Effects of a quantitative trait locus for muscle hypertrophy from Belgian Texel sheep on carcass conformation and muscularity

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ABSTRACT: A QTL for muscle hypertrophy has been identified in the Belgian Texel breed. A population of F_2 and backcross lambs created from crosses of Belgian Texel rams with Romanov ewes was studied. Effects on carcass traits and muscle development of the Belgian Texel breed polygenes and Belgian Texel single QTL were compared. In both cases, carcass conformation and muscularity were improved. The Texel polygenic environment improved conformation mainly through changes in skeletal frame shape. Segments were shorter and bone weight lower. Muscles were more compact, shorter, and thicker. The single QTL affected muscle development. Thickness and weight of muscles were increased. Composition in myosin changed toward an increase of fast contractile type. The relative contribution of hind limb joint to carcass weight was increased. Differences in skeletal frame morphology among the three genotypes of the single QTL were small. Conformation scoring was mainly influenced by leg muscularity. Back and shoulder muscle development, which largely contributed to variability of muscularity, were less involved in the conformation scoring. Lastly, the QTL explains a small part of differences between these Belgian Texel and Romanov breeds for conformation or muscle development. A large part of genetic variability remains to be explored.

Key Words: Carcass, Hypertrophy, Morphology, Muscularity, Myosin Heavy Chains, Sheep

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Introduction

Muscularity, which is defined as muscle thickness relative to skeleton dimensions (Dumont, 1971; Purchase et al., 1991), is an important economic trait at the trade level in northern European countries. In these countries, retail products are commonly carcass joints, and consumers like plump legs and relatively large chops. Muscularity is not directly assessed at the carcass level because muscles are not visible on the external surface. Commercial evaluation of lamb carcasses relies partly on scoring of conformation using the EUROP five-point scale (E, U, R, O and P, where E has a better conformation than P) and partly on scoring of fatness. Conformation is defined by the thickness of both flesh and fat (s.c. and intermuscular) relative to skeletal dimensions (De Boer et al., 1974). Conformation score is subjective and synthetic, based on visual examination of individual parts of the carcass (leg, saddle, loin, thorax and shoulder).

To improve muscularity, breeds with hypertrophied muscle development can be used. Belgian strains of Texel sheep harbor a QTL with considerable effect on muscular development (Marcq et al., 2002). This effect does not seem to be associated with sensory quality degradation. Improvement of muscularity is often accompanied, in other species, by a decrease in meat sensory quality in relation to changes in contractile type (Klont et al., 1998).

The current study was carried out to 1) determine the effect of the Belgian Texel QTL on carcass traits and contractile type, which were evaluated using determination of myosin isoforms; 2) assess whether the conformation scoring accounted for variation in muscularity, particularly in a population segregating muscle hypertrophy; and 3) investigate further nondestructive objective measurements for carcass trait evaluation, especially muscularity.

Materials and Methods

Animals

This study was performed on a population segregating a QTL for muscle hypertrophy. This QTL has been

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identified in the chromosomal region of the myostatin encoding gene (Marcq et al., 2002). Three Belgian Texel rams chosen within a population of "hypertrophied" subjects were mated to 61 Romanov ewes. The Romanov breed is characterized by high prolificacy and maternal characteristics, but poor conformation. In the first generation, three F_1 rams sired by three different Texel rams and selected for their conformation were mated with 95 F_1 ewes and with 99 Romanov ewes producing respectively 147 and 99 litters, during four breeding seasons. Thus, we obtained the experimental population consisting of two groups, backcross (**BC**; n = 197) and F_2 (n = 232), with large variation for morphological traits.

The F_2 and BC lambs were genotyped for two microsatellite markers (BM81124, BULGE20) flanking the myostatin gene to distinguish whether the locus originated from Texel or Romanov sheep. Genetic interval between the two markers was 1 cM. They were located at 107.6 and 108.6 cM, respectively, on chromosome OARQ 2 (de Gortari et al., 1998; Marcq et al., 2002). Experimental population was thus structured into two levels of classification: the two populations, F_2 and BC, for level one, and the three haplotypes according to microsatellite markers, Texel-Texel (**TT**), Texel-Romanov (**TR**), and Romanov-Romanov (**RR**) for level two. In TR haplotype, maternal and paternal origin of the Texel locus was not differentiated. Sizes of these different groups (F_2, BC, TT, TR, and RR) were 232, 197, 55, 211, and 163, respectively. Recombinants were excluded from the analysis. Animals were raised under the same conditions, grouped after weaning, and fed ad libitum with concentrate. Lambs were slaughtered at a BW of 39 kg for males and 33 kg for females.

