHC creates a large spectrum of different fiber types, which leads to a diversity of myofibers far beyond those that can be histochemically identified. Up to now, four MyHC have been identified in pig longissimus at 100 kg body weight (I, IIA, IIX, and IIB), each isoform being coded by its own gene. The presence of these four MyHC was first documented in rats (Bär and Pette, 1988; Schiaffino et al., 1989; DeNardi et al., 1993), mice (Gorza, 1990), guinea pigs (Gorza, 1990), and rabbits (Aigner et al., 1993), whereas IIB MyHC has been suggested to be absent in human skeletal muscle (Smerdu et al., 1994). Analysis of MyHC isoforms in different bovine muscles by RT-PCR reports the expression of type I, IIA, and IIX MyHC and suggests the possibility of non-expression of IIB MyHC (Tanabe et al., 1998). However, the production of specific monoclonals or riboprobes is still required to unambigously define MyHC in bovine muscles.

Skeletal Muscle Development

Ontogeny of Myofibers

In most mammals, ontogeny of myofibers is a biphasic phenomenon. Because porcine muscle possesses a unique structure consisting of clusters of slow fibers surrounded by fast fibers (type grouping), it is a good model to study the progeny of individual muscle fibers throughout gestation. The development of this type grouping has been well-described using the AM-ATPase cytochemical techniques by Ashmore et al. (1973) and Beermann et al. (1978). Briefly, a primary generation forms from 35 to 55 d of gestation (**dg**), followed by a second generation between 55 and 90 to 95 dg. These secondary fibers appear around each primary myotube, presumably using them as a scaffold or framework for organization. The number of secondary fibers around each primary varies from between five and nine in mice and rats (Ross et al., 1987; Ontell et al., 1988) to over 20 in larger animals, such as pigs (Stickland and Handel, 1986). The total number of myofibers (**TNF**) is generally considered to be established by 90 to 95 dg in the pig (Wigmore and Stickland, 1983), and the postnatal increase in size is more dramatic in white- than in red-precursor fibers (Figure 1). Expression of adult MyHC is spatially regulated within the fascicles of myofibers. In pigs, in which muscle exhibits a highly organized pattern and unique distribution of fibers (Suzuki and Cassens, 1980), the expression of MyHC follows the rank order I, IIA, IIX, and IIB from the center to the periphery of the rosettes (Lefaucheur et al., 1998). It is now well documented that MyHC transitions follow an obligatory pathway I ↔ IIA ↔ IIX ↔ IIB (reviewed by Schiaffino and Reggiani, 1994; Pette and Staron 1997), suggesting that the spatial distribution of MyHC observed in pigs must be functionally relevant. It is noteworthy that the biphasic nature of myogenesis is also observed in other species, even though the type grouping is much less pronounced than it is in pigs. However, a large difference in the timing is observed between species in relation to their degree of physiological maturity at birth. In particular, the TNF is reported to increase up to 1 mo after birth in rabbits, which are quite immature at birth (Nougues, 1972).

Contractile Differentiation

Muscle fibers undergo a process of maturation that leads to the pattern of distribution found in the adult. Conventional AM-ATPase histochemistry shows that a subpopulation of secondary fibers, located in the direct vicinity of primary myotubes, matures to type I fibers during the early postnatal period, leading to the typical clusters of type I fibers surrounded by type II fibers in adult pig skeletal muscle. The percentage of type I fibers increases up to 8 wk in pig muscles, suggesting that the early postnatal period could be a critical period when fiber plasticity is quite vulnerable to various stimuli.

Fiber type diversification is accompanied by changes in MyHC polymorphism. As many as nine different MyHC isoforms have been identified in mammalian skeletal muscles, including the extraocular and super-fast MyHC. Each isoform is the product of a different gene belonging to the MyHC gene family (Schiaffino and Reggiani, 1996). Recent data in pig longissimus and semitendinosus muscles report three developmental isoforms (embryonic, fetal/perinatal and α-cardiac) that are transiently expressed during development and four adult isoforms (I, IIA, IIX, and IIB) that begin to appear during development and continue to be expressed in adult muscle (Lefaucheur et al., 1995, 1997, 1998). A simplified scheme of muscle fiber diversification in pig skeletal muscle, based on MyHC transitions, is shown in Figure 2. Primary myotubes are the first to appear and initially express embryonic, fetal, and slow type I MyHC. During the fetal period, they subsequently mature to type I fibers in most muscles but can also give rise to type IIA fibers in highly glycolytic muscles, such as the superficial white portion of pig semitendinosus muscle (Lefaucheur et al., 1995). Secondary fibers begin to appear at 50 to 55 dg and also express embryonic and fetal MyHC during the fetal period. However, unlike primary myotubes, they do not express type I MyHC before late gestation. Perinatally, a subpopulation of secondary fibers in the direct vicinity of primary myotubes begins to express type I MyHC and mature to type I fibers. Some of these fibers transiently express the α-cardiac MyHC before maturing to type I fibers (Lefaucheur et al., 1995, 1997). Adult fast type IIA MyHC is present in some secondary fibers during the fetal period, whereas IIX and IIB appear shortly after birth (Chang et al., 1995 ; Chang and Fernandes, 1997). During the first weeks after birth, secondary fibers that do not express type I MyHC mature to either type IIA, IIX, or IIB fibers. To our knowledge, further study is still needed to describe in detail the temporal and spatial expression of the different MyHC in meat-producing animals during the fetal and postnatal periods.

Embryonic and fetal MyHC are chronologically expressed during myogenesis and successively disappear. A comparison between species (Figure 3) shows that fetal MyHC disappears before birth in bovines, between 10 and 15 d after birth in pigs, and at approximately 30 d in rats and rabbits, indicating a decreasing maturity at birth in the rank order bovine > pig > rabbit = rat, suggesting that overall maturity of animals at birth may be manifested in the musculature as well.

Metabolic Differentiation

Besides changes in MyHC polymorphism, an evolution in muscular energetic metabolism also occurs during development. It can be assessed by biochemical techniques using glycolytic (lactate dehydrogenase, **LDH**) and mitochondrial (isocitrate dehydrogenase, **ICDH**) enzyme activities. Most changes occur after birth ; Figure 4 illustrates the allometric increase in muscle weight (**MW**) and total LDH and ICDH activities (i.e., total amount of enzyme activity in the whole muscle) during postnatal development in pig longissimus (Lefaucheur and Vigneron, 1986). Changes in the shaded areas denote changes in enzyme activities per gram of fresh muscle. It can be seen that glycolytic metabolism (LDH) dramatically increases up to 2 to 3 wk and continues to increase at a slower rate up to 100 kg BW. Conversely, a slight increase in muscle oxidative metabolism occurs up to 2 to 3 wk, followed by a gradual decrease. Muscle metabolism, as a whole, becomes more glycolytic with increasing age. Again, these data identify the early postnatal period as a likely critical period for muscle fiber type diversification. In bovine muscle, however, it is noteworthy that metabolic differentiation starts earlier during the last third of gestation (Gagnière et al., 1998), indicating that bovines are more mature at birth than pigs. Using histochemical techniques on porcine, ovine, and bovine muscles, Ashmore et al. (1972) concluded that αR fibers have the capacity to transform into αW fibers during growth, in accordance with the increasing glycolytic metabolism.

