Growth- and breed-related changes of muscle fiber characteristics in cattle[1]

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ABSTRACT: The objective of this study was to investigate the growth- and breed-related changes of muscle fiber characteristics in cattle and their importance to meat quality. Four cattle breeds with different growth impetus and muscularity were reared and slaughtered under experimental conditions. German Angus as a beef type, Galloway as a hardy type, Holstein Friesian as a dairy type, and double-muscled Belgian Blue as an extreme type for muscle growth were used. Between 5 and 17 bulls of each breed were slaughtered at 0, 2, 4, 6, 12, 18, and 24 mo of age. Muscle fiber traits were determined and classified by computerized image analysis, and several measures of meat quality were also determined, including shear force value, meat color, and i.m. fat content. The postnatal growth of semitendinosus muscle in cattle was characterized by a nearly 10-fold increase of muscle fiber area from birth to 24 mo of age. In the first few months after birth, a transformation of type IIA fibers into IIB fibers was found, whereas type I fibers were nearly unaffected by age. The apparent total muscle fiber number of semitendinosus muscle did not increase during postnatal life. These results confirm that the fiber number is determined in embryonic development. Throughout the study, the double-muscled Belgian Blue (BBDM) bulls had almost twice the fiber number of the other breeds, emphasizing a more extensive hyperplasia of muscle fibers during embryonic development in BBDM compared with the other three breeds. The apparent number of type I fibers was, however, not affected by breed, which suggests that the additional fibers found in BBDM postnatally were type IIB and IIA fibers. We did not find significant differences in muscle fiber total number, muscle fiber type frequencies, or meat quality characteristics among breeds, with the exception of BBDM. Having pooled the four breeds, paler meat was related to a higher frequency of type IIB fibers, a lower area of type IIA and type I fiber, and a higher total muscle fiber number. These findings based on data of double muscling give us some hints for biological causes for the variation of meat quality. Further investigation, in particular within each breed, is necessary to identify the superior fiber traits for bovine meat production.

Key Words: Breed Differences, Cattle, Growth, Meat Quality, Muscle Fibers

Introduction

In animal breeding and husbandry extensive efforts have been focused on the efficient production of leaner meat. Increased muscle mass can principally be achieved by enhancements in muscle fiber number, an increase in fiber size, and(or) fiber transformation from small, slow-twitch fibers to large, fast-twitch fibers. The investigation of muscle fiber characteristics is therefore of practical importance to meat scientists, breeders, and the meat industry to provide a better understanding of the involvement of muscle fibers with regard to the determination of muscle growth and final meat quality traits. Attempts have been made to document the relationships between muscle fiber size and type frequencies in pigs (Staun, 1972; Swatland, 1982; Henckel et al., 1997), as well as the relationships between total muscle fiber number and growth and meat quality (Dwyer et al., 1993; Rehfeldt et al., 1993; von Lengerken et al., 1994). Furthermore, a few studies have estimated the heritability of muscle fiber characteristics and their phenotypic and genetic correlations with growth, carcass, and meat quality traits (Staun, 1972; Fiedler et al., 1997; Larzul et al., 1997).

Previously, Tuma et al. (1962) and Calkins et al. (1981) observed correlations in cattle between fiber diameter, fiber type composition, and meat shear force values. Some more recent studies suggest relationships between fiber type or size and eating quality, especially tenderness in beef (Seidemann et al., 1988; Crouse et al., 1991; Maltin et al., 1998), but the precise relationship remains undefined. Whipple et al. (1990) and Vest-

ergaard et al. (2000b) found no correlations between muscle fiber traits and tenderness. Although the results are variable and sometimes contradictory, the current evidence suggests relationships exist between muscle fiber characteristics and meat quality, particularly in pork (Klont et al., 1998).

The objective of this study was to investigate the growth- and breed-related changes of muscle fiber characteristics in cattle and their importance to meat quality. In this study, we investigated these characteristics in cattle from birth to 24 mo of age, beyond the typical slaughter age for beef cattle.

Materials and Methods

Animals

Bulls of four breeds of cattle with different muscle growth potential were used. The breeds represent German Angus (**GA**) as a beef type, Galloway (**G**) as a hardy type, Holstein Friesian (**HF**) as a dairy type, and double-muscled Belgian Blue (**BBDM**) as an extreme type for muscle growth. Bulls were raised using a tethering system with individual feeding. Calves received a milk replacer diet up to 4 mo of age and were then weaned to a diet consisting of wilted grass silage (1.8 kg dry matter), maize silage (.5 kg dry matter), and concentrates (5.1 kg dry matter) based on barley grain (92% organic matter, 15% crude protein, and 25% crude fiber). The proportion of concentrate in the diet was 70% (DM basis). Animals were restrictively fed concentrates, depending on live weight, and were given ad libitum access to silage. Between 5 and 17 bulls of each breed were slaughtered at 0, 2, 4, 6, 12, 18, and 24 mo of age. All animals were cared for and killed according to German rules and regulations for animal care.

Tissue Collection

After slaughter, chilling at 6°C for 24 h, and dressing, the semitendinosus muscle was removed from the left side of the carcass, trimmed of any external fat, measured (muscle length), and weighed. Muscle cross-section areas were measured on a 1 cm-thick muscle slice using a computerized image analysis system (Quantimet 570, Cambridge Instruments, Leica, Bensheim, Germany) to be used for the calculation of apparent muscle fiber number. Muscle samples (.7 cm^3) for histochemistry taken at the same location as the cross-section areas were measured in the middle region of the muscle (muscle length/2) and .5 cm under the skin (superficial, pale region of semitendinosus muscle) according to the studies of Totland and Kryvi (1991).