Measurements

Subjective and Nondestructive Measurements. Lambs were weighed before departing the farm for slaughter. After slaughter, carcasses were dressed according to commercial practices. Carcasses were weighed and subjectively assessed for conformation and fattening according to the system used for national programs for breeding of reproductive rams. Assessment is based on expanded scales of conformation and fatness of the EUROP system: E, U+, U, R+, R, O+, O, P+, P (decreasing order), and 1, 1+, 2, 2+, 3, 3+, 4, 4+, 5, 5+ (increasing order of fattening), respectively. Scores were translated into continuous and ordinate notation.

Objective and Nondestructive Measurements. The following measures were taken on the whole carcasses (Figure 1): hind leg length between malleolus and symphysis (**Hs**); hind leg length between malleolus and perineeum; hind leg vertical length between malleolus and perineum; back length between bottom of tail and neck at the scapula level (**Bl**); back dorsal width at pelvis (**Bp**); back dorsal width at thorax; back dorsal width at shoulder; angle between the vertical and a line set down the posterior hind leg plump; dorsoventral height at thorax; bone thickness at malleolus; and kidney fat weight.

Objective and Destructive Measurements. Carcasses were split down transversally between the last thoracic vertebra and first lumbar vertebra. Longissimus muscle surface, width, and thickness, and dorsal fat thickness were measured on the thoracic surface of transversal section (Figure 2). Shoulders were then jointed and weighed. Muscle, bone, and fat were separated according to commercial practice with a closer trimming and deboning of the lean. The total separated weights of muscle, fat, and bone were recorded. Muscle, bone, and fat percentage of shoulder were calculated. The lumbar joint and hind limb joint were separated and weighed. The hind leg was transversally cut in the middle of the femur bone and perpendicularly to its length axis. The cuts were photographed and surfaces of the lateral (**Sl**), medial (**Sm**), and anterior muscles were recorded (Figure 3). At this cut level, muscle samples were removed from outer and inner locations of vastus lateralis and semimembranosus muscles (Figure 4). Myosin heavy-chain (**MHC**) isoforms were separated by gradient electrophoresis (Sayd et al., 1998), and the percentage of each isoform (types I, IIa, and IIb) was determined.

The following indexes and ratios were calculated: leg compactness ($100 \times Bp/Hs$); carcass compactness ($100 \times Bp/Bl$); leg index of muscularity ($[Sl + Sm]^{1/2}/Hs$); back index of muscularity ($Ls^{1/2}/Bl$); muscle-to-bone ratio (muscle weight/bone weight); carcass yield (carcass weight/live weight); shoulder yield (shoulder weight/carcass weight); lumbar yield (lumbar weight/carcass weight); and leg yield (leg weight/carcass weight).

Statistics

Analyses were performed to describe morphological variability of population and to study relationships between conformation scoring and objective measurements. Statistical analyses were performed using SAS software (SAS Inst., Inc., Cary, NC).

The GLM procedure was applied for mean comparison between F_2 and BC and between the three genotypes determined by myostatin markers. The model was:

$$X_{ijklmn} = \mu + y_i + s_j + t_k + h_l + sx_m + b_m \times (PV_{ijklmn} - PVREF_m) + E_{ijklmn}$$

where X_{ijklmn} = performance of the nth individual of ith year, of jth sire, of kth genetic type, of lth QTL haplotype, and of mth sex, with μ = general mean; y_i = fixed effect of the ith year, i varying from 1 to 4; s_j = fixed effect of the jth F_1 sire, j varying from 1 to 3; t_k = fixed effect of kth genetic type (F_2 or BC), k varying from 1 to 2; h_l = fixed effect of lth QTL haplotype (TT, TR or RR), l varying from 1 to 3; sx_m = fixed effect of mth sex, m varying from 1 to 2; b_m = regression coefficient of live weight on character for individuals of mth sex; PV_{ijklmn} =