Regulation of Muscle Fiber Type Diversification

Myogenesis involves determination, migration, proliferation, differentiation, and fusion of myoblasts to form myotubes. This cascade of events is under the control of numerous factors that are expressed in a temporally and spatially regulated manner (reviewed by Buckingham, 1996; Molkentin and Olson, 1996; Yun and Wold, 1996; Wigmore and Dunglison, 1998). In vertebrates, at least two famillies of transcription factors, the basic helix-loop-helix (**bHLH**) muscle regulatory factors (**MRF**: myf-5, MyoD, myogenin, MRF-4) and the myocyte enhancer factor 2 (**MEF2**) have been shown to regulate skeletal muscle determination and differentiation. Thus, MRF can convert nonmyogenic cells into myoblasts by inducing the expression of many muscle-specific genes. In the adult rat hindlimb, Hughes and his colleagues (1993) observed a selective accumulation of MyoD and myogenin in fast and slow fibers, respectively. In addition, they showed that cross-reinnervation or thyroid hormone-induced alteration of the fast:slow fiber ratio similarly affected MyoD:myogenin ratios, suggesting a possible role of the different MRF in fiber type determination and transformation. However, gene knock-out models have failed to show a cause-and-effect relationship between specific MRF and muscle fiber types. Theoretically, MRF knock-out models would have provided definitive information regarding shifts in muscle fiber type; however, because the central dogma is that MRF participate in the earliest stages of myogenesis, the objective of many MRF knock-out models was mainly restricted to studying fetal muscle development (Braun et al., 1992; Rudnicki, et al., 1992; Hasty et al., 1993; Nabeshima et al., 1993), and this could have obscured subtle differences in muscle fiber type in these studies. In addition, Rudnicki et al. (1992) reported that the survivability of MyoD –/– mice was substantially lower than that of MyoD +/+ mice and postulated that these mice may not compete well with MyoD +/– and +/+ littermate pups. Thus, we speculate that a lack of functional MyoD protein could reduce the development of fast muscle fibers, which is often considered a prerequisite for increased muscle mass and strength (Schiaffino and Salviati, 1997). This reduced strength attributed to lack of type IIB muscle fibers was further documented in knock-out mice lacking the IIB/X MyHC genes (Leslie et al., 1997). Myogenin knock-out mice failed to form muscle fibers normally, making detection of muscle fiber-specific MRF expression impossible. Furthermore, Olson et al. (1996) pointed out that studies generating MRF-4 knock-outs yielded offspring ranging from complete viability to complete lethality. Therefore, limitations exist regarding the use of gene knock-out models for studying muscle fiber type diversification.

Insulin-like growth factor I (**IGF-I**) is known to strongly influence myogenesis by stimulating both proliferation and fusion of myoblasts (reviewed by Florini et al., 1996). Among hormones, thyroid hormones seem to be particularly important in regulating fiber type maturation and diversification (reviewed by Pette and Staron, 1997). Triiodothyronine stimulates the disappearance of fetal/neonatal MyHC in favor of adult fast isoforms during the perinatal and early postnatal periods and induces transition from slow to fast fibers in adult muscles. Recently, a member of the transforming growth factor-β family, myostatin, has been identified to be a key factor in the regulation of the total number of fibers, its knock-out leading to a dramatic increase in muscle mass through hyperplasia and hypertrophy of muscle fibers in mice (McPherron et al., 1997).

In mammals, different lineages of myoblasts have been suggested to form the basis for the differences between primary and secondary myotubes and the initial maturation of myotubes into slow and fast fibers. However, further refinement of the pattern of MyHC expression also occurs during the postnatal period under the influence of many factors such as contractile activity, neurotrophic and growth factors, hormones, and nutrients (reviewed by Gunning and Hardeman, 1991; Schiaffino and Reggiani, 1996; Pette and Staron, 1997; Brameld et al., 1998). Because MyHC isoforms are coded by separate genes, regulatory sequences present in their promoters and enhancers are involved in controlling their fiber type expression. In the future, a better understanding of the mechanisms underlying this regulation will be of practical importance for the meat industry.

Significance of Myofiber Types for Growth Performance

Muscle weight is a function of total number of fibers (TNF), fiber cross-sectional area (**CSA**), and length. Most researchers agree that muscle growth capacity is positively related to the TNF, a characteristic fixed before birth in most meat-producing farm mammals (Staun, 1963; Miller et al., 1975; Guenther, 1977; Handel and Stickland, 1988; Dwyer et al., 1993). Surprisingly, the relationship between muscle mass and CSA is highly controversial. This could be due to the fact that muscle mass is mainly influenced by TNF, a highly variable trait. Most studies report that glycolytic fibers exhibit the largest CSA, suggesting that, for a given TNF, an increase in the proportion of glycolytic fibers must lead to an increase in muscle weight. When comparing wild and domesticated animals, the well-accepted idea is that domestication has led to changes in myofiber composition toward the glycolytic type (Rahelic and Puac, 1981; Solomon and West, 1985; Weiler et al., 1995). However, Karlsson et al. (1993) did not find any marked effect of selection for high lean tissue growth rate on fiber composition in Swedish Yorkshire pigs. Similarly, no significant relationship was found between myofiber composition of longissimus and growth performance within the Large White breed (Larzul et al., 1997). Conversely, Henckel et al. (1997) reported a positive correlation between muscle gain and the activity of citrate synthase, an oxidative enzyme, and the number of capillaries per fiber in longissimus muscle of Large White and Landrace pigs. In bovines, bulls exhibit a lower proportion of glycolytic fibers and a higher muscle growth capacity than steers. To our knowledge, another unanswered question is the significance of the balance between the expression of IIX and IIB MyHC for muscle growth capacity. Altogether, these data show that the relationship between fiber type composition and growth performance is still unclear and deserves further research. Moreover, growth in length of myofibers is also an important aspect that has been poorly studied. This aspect of muscle fiber growth is undoubtedly involved in the increase in mass of important muscles, such as longissimus, in which muscle fibers are positioned at a 25° angle to the vertebral axis (Davies, 1972).

Factors Influencing Fiber Type Composition

As shown in Table 2, numerous intrinsic and extrinsic factors can potentially be used to manipulate muscle histological characteristics in farm animals.