Histochemistry

Samples were immediately frozen in liquid nitrogen and stored at −70°C. Transverse sections, 10 μm thick, were cut using a Cryostat 2800 Frigocut (Reichert-

Jung, Leica, Bensheim, Germany). For fiber typing in cattle, we adapted the method validated for pigs by Szentkuti and Eggers (1985), based on the technique of Brooke and Kaiser (1970). Sections were reacted for actomyosin Ca^{2+} adenosine triphosphatase stability after alkaline preincubation (pH 10.4) and then stained with azure II (Chroma-Gesellschaft, Schmid GmbH, Köngen, Germany). The reaction is highly sensitive for changes in pH and was finely adjusted to allow for clear discrimination between three fiber types, one slow-twitch (type I) and two fast-twitch fiber types (types IIA and IIB) (Figure 1). In the literature (for review, see Brandstetter, 1996), depending on the author and the histochemistry employed, the three main types of muscle fibers were classified as type I (slow-twitch oxidative, slow oxidative, beta red, or red fibers), type IIA (fast-twitch oxidative, fast oxidative glycolytic, alpha red, or intermediate fibers), or as type IIB (fast-twitch glycolytic, fast glycolytic, alpha white, or white fibers). Terms in the discussion will be used as they were used in the original publications. The method used in this investigation is a new, simplified technique applied to samples taken 24 h after slaughter from birth to 24 mo of age. It can be used for large-scale investigations in cattle.

Image Analysis

A minimum of 300 muscle fibers per animal in randomly selected muscle fiber primary bundles were measured and classified by computerized image analysis (Quantimet 570, Cambridge Instruments). The Quantimet 570 device was equipped with a 3-CCD color camera (Sony, Japan) and a transmission light microscope (Jenaval, Zeiss Jena, Germany). After calibration, image setup, and acquisition, a delineation for enhancing the transition between muscle fibers and connective tissue was made. The dark fibers (type IIB) were detected by their color and measured first. Adjacent fibers were separated by a binary segmentation operation. The result can be corrected interactively; therefore, fibers still touching were separated by drawing a line. Artifacts were deleted and holes were closed. The light fibers (type I) were subsequently detected by their color and measured after elimination of all previously measured fibers from the image via a gray mask operation. For cleaning of the image a binopen operation was used. An interactive correction was possible before measuring the fiber size. The measurement of the gray fibers (type IIA) followed the same procedure as for the white. The resulting units of measure were muscle fiber cross-section area, frequency of each muscle fiber type, and muscle fiber number per square centimeter. The apparent total muscle fiber number of semitendinosus muscle was calculated from the muscle cross-section area and muscle fiber density (fiber number per square centimeter).

Meat Quality Traits

We used standard procedures of our laboratory for determination of meat quality traits: shear force value at d 1, meat color (brightness), and i.m. fat content of semitendinosus muscle. Tenderness was estimated by measuring the shear force with the Warner-Bratzler shear force measuring equipment (Emerson Electric,

Figure 1. Cross-sections of semitendinosus muscle from (A) newborn and (B) 24-mo-old Holstein Friesian bulls. Histochemical staining of fiber types with ATPase.

St. Louis, MO). A muscle sample of approximately 250 g and 4 cm in thickness was wrapped in aluminum foil and heated in an oven at 160°C for 75 min and then cooled for 90 min. Three cylinders of meat were cut with a sharpened metal tube 2.54 cm in diameter. These cylinders were cut and the average value of the maximal forces was taken as shear force value (Otto and Stang, 1975). Brightness was measured with a Minolta CR 200 (Minolta GmbH, Ahrensburg, Germany) with triplicate measurement on the freshly cut surface of semitendinosus 24 h postmortem using the parameter L* (L = 0 designates black and L = 100 designates pure white). The i.m. fat content of semitendinosus muscle samples was obtained via the Soxhlet extraction method using petroleum ether as the solvent and determined gravimetrically after evaporating the extracting solvent.

Statistics

The experimental units were bulls of four breeds, slaughtered at a predetermined stage of age. The data were submitted for analysis of muscle fiber and meat quality traits with a two-way classification model using the GLM procedure of SAS (1988). The factors considered were age and breed and the interaction between them. We computed pair-wise comparisons between the least square means of the factor levels and of the subgroups (i.e., bulls of the same breed slaughtered at the same age) by applying the PDIFF option of the LSMEANS statement of SAS to the effect of age group, breed, and age group × breed. Along with the standard errors, the standard deviations of the subgroups are presented in order to show the variance heterogeneity caused by different age groups and breeds. For the investigation of changes of the fiber traits in dependence on age, linear regression has been applied to three age groups (0 to 2 mo, 2 to 6 mo, and 6 to 24 mo) by using the procedure REG of SAS.

The relationship between muscle fiber characteristics and meat quality traits was analyzed by the CORR procedure of SAS. The simple Pearson's correlation coefficient describing the relationship among all bulls and the partial Pearson's correlation coefficient describing the relationship among bulls of the same age group were determined. This turned out to be essential because for some traits the coefficients were positive over all age groups but negative within the age groups. An analysis within breeds or age groups was only performed if noted.