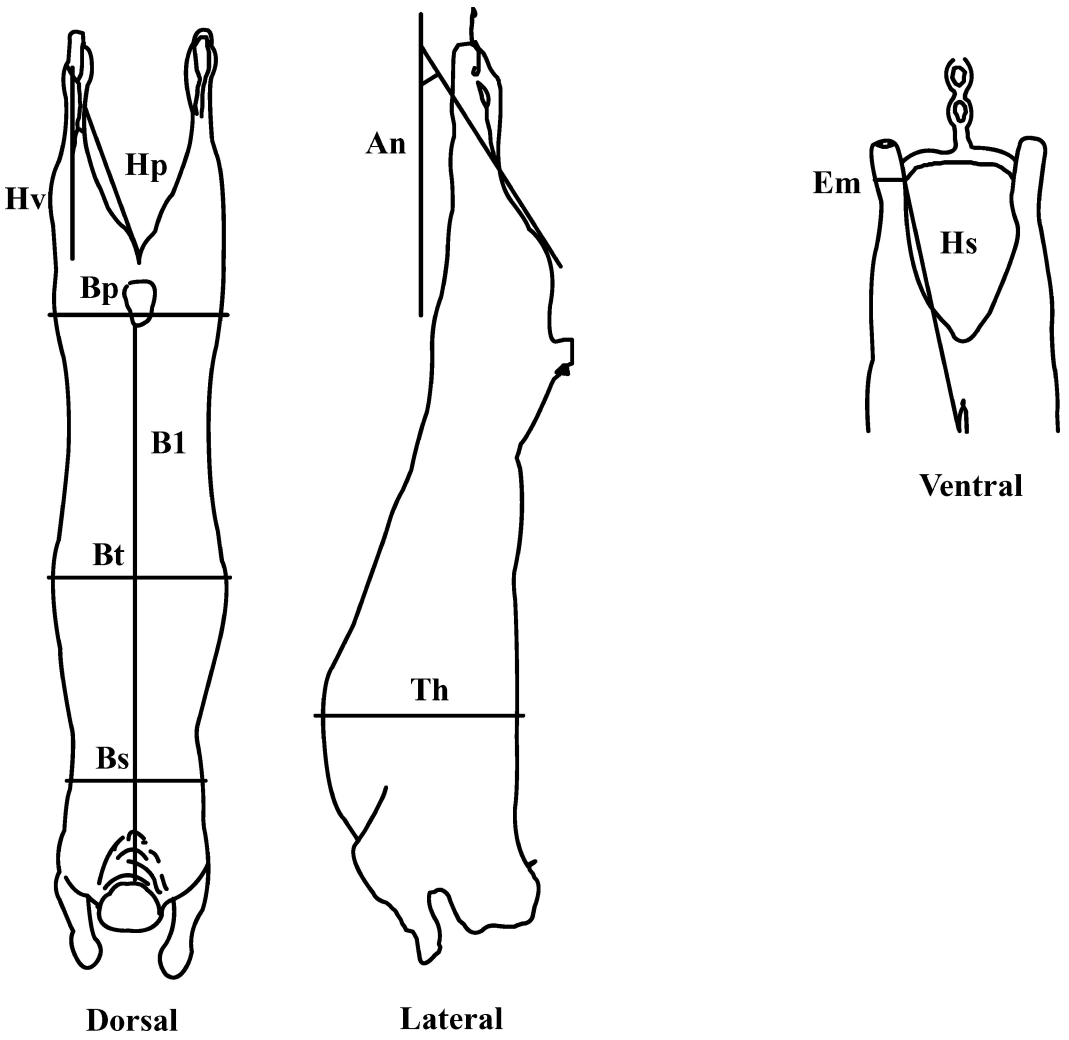

Figure 1. Illustration of dorsal, lateral and ventral carcass measurements. Hs = hind leg length between malleolus and symphysis; Hp = hind leg length between malleolus and perineeum; Hv = hind leg vertical length between malleolus and perineum; Bl = back length between bottom of tail and neck; Bp = back dorsal width at pelvic; Bt = back dorsal width at thorax; Bs = back dorsal width at shoulder; An = angle between the vertical and a line set down the posterior hind leg plump; Th = dorso ventral height at thorax; Em = bone thickness at malleolus.

live weight of the nth individual of ith year, of jth sire, of kth genetic type, of lth QTL haplotype, and of mth sex; $PVREF_m$ = fixed live weight to which performance of individual of mth sex is adjusted (33 kg for females – 39 kg for males); and E_{ijklmn} = random residual value ~$N(0, \sigma^2_E)$.

For further analysis, data were preadjusted for sex and live weight effects. Additive or dominance effects of the QTL affecting a trait were respectively calculated with: TT – RR and TR – (TT+RR)/2. A positive value for TT – RR and for TR – (TT+RR)/2 correspond to additive and dominance effects, respectively.