Muscle

Muscle type, location, and function are undoubtedly the most important factors that influence fiber type composition within an animal. Generally, deep muscles involved in maintaining posture are more oxidative and contain more type I fibers than more superficial muscles involved in rapid movements (Ono et al., 1995). Muscle fiber composition can also dramatically change within the same muscle. The proportion of type I fibers in pig semitendinosus muscle ranges from approximately 4% in the superficial white portion to 45% in the deep red portion (Beermann et al., 1990). In cattle, the increase in fiber diameter stops later in the light than in the dark area of semitendinosus muscle, coinciding with an increase in the percentage of αW fibers in the light area (Dreyer et al., 1977). The occurrence of giant fibers is also influenced by the type of muscle. Thus, Solomon and Eastridge (1987) found more giant fibers in triceps brachii (23% βR) than in semimembranosus (11% βR) muscle, which contradicts findings of Rahelic and Puac (1981), who observed more giant fibers in muscles with the lowest percentages of βR fibers.

Species

The total number of fibers and the proportion and spatial distribution of fiber types of a given muscle vary between species. It is well-documented that body size is much more related to TNF than fiber CSA (reviewed by Plaghki, 1985). Mean CSA of muscle fibers in longissimus is approximately 3,000 μm^2 in 500-kg Montbéliard bulls (Brandstetter et al., 1998a), 3,400 μm^2 in 100-kg Large White pigs (Lefaucheur et al., 1992), and 2,800 μm^2 in 2.2-kg New Zealand rabbits (Alasnier et al., 1996). The proportions of conventional type I, IIA, and IIB fibers in longissimus muscle are 35, 24, and 41% in Montbéliard bulls

(Brandstetter et al., 1998a); 10, 7, and 83% in Large White pigs (Larzul et al., 1997); and 1, 6, and 93% in New Zealand rabbits (Gondret et al., 1996), respectively, denoting a positive relationship between the proportion of slow-twitch type I fibers and body size.

Breed

Within a species, the most important factors that influence fiber type composition of a given muscle are probably genetic factors, in particular the breed. However, because mature body size can be highly different between breeds, differences can vary depending on weight, age, or degree of maturity expressed as a percentage of adult body weight. Thus, studies carried out in lambs (Solomon et al., 1981) and cattle (Dreyer et al., 1977) showed that early-maturing breeds had more αW fibers and fewer αR fibers than late-maturing breeds when compared at similar slaughter weights or chronological ages. Because αR fibers have the capacity to transform into αW fibers during postnatal development (Ashmore et al., 1972), physiological maturity may have contributed to the higher percentage of αW fibers in early-maturing animals, as suggested by Solomon et al. (1986). These authors concluded that the degree of conversion of αR to αW fibers can help to identify physiological maturity in market-weight animals. Concerning fiber size, several studies carried out in bovine and ovine muscles reported larger fiber diameters in early- than in late-maturing animals compared at similar ages or weights (Dreyer et al., 1977; Guenther, 1977; Solomon et al., 1981), possibly as a consequence of advanced maturity in early-maturing animals. However, strong differences between breeds have also been reported at similar stages of growth. In the adult, Meishan pigs, which exhibit a low muscle growth potential, have a higher oxidative and a lower glycolytic metabolism, in addition to a decrease in TNF and fiber size (Bonneau et al., 1990). Several other studies show that wild breeds of pigs contain more oxidative and less glycolytic fibers than domesticated ones, as well as smaller fibers (Rahelic and Puac, 1981; Weiler et al., 1995). Finally, Large White pigs are reported to contain more type I fibers than miniature pigs (Stickland and Handel, 1986), which may be necessary to support their increased weight. Interestingly, giant fibers resembling βR or αR fibers are found in wild pigs (Solomon and Eastridge, 1987), suggesting that the giant fiber syndrome is not necessarily associated with breeding for muscularity.

Major Genes

In different species, several major autosomal genes influence muscle fiber type composition of valuable muscles (Table 3). These are the halothane (**RYR1**) and RN genes in the pig, the myostatin gene in double-muscled cattle (Grobet et al., 1997; Kambadur et al., 1997; McPherron and Lee, 1997), and the Callipyge gene in sheep. Halothane, myostatin, and Callipyge genes lead to a dramatic muscular hypertrophy. However, only the myostatin gene in cattle is associated with an increase in TNF. This hyperplasia has been associated with prolonged proliferation of myoblasts and delayed myotube formation in vitro (Quinn et al, 1990), as well as in vivo (Picard et al., 1995). The RYR1, myostatin, and Callipyge genes increased both the percentage and CSA of glycolytic fibers. Conversely, the RN gene mainly increased the CSA of fast oxido-glycolytic fibers, leading to a decrease in relative area of glycolytic fibers and a shift toward a more oxidative and less glycolytic metabolism. Carriers of the RN gene exhibit a higher glycogen content in white muscles in vivo and 24 h after slaughter (reviewed by Sellier and Monin, 1994), in particular in glycolytic fibers (Marinova et al., 1992). This leads to a lower ultimate pH and water-holding capacity of cooked meat. Those interested in meat research should always keep in mind that all these genes strongly influence meat quality traits (Sellier and Monin, 1994; Koohmaraie et al., 1995; Clinquart et al., 1998) and could mask the direct effects of fiber type composition on meat quality.

Individual

There is a large individual variation in fiber type composition between animals of the same breed reared in the same environment. An experiment using 383 Large White pigs, free of the RYR1 and RN genes, showed that relative area of type I fibers in longissimus muscle ranged from 2.1 to 18.4% (mean = 6.7 ± 1.8%) and was highly heritable ($h^2 = .46$, Larzul et al., 1997), which suggests that it can be manipulated by conventional selection from a biopsy. Therefore, selection experiments based on histochemical characteristics to study the correlated selection responses on growth performance and meat quality may be useful to determine the specific role of fiber types in determining meat quality. The total number of fibers has also been shown to be quite variable, ranging from 292×10^3 to 958×10^3 in the semitendinosus muscle within an F_2 population of 364 Large White × Meishan pigs (Lefaucheur et al., unpublished data), and heritable ($h^2 = .22$ to $.88$) (Staun, 1963; 1972; Dietl et al., 1993; Larzul et al., 1997). However, the direct measurement of TNF on living animals is difficult. Therefore, identification of a marker for evaluating TNF is necessary.

In the future, meat scientists investigating the effects of nutritional or environmental factors on muscle fiber type composition and meat quality should be aware of the large effects that genetic variability can have on experimental results. Using an animal for its own control through biopsies or using clones could dramatically increase the power of experimental designs.