Results and Discussion

Muscle Fiber Size

The increase of carcass weight and the growth of semitendinosus muscle of different breeds are shown in Tables 1 and 2. We found that the breeds (GA, G, HF, and BBDM) exhibited 50-, 43-, 36-, and 34-fold (respectively) increases in carcass weight and 31-, 27-,
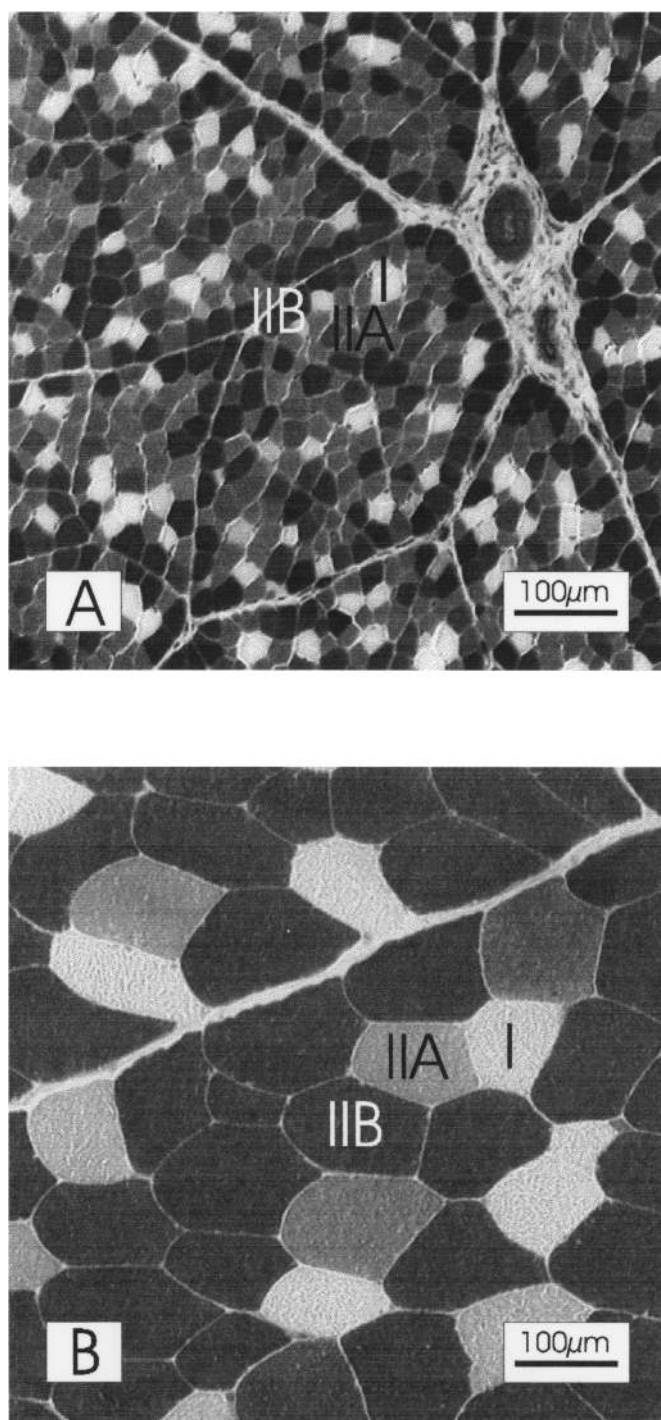
Table 1. Carcass weight of different cattle breeds during growth (kg)[a,b]

Breed	0	2	4	6	12	18	24	Mean
GA								
LS mean	8.5^c	48.8^d	81.2^{eC}	100.8^{eC}	212.2^{fC}	330.2^{gC}	429.4^{hC}	173.0^C
SD	1.1	6.7	13.1	11.9	16.7	23.3	20.8	
n	6	5	6	10	10	14	17	
G								
LS mean	10.7^c	46.1^d	66.1^{deC}	86.5^{efC}	186.2^{gD}	262.3^{hD}	357.6^{iD}	145.1^D
SD	4.8	9.2	12.7	9.4	17.5	29.1	26.6	
n	8	8	7	11	10	14	14	
HF								
LS mean	11.2^c	43.5^d	72.4^{eC}	100.6^{fC}	217.9^{gC}	317.8^{hC}	401.0^{iE}	166.3^C
SD	2.3	3.3	4.4	13.4	18.2	34.9	34.1	
n	6	10	10	10	10	12	12	
BB								
LS mean	15.9^c	50.8^d	102.0^{eD}	125.6^{fD}	264.3^{gE}	395.9^{hE}	475.6^{iF}	204.3^E
SD	4.6	4.9	14.8	20.5	11.2	63.1	37.5	
n	9	9	10	8	9	16	14	
Mean	11.6^c	47.3^d	80.4^e	103.4^f	220.2^g	326.6^h	415.9^i	

[a]The sources of variation included in the analysis were age group ($P = .0001$), breed ($P = .0001$), and their interaction ($P = .0001$). Standard errors may be evaluated by SE = $24.9/\sqrt{n}$ per subgroup.

[b]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

[c,d,e,f,g,h,i]Means with different superscripts are significantly different ($P < .05$); lowercase letters refer to differences between the age groups and capital letters to differences between the breeds.

19-, and 25-fold (respectively) increases in muscle weight from birth to 24 mo. The increase in muscle weight during growth was the result of the increase in muscle fiber cross-sectional area (approximately 9 to 10-fold) (Table 3) and the increase in muscle length (approximately two- to threefold) (data not shown). The double-muscling of the BBDM was already apparent in the weight of the semitendinosus at birth. Muscle mass can be enhanced through an increase in muscle fiber number and/(or) an increase in fiber size.

The 9-to 10-fold increase in mean muscle fiber cross-sectional area from birth to 24 mo was nearly linear

Table 2. Semitendinosus muscle weight of different cattle breeds during growth (g)[ab]

Breed	0	2	4	6	12	18	24	Mean
GA								
LS mean	107^{cCD}	403^{cdCE}	702^{deC}	824^{eC}	1,748^{fC}	2,565^{gC}	3,326^{hC}	1,382^C
SD	24	61	113	121	143	255	330	
n	6	5	6	10	10	14	16	
G								
LS mean	100^{cC}	360^{cdD}	497^{deD}	685^{eC}	1,521^{fCD}	2,148^{gD}	2,648^{hD}	1,137^D
SD	25	86	121	94	198	375	347	
n	8	8	6	11	10	14	14	
HF								
LS mean	151^{cC}	317^{cdCD}	562^{deD}	722^{fC}	1,604^{fD}	2,344^{gD}	2,832^{hD}	1,219^D
SD	42	45	75	128	208	255	359	
n	6	10	10	10	10	8	10	
BB								
LS mean	214^{CD}	500^{cdE}	1,032^{eE}	1,349^{eD}	3,136^{fE}	5,261^E	5,432^{gE}	2,418^E
SD	61	81	195	279	418	700	715	
n	9	9	10	8	9	8	14	
Mean	143^c	395^d	698^e	895^f	2,002^g	3,080^h	3,560^i	

[a]The sources of variation included in the analysis were age group ($P = .0001$), breed ($P = .0001$), and their interaction ($P = .0001$). Standard errors may be evaluated by SE = $299/\sqrt{n}$ per subgroup.