A principal component analysis (**PCA**) was performed with the PRINCOMP procedure of SAS, including 16 objective linear, angular, and surface measurements (marked with a superscript "e" in Table 1). Conformation scoring, weights, and ratios were not included. Correlations of variables with the first three components were calculated.

A forward stepwise procedure of regression analysis was used with the REG procedure to explain conformation score. Independent variables were added until they reach a significance level of $P > 0.15$. Independent variables used for the model included every carcass measurement except for carcass weight and carcass yield.

Results and Discussion

Genetic Effects on Carcass and Muscle Characteristics

Means and genetic effects on muscle and carcass measurements are presented in Tables 1, 2, and 3. Figure 5 summarizes the genetic differences in phenotypic measures that can be attributed to the polygenic breed

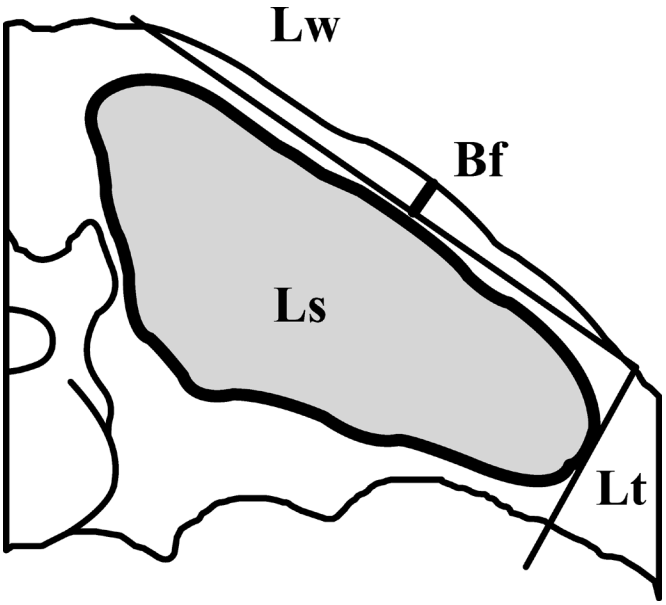

Figure 2. Illustration of measurements of the transversal section of longissimus muscle. Ls = longissimus muscle surface; Lw = longissimus width; Lt = longissimus thickness; Bf = back fat thickness.

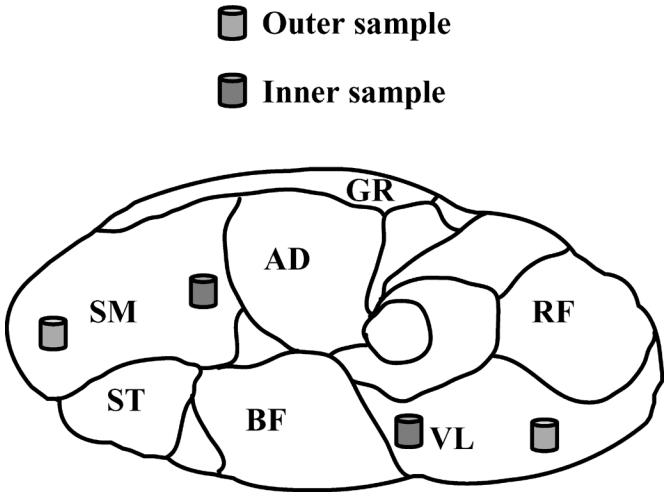

Figure 4. Location of samples in transversal cut of leg. SM = semimembranosus; AD = adductor; GR = gracilis; RF = rectus femoris; VL = vastus lateralis; BF = biceps femoris; and ST = semitendinosus muscles.

effect or to a single QTL effect. To compare traits, differences were expressed in residual standard deviations.

The Texel Breed Polygenic Effect. In contrast with growth traits, no additional maternal genetic effect or heterosis effect were observed on carcass traits (Ch'ang and Evans, 1985). Slaughtering at a fixed weight avoided these effects (Farid, 1989). Thus differences between F_2 and BC originate from a polygenic breed effect corresponding to the substitution of 25% of genes from Texel origin by 25% of genes from Romanov origin. Conformation scoring and muscularity indexes were higher in F_2. The back of F_2 was shorter, wider especially at the shoulder level, less deep, and the limbs were shorter. Carcasses of F_2 were more compact.