Sex

Sex has been reported to have no effect on muscle fiber number in mice (Rowe and Goldspink, 1969) and meat-producing animals (Staun, 1963; Seideman et al., 1984; Dwyer et al., 1994). However, it can strongly influence muscle fiber type composition. In cattle, castration decreases CSA of myofibers and strongly increases the proportion of glycolytic fibers at the expense of fast oxido-glycolytic ones (Dreyer et al., 1977; Young and Bass, 1984; Clancy et al., 1986; Seideman et al., 1986), leading to a more glycolytic and less oxidative metabolism as measured by enzyme activities (Brandstetter et al., 1998b). The higher proportion of glycolytic fibers in steers may expedite the postmortem aging process. It is likely that testicular hormones are responsible for the paucity of glycolytic fibers in bulls. However, administration of testosterone to castrated guinea pigs induced a change from αR to αW fibers (Bass et al., 1971; Lyons et al., 1986). Further research is needed to understand the mechanisms of action of androgens on fiber types. In pigs, most studies have documented differences between females and castrated males (barrows). Generally, females exhibit larger fibers, with no difference in fiber type percentages and relative areas (Miller et al., 1975; Sosnicki, 1987; Solomon et al., 1990; Ender, 1995; Weiler et al., 1995; Larzul et al., 1997). Fiber type percentages were also found to be similar in longissimus muscle of boars (Solomon et al., 1990). However, in a recent study carried out on longissimus muscle from 165 female and 152 intact male Large White pigs at 70 kg BW, we found a significantly higher relative area of type I fibers in intact male pigs (7.6 ± 2.2%) than in females (6.7 ± 2.5%) ($P < .001$), suggesting that castration decreases relative area of type I fibers in pigs.

Fetal Nutrition

Undernutrition during the fetal period, leading to runting in pigs, has been shown to specifically decrease the number of secondary fibers, leading to a permanent decrease in postnatal muscle growth potential (Hegarty and Allen, 1978; Powell and Aberle, 1980, 1981; Wigmore and Stickland, 1983; Handel and Stickland, 1987). At similar BW, runt pigs exhibit larger muscle fiber diameters than control pigs (Hegarty and Allen, 1978; Powell and Aberle, 1981), as well as fatter carcasses, likely in relation to a higher physiological maturity. In contrast, overnutrition of the sow between 25 and 50 d of gestation (dg) (Dwyer et al., 1994) or injection of growth hormrone between 10 and 24 dg (Rehfeldt et al., 1993) can increase the TNF in developing pigs. The exact mechanism for this phenomenon, however, remains unknown.

Postnatal Nutrition

Feed restriction (30% of ad libitum intake) between 7 and 100 kg BW did not change fiber type percentages in pig longissimus and tibialis cranialis muscles; however, an increase in myofiber CSA was observed, in accordance with a higher lean meat content in feed-restricted animals (Lefaucheur, 1989). Conversely, feed restriction (50% of ad libitum) at an early stage (between 3 and 7 wk of age) did not change myofiber type proportion in longissimus muscle but led to a dramatic increase in proportion of type I fibers (+43%) in the red rhomboideus muscle (Harrison et al., 1996). In this last experiment, CSA of all fibers was lower in feed-restricted piglets because of a lower body weight. According to these authors, because the energy expenditure per unit tension developed is lower in type I fibers, a selective increase in the proportion of type I fibers during a period of reduced energy availability would be physiologically relevant to spare energy. In pigs, protein restriction has been shown to decrease glycolytic metabolism and increase intramuscular fat content and tenderness (Karlsson et al., 1993). The balance between energy, protein, and amino acids plays an important role in determining feed efficiency and lean tissue growth rate (Campbell, 1988). Thus, an excess of energy leads to fatter animals at a given body weight, which is likely to increase intramuscular fat and reduce fiber size, in relation to a lower lean meat content. However, few studies have been conducted to establish the relationship between these aspects.

In lactating sows in which feed intake does not meet the nutrient requirement for milk production and maintenance, an important loss of body fat (Whittemore et al., 1980) and muscle tissue (Etienne et al., 1985) occurs. In longissimus muscle, this is accompanied by a selective decrease in CSA of glycolytic fibers, an increase in relative area of type I fibers, and a general reduction of both oxidative and glycolytic metabolisms (Lefaucheur, 1990). These changes are similar to those observed in laboratory animals after a period of starvation, restricted feeding, or glucocorticoid treatments. Because the musculature represents approximately 40% of the body mass of the sow after farrowing and predominantly consists of fast glycolytic muscles, fast glycolytic fibers are likely to represent a substantial portion of the available protein reserves for the sow.

In lambs, feed restriction has been reported to induce atrophy of muscle fibers and increase the percentage of αR fibers at the expense of αW fibers (Solomon et al., 1994c). Following a period of restriction, compensatory growth has been shown to increase glycolytic metabolism while decreasing oxidative metabolism in bulls (Brandstetter et al., 1998b). However, no such effects were oberved in steers. Finally, the energetic density of the diet (2.79 vs 1.87 Mcal ME/kg diet) was shown to influence fiber type composition in lambs given ad libitum access to feed and slaughtered at 45 kg BW (Solomon and Lynch, 1988). In particular, longissimus muscles from lambs fed the lower-energy diet contained more αR and fewer αW fibers, exhibited a lower rate of postmortem pH decrease, and were more tender and slightly more juicy than the longissimus muscles from lambs fed the higher-energy diet.

Ambient Temperature

Ambient temperature is an environmental factor that can influence muscle fiber type composition and muscle energy metabolism. Long-term exposure to cold can increase the proportion of type I fibers (Table 4). This is generally accompanied by an increase in oxidative metabolism (Lefaucheur et al., 1991; Herpin and Lefaucheur, 1992). Recent experiments carried out between birth and 5 d in pig showed that cold exposure (24 to 15°C vs 34 to 30°C) induced a dramatic increase in type I and α-cardiac MyHC in both longissimus and rhomboideus muscles (Lossec et al., 1998). The cold environment also induced an increase in oxidative enzyme activities in both muscles, whereas glycolytic metabolism was unaffected. The physiological significance of these changes is probably related to an increase in cold-induced thermogenesis. However, to what extend these adaptations are the result of sustained shivering or to changes in substrate availability or hormonal levels, in particular of thyroid hormones, remains to be determined. Conversely, exposure to a warm environment (31 vs 18°C) between 9 and 33 kg decreased both oxidative and glycolytic metabolisms, in particular in white muscle, indicating a general reduction of muscle energy metabolism (Rinaldo and Le Dividich, 1991). From a practical point of view, the more severe response of red muscles to a cold environment could lead to increase heterogeneity of the color between muscles, leading to reduced consumer acceptability.