[b]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

[c,d,e,f,g,h,i]Means with different superscripts are significantly different ($P < .05$); lowercase letters refer to differences between the age groups and capital letters to differences between the breeds.

Table 3. Mean muscle fiber cross-sectional area in semitendinosus muscle of different cattle breeds during growth $(\mu m^2)^{ab}$

Breed	Slaughter age, mo							Mean
	0	2	4	6	12	18	24	
GA								
LS mean	618[c]	1,348[c]	2,268[dC]	2,244[d]	3,636[e]	5,005[fC]	6,631[gC]	3,107[C]
SD	9	168	435	381	556	756	1,344	
n	2	5	6	10	10	11	13	
G								
LS mean	618[c]	893[c]	1,829[dC]	1,682[d]	3,576[e]	4,272[fD]	6,018[gD]	2,698[D]
SD	175	348	430	259	728	763	88	
n	4	7	7	11	10	12	3	
HF								
LS mean	550[c]	1,237[cd]	1,773[deCD]	1,888[e]	3,154[f]	3,562[fE]	4,812[gE]	2,425[D]
SD	72	192	396	415	1,004	611	1,085	
n	5	10	10	10	10	10	10	
BB								
LS mean	558[c]	905[cd]	1,462[deD]	1,963[e]	3,500[f]	5,179[gC]	5,058[gDE]	2,661[D]
SD	159	298	212	521	873	1,125	1,024	
n	9	6	7	8	9	14	12	
Mean	586[c]	1,096[d]	1,833[e]	1,944[e]	3,467[f]	4,504[g]	5,630[h]	

[a]The sources of variation included in the analysis were age group ($P = .0001$), breed ($P = .0001$), and their interaction ($P = .0001$). Standard errors may be evaluated by SE = $722/\sqrt{n}$ per subgroup.

[b]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

[c,d,e,f,g,h]Means with different superscripts are significantly different ($P < .05$); lowercase letters refer to differences between the age groups and capital letters to differences between the breeds.

(r^2: GA = .86, G = .87, HF = .79, BBDM = .81), indicating that hypertrophy determined the postnatal muscle growth. Between 4 and 6 mo of age, the rate of fiber cross-sectional area increase slowed ($P > .19$) (Table 3 and split for fiber types in Figure 3). This retardation of muscle growth can be attributed to weaning, the developmental stage at which calves change from being monogastrics to ruminants. They require a period of several weeks to adapt to solid feed and during this time are in a state of undernutrition. Double-muscled Belgium Blue bulls showed a retardation of growth in semitendinosus muscle weight and muscle fiber cross-sectional area from 18 to 24 mo of age. After comparing the weights of different muscles from 0 to 24 mo of age in BBDM, we observed a retardation only of semitendinosus muscle following a higher growth rate; we did not observe this retardation in other muscles at other stages of growth. Perhaps the semitendinosus reached a growth plateau at this age. In order to elucidate this finding more research is needed. The group of BBDM grew more slowly than the other groups from 18 to 24 mo of age. This was an unexpected result in this investigation and was caused by a lack of experience in working with BBDM at this late age. We repeated the statistical analysis ignoring this group. There were no statistical differences.

Between the beef breed GA and the other breeds we found highly significant differences in fiber area. In particular, the differences between GA and HF were associated with differences in muscle weight (Table 2), because the apparent muscle fiber numbers were not

significantly different between these breeds (Table 4). The mean fiber area of BBDM was not greater than that of G and HF (Table 3), therefore, we conclude that the greater muscle weight in double-muscled cattle is not the result of muscle fiber hypertrophy. At all ages tested, a comparison between fiber size and type revealed type I fibers to be the smallest, type IIB to be the largest and type IIA to be intermediate in size, in accordance with the findings of Brandstetter et al. (1996). Type I fibers were lesser in both frequency (Figure 2) and size (Figure 3) in BBDM than in the other breeds. This led to a still more pronounced decrease in relative area of type I fibers in BBDM bulls compared to those of other breeds.

Apparent Muscle Fiber Number

The analysis of variance demonstrated a highly significant influence of breed and no influence of age ($P = .77$) on apparent muscle fiber number (Table 4). The constant fiber number demonstrated for all ages agrees with the fact that the fiber number is determined in embryonic development and does not increase during postnatal development (Luff and Goldspink, 1970; Rehfeldt et al., 1987). Apparent muscle fiber number of semitendinosus from BBDM bulls was, on average, about twice that of semitendinosus from other breeds. This emphasizes that a more extensive hyperplasia of muscle fibers (increase in muscle fiber number during prenatal growth and development) in BBDM than in the other three breeds was responsible for the higher

muscle weights. The apparent number of type I fibers was slightly affected by breed ($P = .08$). The only significant pairwise comparison between breeds appeared between G and BBDM; this implies that the additional fibers found in the BBDM were mostly type IIB and IIA fibers. Interpretation of these data should take into account that apparent fiber number is only a rough measurement and the results are highly variable. Picard et al. (1998) showed that muscle differentiation of double-muscled fetuses is delayed, a consequence of a higher proliferation phase and a latency phase of fusion. Therefore, at birth double-muscled cattle have a higher total number of muscle fibers and more fast-twitch fibers than cattle with normal musculature. Previously, Ouhayoun and Beaumont (1968) compared double-muscled and normal animals at 3, 15, and 20 mo of age and found smaller fibers and a greater fiber number in double-muscled animals. Grobet et al. (1997) demonstrated that a mutation in the bovine myostatin gene is responsible for the double-muscled phenotype.