Exercise

Studies using electric stimulation have shown that contractile activity per se strongly influences myofiber composition (reviewed by Pette and Staron, 1997). The general idea is that increased activity induces a transition in the order IIB → IIX → IIA → I, whereas decreased activity results in transitions in the opposite direction. A recent experiment using long-term electrical stimulation in rabbit skeletal muscle reported α-cardiac MyHC as being intermediate between type IIA and I MyHC (Peuker et al., 1998). Experiments using pigs showed that both exercise training and spontaneous physical exercise can influence muscle physiological traits but do not affect the same muscles (Petersen et al., 1998). One explanation is that animals can either walk, trot, gallop, or jump depending on the experimental design, which does not activate the same muscles. These data show that exercise training studies are likely unsuitable for predicting the effects of spontaneous exercise occurring in outdoor or free-range rearing systems (Petersen et al., 1998). Collectively, however, most accounts show that physical exercise increases oxidative metabolism and decreases glycolytic metabolism in muscles involved in the exercise (reviewed by Essén-Gustavsson, 1993).

Growth-Promoting Agents

Growth-promoting agents can influence muscle growth and muscle fiber type composition in farm animals, in particular growth hormone (**GH**), β-agonists, and steroids. The anabolic action of GH on muscle development in pigs was first analyzed by Turman and Andrews (1955) and Machlin (1972) and has been extensively studied since (reviewed by Cannon et al., 1995 and Aalhus et al., 1997). Most research reports a general increase in CSA of all fibers, without any change in percentage of each fiber type (Beerman et al, 1987; Solomon et al., 1988, 1991a). A dramatic decrease in intramuscular fat content is consistently observed in GH-treated animals. Though no major effect of GH treatment on meat quality is usually reported, several studies indicate an increase in shear force (Solomon et al., 1988, 1990, 1991a, 1994a; Rehfeldt and Ender, 1993), as well as a higher incidence of pale, soft, and exudative (PSE) muscle (Solomon et al., 1990, 1991a). Even though a direct effect of GH on muscle fibers is not ruled out, it is widely accepted that most of the anabolic effects of GH would be mediated by increased levels of IGF-I originating from the liver and from paracrine and autocrine secretions. In β-agonist-fed lambs, muscle hypertrophy is associated with a selective increase in CSA of glycolytic fibers, whereas effects on fiber type composition are unclear (Beermann et al., 1987; Kim et al., 1987). In pigs, treatment with β-agonists increased the frequency of type IIB fibers, mainly at the expense of type IIA fibers, resulting in lower activities of oxidative enzymes (Oksbjerg et al., 1990, 1994a,b) and a lower concentration of heme pigment in meat (Warris et al., 1990). An increase in meat toughness was observed in β-agonist-fed animals, in particular in lambs, because of a reduced postmortem proteolysis due to an increased calpastatin activity (Koohmaraie et al., 1991). Finally, steroids are anabolic hormones whose growth-promoting effects are well-known in cattle (Bramble et al., 1998). Treatment of steers with trenbolone acetate and estradiol increases the percentage of fast-twitch oxido-glycolytic fibers at the expense of fast-twitch glycolytic fibers in longissimus, indicating a shift toward a more oxidative metabolism (Clancy et al., 1986). Furthermore, a specific increase in CSA of red fibers was also observed.

Transgenic Animals

Production of transgenic mice expressing the rat growth hormone gene driven by metallothionin-1 promoter (Palmiter et al., 1982) suggested that similar improvements of growth could be achieved in farm animals. In pigs, this technology resulted in slightly enhanced feed efficiencies and growth rates, with a marked reduction in carcass and intramuscular fat deposition (Solomon et al., 1994b, 1997). Unfortunately, these transgenes had a high incidence of joint pathology, gastric ulcers, and infertility associated with abnormally high levels of GH and IGF. Interestingly, the effects of GH trangenesis on longissimus muscle morphological characteristics differ from those of GH injections in pigs (Solomon et al., 1991b). The percentage of intermediate fibers was increased at the expense of red fibers in transgenic pigs, yet fiber type proportions were not affected by pGH administration. On the contrary, all three fiber types increased in size as a result of pGH administration, whereas red fibers were larger, and intermediate and white fibers smaller, in GH transgenic pigs. Another strategy consisted of producing transgenic mice that expressed

IGF-I only in skeletal muscle by coupling the foreign IGF-I gene with the avian skeletal α-actin promoter. These mice had a dramatic increase (50×) in skeletal muscle IGF-I, without any change in serum IGF-I (Coleman et al., 1995). Transgenic overexpresion of IGF-I elicited pronounced hypertrophy of all classes of myofibers, with a shift in muscle fiber type composition toward more oxidative fibers. Similar studies were carried out in pigs (Bee et al., 1997; Pursel et al., 1998). A moderate general increase in myofiber size without any change in fiber type composition was observed in longissimus muscle. The hypertrophic response was greatest for βR, followed by αR and αW fibers. Interestingly, no health problems were noted. Sutrave et al. (1990) showed that transgenic mice expressing a truncated chicken c-ski cDNA linked to a mouse sarcoma virus long terminal repeat promoter exhibited reduced body fat and muscular hypertrophy, with a selective hypertrophy of IIB and IIX fibers. Pursel and Rexroad (1993) reported that expression of this transgene in swine resulted in disappointing results due to a wide range of phenotypes among animals. As mentioned earlier, scientists recently identified myostatin or GDF-8, whose inactivation led to a dramatic increase in muscle mass by increasing TNF and fiber CSA in mouse and cattle (Grobet et al., 1997; Kambadur et al., 1997; McPherron and Lee, 1997; McPherron et al., 1997). Therefore, manipulation of the myostatin gene is a promising means to develop meatier strains in different species of farm animals. In the future, genomic mapping of farm animals will probably identify more economically important genes that could be used to produce new transgenics with improved muscle mass and meat quality. However, the efficiency of gene transfer and subsequent temporal and spatial control requires more research.

Significance of Muscle Fiber Type for Meat Quality

Scientists have long been aware that fiber type composition and fiber cross-sectional areas are important factors influencing many of the peri- and postmortem biochemical processes, and thereby meat quality. The biochemical characteristics of individual fiber types (Table 1) can help to predict the significance of muscle fiber type for meat quality.

Water-Holding Capacity

Both the rate and extent of postmortem (**p.m.**) pH decline influence several meat quality characteristics (Monin, 1988). In particular, a high rate, as well as a large extent, of p.m. pH decline can alter water-holding capacity of fresh and cooked pork, as a consequence of protein denaturation. The rate of p.m. pH decline is related to Ca^{++} flux in the sarcoplasmic reticulum, AM-ATPase activity, muscle buffering capacity, and muscle temperature. The extent of p.m. pH decline is determined by the conversion of glycogen to lactic acid and mainly depends on muscular glycogen content at slaughter. Initial glycogen content present at slaughter is usually estimated by the glycolytic potential, as described by Monin and Sellier (1985).

A recent study using longissimus muscle samples from Large White pigs showed that increasing the proportion of αW fibers increased the rate and extent of p.m. pH decline, leading to a higher reflectance and cooking loss (Larzul et al., 1997). This indicates a negative effect of glycolytic fibers on some aspects of meat quality in pigs, in accordance with the fact that glycolytic fibers exhibit a high AM-ATPase activity and glycogen levels (Table 1). However, the rate of p.m. pH decline has also been shown to be similar between the porcine longissimus and semispinalis capitis muscles, although semispinalis capitis muscle contained more type I fibers (40 vs 8 %) (Lefaucheur et al., 1991, 1992). This could be explained by a lower buffering capacity in semispinalis capitis and(or) differences in muscle temperature that would compensate for differences in AM-ATPase activity. In contrast, relationships between fiber type composition and extent of p.m. pH decline are well-established, the ultimate pH being positively related to oxidative capacity and proportion of type I fibers and negatively related to glycogen content (Laborde et al., 1985; Talmant et al., 1986). Several studies have identified myofiber CSA, in particular that of αR fibers, as being more prone to causing meat deficiencies in pigs by increasing the rate of p.m. pH decline (Klosowska et al., 1975; Larzul et al., 1997), Minolta L* values (Larzul et al., 1997), and instrumental toughness (Maltin et al., 1997) and decreasing water-holding capacity (Klosowska et al., 1975; Lengerken et al., 1994). However, the direct influence of CSA on water-holding capacity remains to be established.

Color

Increasing the proportion of red fibers is known to increase redness of meat and myoglobin content (Klosowska et al., 1975; Whipple et al., 1992; Henckel et al., 1997). However, most research also shows that color stability is inversely related to oxidative metabolism, in particular in bovines (Renerre, 1984). Thus, an increase in the proportion of glycolytic fibers could have beneficial effects in bovines by improving color stability, which is one of the most important characteristics for consumer acceptability.

Eating Quality

Identification of a superior fiber type for eating quality has not been reported and may vary between species. In lambs, a positive relationship between the proportion of type I fibers and juiciness and flavor has been reported by Valin et al. (1982). Similarly, increasing percentage or relative area of type I fibers improved tenderness and juiciness in longissimus muscle in cattle (Maltin et al., 1998). A positive correlation between the percentage or percentage area of αW fibers and tenderness has also been found in bovines (Seideman et al, 1986). This was not confirmed by Solomon and Lynch (1988), who found that increasing the percentage of αR fibers at the expense of αW fibers through dietary manipulation improved tenderness and juiciness. Relationships between histological characteristics and sensory quality of pork are also highly controversial (Sosnicki, 1987; Maltin et al., 1997; Henckel et al., 1997). Surprisingly, a study using Danish Large White and Landrace pigs showed a positive relationship between activity of LDH, a glycolytic enzyme, and color, flavor, juiciness, and tenderness of pork chops (Henckel et al., 1997). Similarly, a positive relationship between percentage of glycolytic fibers and instrumental tenderness was found by Karlsson et al. (1993) in pigs fed a low-protein diet.

Although controversial, there seems to be a positive relationship between intramuscular fat (**IMF**) and palatability of meat (reviewed by Cannon et al., 1995). In particular, increasing IMF up to 2.5% improved tenderness and juiciness of pork chops (Devol et al., 1988). Data from an experiment using the longissimus muscle of Large White pigs failed to show phenotypic and genetic correlations between myofiber type composition and IMF content (Larzul et al., 1997). Thus, even though oxidative fibers contain more triglycerides than glycolytic fibers (Essen-Gustavsson et al., 1994), these lipids represent a small proportion of total IMF, as compared with triglycerides located in intramuscular fat cells between fibers. Other studies using different muscles confirmed the absence of a relationship between IMF content and fiber type composition in pigs (Leseigneur-Meynier and Gandemer, 1991). The fact that manipulation of the diet can dramatically change IMF content (Candek-Potokar et al., 1998b) without any clear effects on myofiber type composition (Candek-Potokar et al., 1998a) also supports these results. A practical implication is that total IMF content and myofiber type composition can be manipulated independently. Positive correlations between the percentage or relative area of αW fibers and various indices of fat (subcutaneous and intramuscular fat) were observed in bovine (Seideman et al., 1986) and ovine (Hawkins et al., 1985) muscles. Because percentage of αW fibers and intramuscular fat content normally increase with weight (Solomon et al., 1986), these correlations can be interpreted in terms of physiological maturity. Contrary to data regarding total IMF content, a close relationship exists between fiber type composition and the content and nature of phospholipids (Leseigneur-Meynier and Gandemer, 1991; Alasnier et al., 1996). In particular, oxidative muscles contain more phospholipids than glycolytic muscles. Because phospholipids are major determinants of cooked meat flavor (Meynier and Gandemer, 1994), muscle fiber type composition is likely to influence flavor.

Increasing muscle fiber CSA, in particular that of αR fibers, has been associated with lower instrumental tenderness in pork (Maltin et al., 1997). At a commercial BW, no consistent phenotypic correlations between CSA and IMF have been reported in pigs (Sosnicki, 1987; Essén-Gustavsson et al., 1994; Larzul et al., 1997). However, recent results indicate a significant positive genetic correlation (r_g = .68) between IMF and CSA in Large White pig longissimus muscle (Larzul et al., 1997).

Postmortem Maturation of Meat

Another important aspect of meat quality deals with postmortem maturation, which leads to decreased shear force values and improved tenderness. As shown by Dransfield et al. (1981), 80% of tenderizing occurs within approximately 4 d in pork, 8 d in lamb, and more than 10 d in beef. Several studies have shown that maturation rate is faster in fast twitch than in slow twitch oxidative muscles (reviewed by Seideman, 1986; Ouali et al., 1988; Totland et al., 1988; Ouali, 1990). The role of proteases and their inhibitors in regulating toughening and tenderization processes of meat (Koohmaraie, 1996) could explain differences of maturation between muscles. Indeed, a study including different muscles in cattle, pigs, and sheep reported that the calpain/calpastatin ratio is higher in fast-twitch glycolytic than in slow-twitch oxidative mucles (Ouali and Talmant, 1990), which could partly explain the faster rate of maturation in glycolytic muscles. From a practical point of view, increasing the proportion of glycolytic fibers could have beneficial effects on tenderness in beef by increasing the rate of p.m. maturation and subsequent instrumental tenderness (Seideman et al., 1986). However, Maltin et al. (1998) found the opposite for sensory tenderness in bull meat allowed to mature for 14 d at 2°C.