Muscle Fiber Type Frequencies

Muscle fiber transformation is well-documented in rodents, pigs, and sheep (for review, see Pette and Staron, 1997). In cattle, however, contradictory results have been published, leading to conflicting views regarding fiber type changes with age. To our knowledge, the present study is the first to provide ontogeny data on this subject from birth to 2 y of age in several breeds of cattle.

The main fiber type changes occurred in the first few months of life (Figure 2). We found that the linear regression coefficients of the fiber type frequencies differed significantly from 0 mainly in the first 2 mo (Table 5). Increasing age from birth to 2 mo resulted in an increased frequency of type IIB fibers and a decreased frequency of type IIA fibers in all breeds. Type I fiber frequency remained constant; therefore, the increased frequency of type IIB fibers occurred at the expense of type IIA fibers. From 2 to 6 mo, the changes of type IIA fibers into type IIB fibers strongly decreased. This is documented by decreased values of the linear regression coefficients as well as lower significance values. From 6 to 24 mo linear changes seldom occurred. Picard et al. (1995) showed the percentage of type I fibers rose significantly in male Montbeliard cattle between 66 and 170 d of age. This increase was not observed in the breeds investigated here. Our findings on type IIA to type IIB fiber conversion partly agree with those of Jurie et al. (1995). They found in semitendinosus muscle of male Limousin cattle between 1, 6, and 12 mo of age a conversion of fast oxidative glycolytic fibers to fast glycolytic fibers. After 12 mo of age, the fiber type frequency was constant. In our investigation the conversion had occurred as early as 6 mo. The large decline in type IIB fiber proportion at the last slaughter age of 16 mo as reported by Brandstetter et al. (1998) was not observed in our study. In GA and G we found a significant but very small decrease of frequency of type IIB fibers. A larger sample size and the use of four cattle breeds gives credence to our results.

Similar results were observed in porcine longissimus biopsies from 70 to 220 d of age (Wegner et al., 1993b). From 70 to 100 d of age we found an increase ($P < .05$)

Table 4. Apparent total fiber number in semitendinosus muscle of different cattle breeds during growth ($\times 10^6$)[ab]

Breed	\	Slaughter age, mo						Mean
	0	2	4	6	12	18	24	
GA								
LS mean	2.09[C]	1.85[C]	1.63[C]	1.66[C]	1.78[C]	1.84[C]	1.71[C]	1.79[C]
SD	.04	.42	.33	.35	.25	.29	.40	
n	2	5	6	10	10	11	11	
G								
LS mean	1.30[C]	1.56[C]	1.41[C]	1.89[C]	1.70[C]	1.73[C]	1.59[C]	1.60[C]
SD	.29	.31	.29	.24	.27	.40	.15	
n	4	7	6	11	10	12	3	
HF								
LS mean	1.97[C]	1.68[C]	1.58[C]	1.82[C]	1.82[C]	2.00[C]	1.83[C]	1.82[C]
SD	.36	.38	.30	.52	.39	.41	.30	
n	5	10	10	10	10	7	8	
BB								
LS mean	3.49[D]	3.55[D]	3.56[D]	3.06[D]	3.12[D]	3.46[D]	3.36[D]	3.37[D]
SD	1.20	1.18	.98	.83	.42	.67	.53	
n	9	6	7	8	9	7	12	
Mean	2.21	2.16	2.05	2.11	2.10	2.26	2.12	

[a]The sources of variation included in the analysis were age group ($P = .77$), breed ($P = .0001$), and their interaction ($P = .59$). Standard errors may be evaluated by $SE = .521/\sqrt{n}$ per subgroup.

[b]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

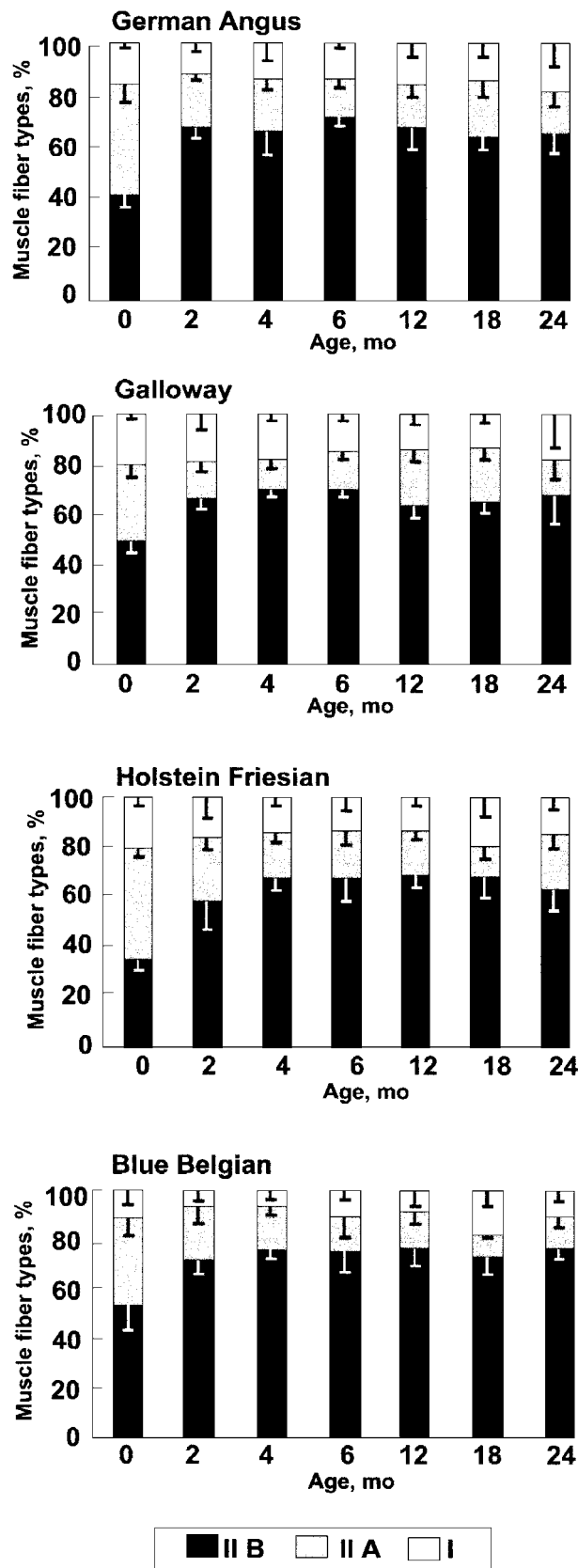[c,D]Means with different superscripts are significantly different ($P < .05$) between breeds.