As evidenced by the presented data, the superior fiber type for meat quality has not been identified. Moreover, this could differ between species. Indeed, increasing glycolytic fibers could be beneficial in beef by stabilizing color and increasing rate of p.m. maturation, whereas it could decrease water-holding capacity in pork. In the future, highly controlled experiments need to be conducted to examine the specific role of variation in muscle fiber characteristics in determining meat quality.

Final Remarks

Meeting the challenge of optimizing efficiency and enhancing meat quality requires a thorough understanding of the mechanisms that regulate muscle fiber development and diversification, as well as a better knowledge of the relationships with meat quality and growth performance. This review shows that muscle fiber type composition is highly variable and can be modified by genetic and environmental factors. The discovery of major genes with a strong effect on muscle development opens new research areas to better understand the origin of the variability of muscle fiber type composition in farm animals. Advances in genetic engeneering open new areas for producing transgenic farm animals once genes controlling muscle growth and meat quality have been identified. However, the relatively high heritability of some histochemical characteristics also suggests that conventional techniques are possible for selecting populations of animals differing in muscle fiber type compositions. Once established, these populations could be used to determine the significance of muscle fiber type in controlling growth performance and meat quality and to identify the superior fiber type for meat production. In light of recent data revealing the presence of at least four adult myosin heavy chains (MyHC) in the pig, the significance of MyHC polymorphism for meat production and a better understanding of the mechanisms underlying their expression are needed. From a practical point of view, because of the dramatic changes that occur during the early postnatal period, altering muscle fiber type at this time seems possible. Finally, because of the influence of total number of fibers (TNF) on muscle growth capacity, and perhaps meat quality, a better understanding of the mechanisms that regulate TNF is a major issue. Increasing TNF without increasing muscle fiber size may be the most plausible strategy for increasing the productivity of meat animals without compromising meat quality.

Implications

Muscle fiber type composition is highly variable and can be influenced by many intrinsic and extrinsic factors. The difficulty of controlling all of these factors within an experiment makes the identification of a strong correlation between fiber type, meat quality, and growth performance complicated. In particular, meat scientists investigating the effects of nutritional or environmental factors on muscle fiber type composition and meat quality must take into account the large effects that individual and genetic variability can have on experimental results. Conventional selection and the identification of new genes controlling the total number of fibers, their types, and meat quality are promising ways to improve meat quality while optimizing growth performance. However, more basic research is still needed to better understand the mechanisms underlying myogenesis in farm animals.

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Notes

1. Contribution from the Purdue University Agricultural Research Programs Journal Paper No. 16,281.
2. Correspondence.

Table 1. Biochemical characteristics of individual fiber types
(+, low; ++, medium; +++, high)

Contractile type	Slow-twitch (type I or β)	Fast-twitch (type II or α)	
Metabolic type	Oxidative	Oxido-Glycolytic	Glycolytic
Fiber type[ab]	βR	αR	αW
	I	IIA	IIB
AM-ATPase[c]	+	++	+++
Buffering capacity[d]	+	+++	+++
Glycogen[e]	+	+++	+++
Myoglobin[f]	+++	+++	+
Lipids[g]	+++	++	+
Capillary density[h]	+++	+++	+
Diameter[i]	+	+, ++	+++

[a]Ashmore and Doerr, 1971; [b]Brooke and Kaiser, 1970; [c]Bottinelli et al., 1994; [d]Talmant et al., 1986; [e]Peter et al., 1972; [f]Morita et al., 1970; [g]Essen-Gustavsson et al., 1994; [h]Hudlicka, 1985; [i]Kiessling and Hansson, 1983; Larzul et al., 1997.

Table 2. List of some factors influencing histological traits

	Total	Fiber type	
Item	no. of fibers	Percentage	Diameter
Muscle	***[a]	***	**
Species	***	**	*
Breed	***	**	*
Individual	**	**	**
Sex	NS	**	**
Fetal nutrition	**	*	**
Postnatal nutrition	NS	*	**
Ambient temperature	NS	**	*
Exercise	NS	**	**
Growth-promoting agents (postnatal)			
Growth hormone	NS	NS	**
β-Agonists	NS	**	**
Steroids	NS	**	**

[a]Intensity of effects (***, very strong; **, strong; *, medium; NS, not significant).

Table 3. Effects of major genes on histochemical traits of valuable muscles in different species

	Major genes				Transgenes	
Item	Halothane[a]	Double-muscling[b]	Callipyge[c]	RN[d]	GH[e]	IGF-I[f]
Species	Pig	Cattle	Sheep	Pig	Pig	Pig
Total no. of fibers	=	↗	=	=	ND[h]	ND
White fibers						
Number, %	↗	↗	↗	↘	=	=
CSA[g], µm^2	↗	↗	↗	=	↘	↗
Relative area, %	↗	↗	↗	↘	↘	↘
Red fibers						
CSA, µm^2	↗	=	=	↗	↗	↗

[a] Lindholm et al., 1977; Essén-Gustavsson et al., 1992, Depreux et al., 1998.

[b] Holmes and Ashmore, 1972; Ashmore et al., 1974; Swatland and Kieffer, 1974; West, 1974.

[c] Koohmaraie et al., 1995; Carpenter et al., 1996.

[d] Lebret et al., 1998.

[e] Solomon et al., 1991b.

[f] Bee et al., 1997.

[g] Not determined.

[h] Cross-sectional area.

Table 4. Effect of ambient temperature on percentage of type I fibers in pig skeletal muscle

Stage	Temp.,°C	Muscle	Type I
3 wk–6 mo[a]	28 vs 12	Longissimus	NS
		Semispinalis	+37%**
3 wk–8 wk[b]	25 vs 8	Longissimus	NS
		Rhomboideus	+22%*
3 wk–7 wk[c]	6 vs 10	Longissimus	+ 38%*
		Rhomboideus	+71%***

[a] Lefaucheur et al., 1991.

[b] Herpin and Lefaucheur, 1992.

[c] Harrison et al., 1996.

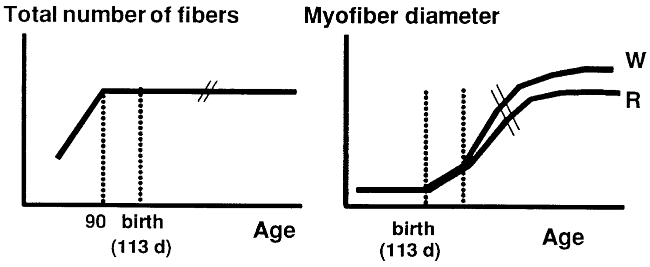

Figure 1. Morphologic changes in pig skeletal myofibers during development (adapted from Cooper et al., 1970; Thurley, 1972; Ashmore et al., 1973; Stickland and Goldspink, 1973; and Swatland, 1973).