Figure 2. Changes of fiber type frequencies during growth. Results are expressed as least squares means (columns) and standard deviation (bars).
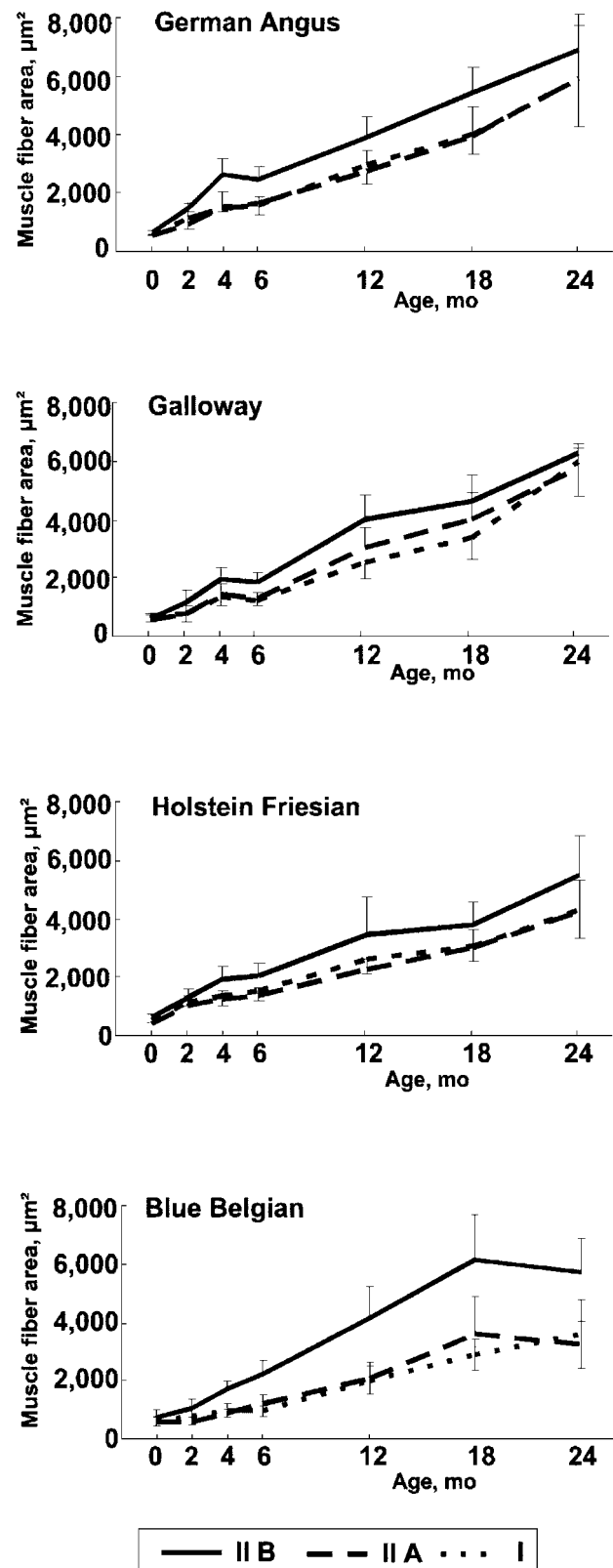
Figure 3. Changes of fiber area during growth. Results are expressed as least squares means (columns) and standard deviation (bars).

Table 5. Linear regression coefficients of fiber type frequencies of different cattle breeds during growth[a]

Fiber type	Slaughter age, mo											
	0, 2				2, 4, 6				6, 12, 18, 24			
	GA	G	HF	BB	GA	G	HF	BB	GA	G	HF	BB
Frequency of type I	−1.9	−2.0	−2.0	−2.6†	.45	−.7	−.7	1.1*	.2	.1	.2	.1
Frequency of type II A	−11.1**	−7.9**	−9.7***	−6.6**	−1.6**	−.04	−1.6**	−1.9†	.1	.2	.1	−.2
Frequency of type II B	13.0***	9.8***	11.6***	9.3***	1.2	.8	2.2*	0.8	−.3*	−.3*	−.2	.0

[a]GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

† $P < .10$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

in type IIB fiber frequency (62 to 70%) and from 100 to 220 d of age no further alterations were observed.