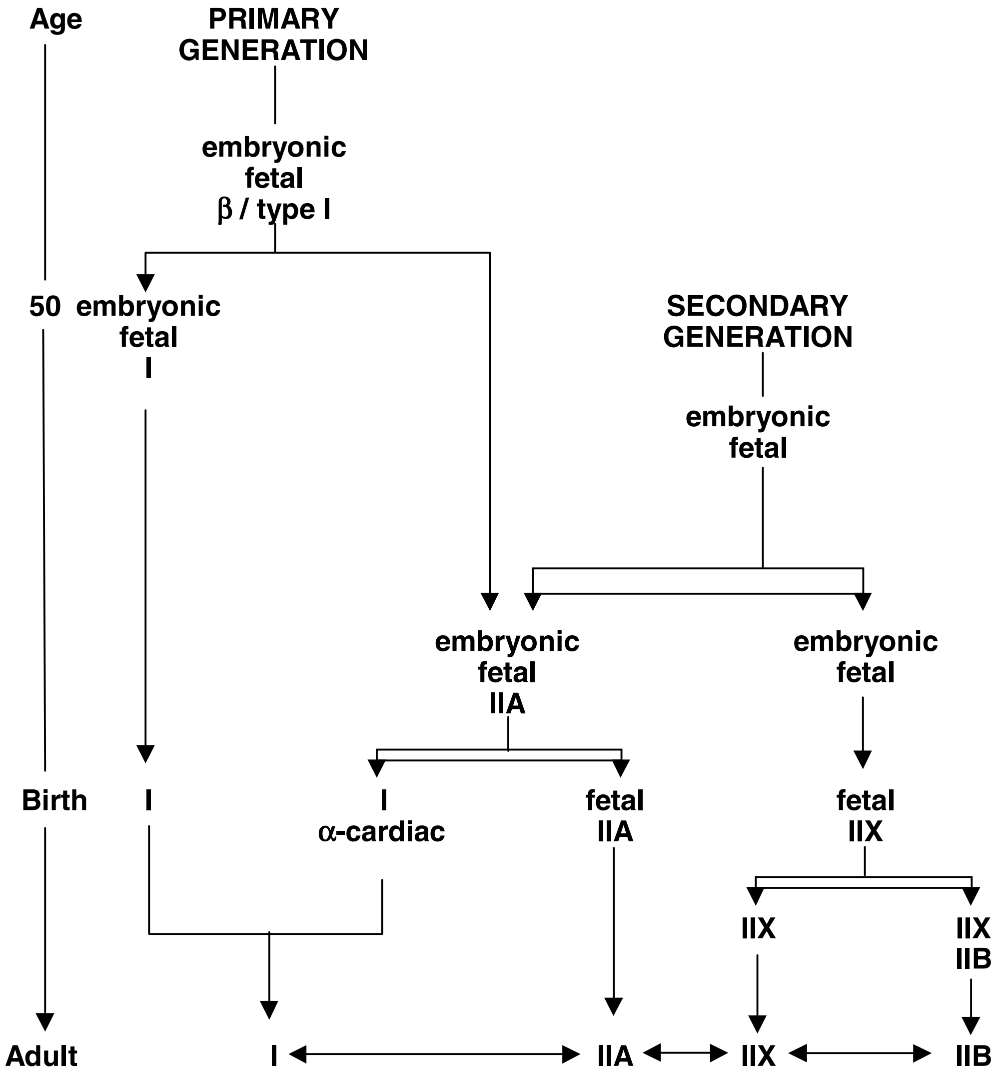

Figure 2. Schematic representation of fiber type differentiation in developing skeletal muscle of pigs based on myosin heavy chain isoform transitions (adapted from from Lefaucheur et al., 1995, 1997; and Chang et al., 1993, 1995, 1997).

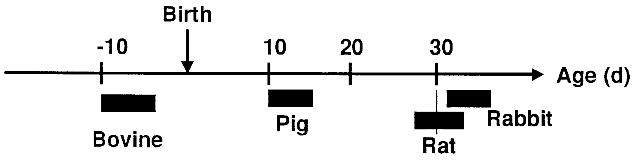

Figure 3. Disappearance of the fetal myosin heavy chain in skeletal muscle of different mammalian species.

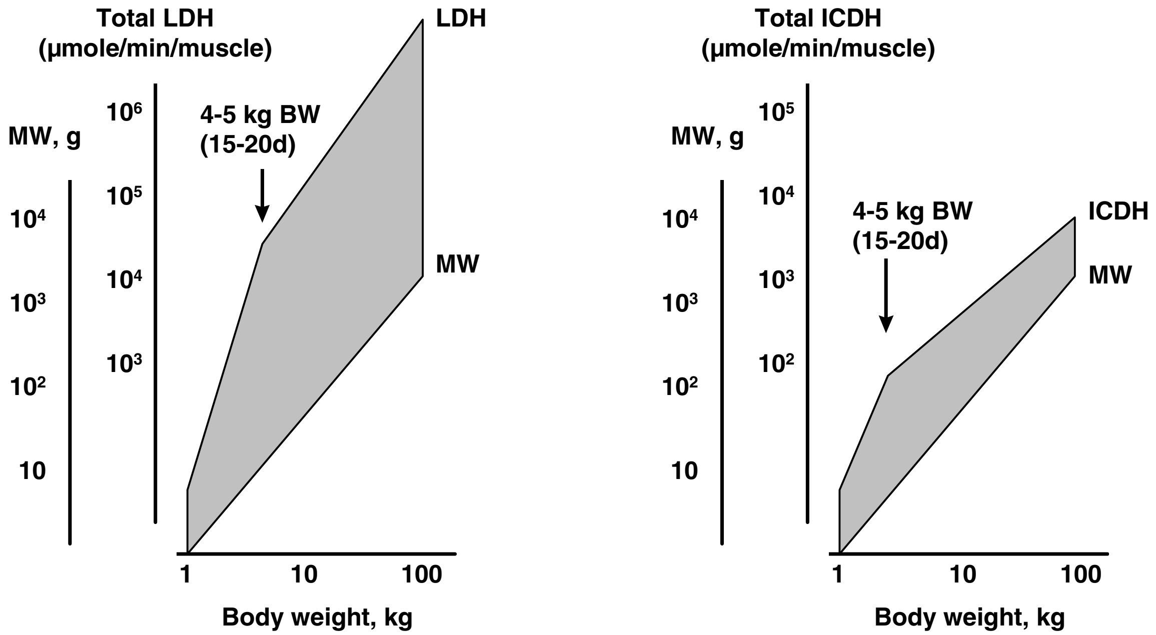

Figure 4. Allometric increases in muscle weight (MW), total lactate dehydrogenase (LDH), and isocitrate dehydrogenase (ICDH) activities in pig longissimus during the postnatal period (adapted from Lefaucheur and Vigneron, 1986).