Previously, Kelly and Rubinstein (1980) reported that rat muscles contract slowly at birth and increase their speed during the first few weeks of life. This relatively early fiber type transition was observed in all breeds that we studied. Postnatally, the phenotypic profiles of muscle fibers can change by responding to altered functional demands. The results from Vestergaard et al. (2000a) showed that muscles of young bulls in an extensive production system had relatively more slow-contracting fibers, better vascularization, and higher oxidative metabolic potential than with muscles of intensively fed young bulls housed in tie stalls. The profiles of muscle fibers can also change by a variety of signals (e.g., crossinervation, exercise, immobilization, and electrostimulation; Pette and Staron, 1997). In normal healthy cattle, such as those in our investigation, such factors were not involved. Growth hormone does not affect muscle fiber type proportions (Vestergaard et al., 1995). In our previous work with growing bulls (Wegner et al., 1993a) we found no significant influence of Zeranol on muscle fiber type frequencies. Swatland (1995) mentioned that muscle fibers undergo a continual alteration throughout life as an adaptation to changing functional demands, and that "fiber type" merely reflects the constitution of a fiber at any particular time. We conclude that during normal growth in cattle the transformation of type IIA fibers into type IIB fibers is completed 2 to 6 mo after birth, depending on the breed. The frequency of type I fibers is nearly the same at birth as at 24 mo of age. These findings are in accordance with the relative physiological maturity of cattle at birth in comparison to other mammals.

Variance analysis of fiber type IIB frequencies showed an effect of breed ($P = .0001$) and age ($P = .0001$) but no effect of their interaction ($P = .1$). The least squares mean of breed BBDM (71.9%) differed significantly ($P = .0001$) from the least squares means of the GA, G, and HF breeds, which were 62.8, 64.2, and 61.5%, respectively (Figure 2). Our findings in BBDM are in accordance with those of many authors (Holmes and Ashmore, 1972; West, 1974; for review, see Fiems et al., 1995). Stavaux et al. (1994) analyzed muscle biopsies for fiber types and size from BBDM and HF calves at 2 and 7 mo of age. Independently of age, slow-twitch fiber frequency and area were significantly lower in BBDM than in HF muscles. The area of intermediate fibers was significantly smaller in BBDM than in HF, and fast-twitch fiber frequency and area were greater in BBDM. We could extend and confirm these findings for a wide range of ages, from birth to 24 mo. Previously, Ashmore et al. (1972) reported in their basic work about the postnatal development of muscle fiber types that the increasing degree of muscularity in domestic animals is achieved by practices (i.e., domestication and selection) that favor transformation of intermediate fibers to fast-twitch fibers.

Relationship to Meat Quality

The relationship between variations in muscle fiber characteristics in farm animals and the ultimate eating quality of meat has been studied for many years (see Introduction). Conclusions from these studies suggest relationships between fiber type and size and eating quality, particularly in pigs, but the precise relationship in cattle remains undefined. The main goal of our study was to investigate the growth- and breed-related changes of muscle fiber characteristics in different cattle breeds. Relationships to meat quality were an additional result. In our investigations, the meat quality traits measured (meat color [Table 6], shear force value [Table 7], and i.m. fat [Table 8]) were not significantly different among GA, G, and HF breeds. The BBDM animals had significantly less i.m. fat and paler meat than the other breeds but nearly similar shear force. The findings for BBDM agree with results of Uytterhaegen et al. (1994) and other authors (for review, see Fiems et al., 1995). The correlation coefficients between muscle fiber characteristics and meat quality traits of semitendinosus muscle are shown in Table 9. It is clear that paler meat and lower i.m. fat are related to a higher frequency of type IIB fibers, a lower area of type IIA

Table 6. Brightness[a] of semitendinosus muscle of different cattle breeds during growth (%)[bc]

Breed	0	2	4	6	12	18	24	Mean
				Slaughter age, mo				
GA								
LS mean	48.8[dDE]	44.3[eD]	40.3[fgD]	44.2[e]	43.0[ef]	38.9[ghD]	37.1[hD]	42.4[D]
SD	1.7	2.1	3.4	3.7	2.1	2.3	1.7	
n	5	5	5	10	10	14	17	
G								
LS mean	46.1[dD]	45.0[deD]	44.4[deE]	43.3[ef]	41.4[f]	38.6[gD]	37.9[gD]	42.4[D]
SD	4.4	2.8	2.8	3.1	3.8	2.0	1.5	
n	7	7	7	11	10	14	14	
HF								
LS mean	50.1[dE]	44.4[eD]	42.8[eE]	44.6[e]	43.3[e]	40.0[fD]	36.9[gD]	43.2[D]
SD	1.7	1.6	2.6	2.9	2.2	1.8	2.8	
n	6	10	10	10	10	12	12	
BB								
LS mean	46.9[dfD]	50.0[eE]	48.6[deF]	45.7[fh]	43.1[g]	44.0[ghE]	40.8[iE]	45.6[E]
SD	2.2	3.2	2.5	3.3	3.3	2.0	2.4	
n	9	9	10	8	9	16	14	
Mean	48.0[d]	45.9[e]	44.0[f]	44.5[f]	42.7[g]	40.3[h]	38.2[i]	

[a]Brightness was measured with a Minolta CR 200 (Minolta GmbH, Ahrensburg, Germany) with triplicate measurement on the freshly cut surface of semitendinosus 24 h postmortem using the parameter L* (L = 0 designates black and L = 100 designates pure white).

[b]The sources of variation included in the analysis were age group (P = .0001), breed (P = .0001), and their interaction (P = .0001). Standard errors may be evaluated by SE = $2.59/\sqrt{n}$ per subgroup.

[c]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

[d,e,f,g,h,i]Means with different superscripts are significantly different (P < .05); lowercase letters refer to differences between the age groups and capital letters to differences between the breeds.

Table 7. Shear force values[a] of semitendinosus muscle of different cattle breeds during growth (kg)[bc]

Breed	2	4	6	12	18	24	Mean
			Slaughter age, mo				
GA							
LS mean	15.9[de]	13.2[deD]	12.9[d]	15.5[eD]	12.7[de]	13.7[de]	14.0[DE]
SD	2.6	6.7	4.6	2.9	1.3	1.6	
n	5	5	8	10	13	15	
G							
LS mean	13.7[de]	18.7[dEG]	14.0[e]	13.6[deDEF]	14.3[de]	14.1[de]	14.8[DE]
SD	3.1	6.9	2.3	2.2	2.1	3.2	
n	3	2	11	10	13	14	
HF							
LS mean	16.5[d]	14.0[deDEF]	13.4[e]	12.0[ef]	12.2[e]	13.2[e]	13.5[D]
SD	2.1	3.5	3.4	2.5	.9	1.8	
n	10	9	10	10	5	11	
BB							
LS mean	14.3[d]	18.2[eG]	12.5[d]	15.6[deDE]	14.4[d]	14.4[d]	15.0[E]
SD	3.5	4.1	5.2	6.5	1.2	4.2	
n	5	7	8	9	7	9	
Mean	15.1[de]	16.0[e]	13.2[f]	14.2[ef]	13.4[f]	13.9[f]	

[a]Tenderness measuring was described by Otto and Stang (1975).

[b]The sources of variation included in the analysis were age group (P = .01), breed (P = .15), and their interaction (P = .16). Standard errors may be evaluated by SE = $3.29/\sqrt{n}$ per subgroup.

[c]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

[d,e,f,g]Means with different superscripts are significantly different (P < .05); lowercase letters refer to differences between the age groups and capital letters to differences between the breeds.

Table 8. Content of i.m. fat[a] of semitendinosus muscle of different cattle breeds during growth (%)[bc]

| Breed | Slaughter age, mo | | | | | | | Mean |
	0	2	4	6	12	18	24	
GA								
LS mean	.43[d]	.32[d]	1.4[eD]	.64[dfD]	1.1[efD]	2.4[gD]	2.4[gD]	1.2[D]
SD	.11	.06	.77	.28	.38	1.2	1.1	
n	5	5	5	10	10	14	15	
G								
LS mean	.49[d]	.55[de]	.51[dE]	.72[dD]	1.1[deD]	1.2[eE]	2.9[fE]	1.1[D]
SD	.32	.10	.34	.27	.37	.85	1.1	
n	6	4	4	11	10	14	14	
HF								
LS mean	.39[d]	.22[d]	.24[dE]	.77[dD]	1.4[eD]	1.5[eE]	2.6[fDE]	1.0[D]
SD	.14	.12	.05	.30	.54	.57	1.2	
n	6	10	10	10	10	5	12	
BB								
LS mean	.22	.23	.19[E]	.14[E]	.39[E]	.43[F]	.64[F]	.32[E]
SD	.07	.25	.06	.05	.12	.26	.43	
n	7	6	7	8	9	7	14	
Mean	.38[d]	.33[d]	.60[d]	.57[d]	1.0[e]	1.4[f]	2.1[g]	

[a]The i.m fat content was obtained via the soxhlet extraction method using petroleum ether as the solvent and determined gravimetrically after evaporating the extracting solvent.

[b]The sources of variation included in the analysis were age group ($P = .0001$), breed ($P = .0001$), and their interaction ($P = .0001$). Standard errors may be evaluated by SE $= .646/\sqrt{n}$ per subgroup.

[c]Values are least squares means (LS means), standard deviation (SD) of the trait in the subgroup, and number (n) of observations per subgroup defined by slaughter age and breed. GA = German Angus, G = Galloway, HF = Holstein Friesian, and BB = Belgian Blue.

[d,e,f,g]Means with different superscripts are significantly different ($P < .05$); lowercase letters refer to differences between the age groups and capital letters to differences between the breeds.

and type I fibers, and a higher total muscle fiber number. These are the traits that differ between BBDM and the other breeds. Shear force was not significantly correlated with muscle fiber traits. We found no significant correlations between muscle fiber characteristics and meat quality in GA, G, and HF. The findings based on data of BBDM give us only some hints about the biological causes of variation in meat quality.

Porcine muscle hypertrophy is associated with large muscle fibers, a high percentage of fast-twitch fibers, and inferior meat quality (PSE) (Swatland, 1982; Weg-

ner et al., 1990; Fiedler et al., 1999). Factors other than fiber cross-sectional area per se are responsible for alteration of meat quality (e.g. sarcoplasmatic reticulum calcium channel disregulation) (Rempel et al., 1995; Küchenmeister et al., 1999). Further investigation, in particular within each breed, is necessary to identify the superior fiber characteristics for bovine meat production.

Implications

The muscularity of cattle results from the total number of muscle fibers at birth, the transformation of type IIA fibers into type IIB fibers, and the hypertrophy of all muscle fiber types postnatally. Excessive muscle hypertrophy in double-muscled Belgian Blue bulls is due to more extensive fiber hyperplasia prenatally and fiber type conversion postnatally, rather than to hypertrophy of muscle fibers alone. With the exception of the double-muscled cattle, the muscle fiber characteristics of cattle have only slightly been altered by breeding (in contrast to pigs) and therefore have no effect on beef quality. In the double-muscled Belgian Blue animals, meat quality problems were found and were likely due to altered fiber type frequencies and lower areas of type IIA and type I fibers associated with this breed.

Table 9. Pearson partial correlation coefficients between muscle fiber characteristics and selected meat quality traits of semitendinosus muscle[a]

Muscle fiber characteristics	Brightness	Shear force	i.m. Fat
Area type IIB	−.02	.07	−.02
Area type IIA	−.26***	.01	.15*
Area type I	−.22**	.07	.17*
Frequency type IIB	.27***	.06	−.27***
Frequency type IIA	−.20**	.03	.23**
Frequency type I	−.18*	−.13†	.14†
Total muscle fiber number	.40***	.16*	−.29***

[a]n = 180.
†$P < .10$.
*$P < .05$.
**$P < .01$.
***$P < .001$.

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