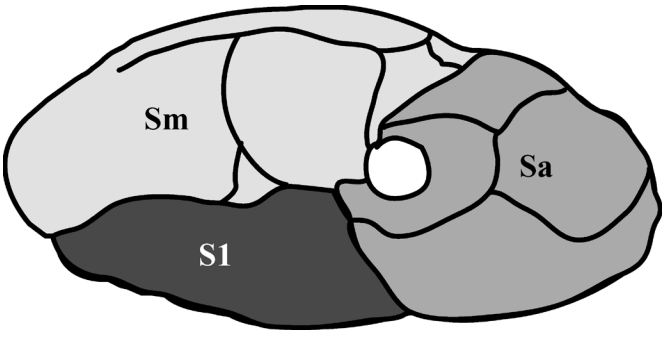

Figure 3. Illustration of measurements of muscular regions in transversal section of leg. Sa = anterior surface; Sl = lateral surface; and Sm = medial surface.

Transversal sections of limb and back muscles were larger in F_2 than in BC, except muscles of anterior surface of the thigh. The angle of plump was higher in F_2. Carcass and lumbar joint yields were higher in F_2 than in BC. Leg and shoulder yields were not different between F_2 and BC. Values of fat and muscle weight were slightly higher in F_2. Bone percent was lower in F_2. Differences in muscle myosin isoform composition were small.

The Muscle Hypertrophy QTL Effect. Differences between TT and RR genotypes correspond to the effect of the QTL for muscle hypertrophy apart from the polygenic Texel or Romanov background. For most of the traits, the QTL effect was additive. Conformation score and muscularity indexes increased with the Texel QTL. Carcass and leg length were slightly shorter with the Texel QTL. Back widths at pelvic and shoulder levels were wider in animals carrying the Texel QTL. Width and depth of thorax did not differ among haplotypes. Transversal sections of longissimus and thigh muscles were larger for Texel QTL, especially for muscles of the posterior surface of the thigh. Angle of plumpness increased with Texel QTL.

Carcass yield and hind limb yield were higher in haplotype TT than in haplotype RR. Muscle percent was increased for animals carrying the Texel QTL. Bone percent and different measurements of fat (shoulder fat weight, back fat thickness, kidney fat weight, and fat scoring) were lower in TT than in RR. The MHC-IIb isoform percentage increased, whereas MHC-I and MHC-IIa isoform percents decreased according to the presence of the Belgian Texel QTL. Most traits, such as pelvic width, leg plumpness, carcass and parts of carcass weights, carcass yield, and muscle weight, showed negative values, indicating a recessive effect of the QTL.

Table 1. Means of carcass and dissection measurements and genetic effects

			Population		QTL effect			
Measurements	Mean	SD	Test[a]	F_2 – BC[b]	Test[a]	TT – RR[c]	Test[a]	TR – (TT + RR)/2[d]
Conformation scoring	5.0	1.003	***	1.396	***	1.174	NS	–0.048
Back width, cm								
At pelvis[e]	22.49	0.534	***	0.431	***	0.55	*	–0.133
At thorax[e]	22.8	1.172	***	0.736	NS	0.048	NS	–0.045
At shoulder[e]	18.27	0.827	***	1.175	***	0.647	NS	–0.115
Length, cm								
Carcass length[e]	61.5	1.916	***	–1.44	***	–1.03	NS	0.076
Thoracic deepness[e]	253.7	6.217	***	–4.69	NS	–1.09	NS	–0.901
Leg length at symphysis[e]	34.9	1.029	***	–1.35	***	–0.588	NS	–0.099
Leg length at perineum[e]	20.3	1.262	***	1.79	*	–0.497	NS	–0.14
Vertical leg length[e]	19.1	1.302	***	–2.00	***	–0.631	NS	–0.174
Thickness								
Angle leg plumpness, degrees[e]	30.4	2.436	***	3.151	***	3.206	*	–0.528
Thigh medial surface, cm^{2e}	64.6	6.308	***	5.424	***	7.039	NS	0.052
Thigh lateral surface, cm^{2e}	30.6	2.859	***	2.080	***	2.422	NS	–0.427
Thigh anterior surface, cm^{2e}	44.5	4.816	NS	0.127	***	4.112	NS	–0.364
Longissimus surface, cm^{2e}	13.9	1.452	***	1.721	***	1.511	NS	0.011
Longissimus thickness, cm[e]	3.30	0.246	***	0.244	***	0.212	NS	–0.01
Longissimus width, cm[e]	5.98	0.372	*	0.135	***	0.281	NS	–0.021
Index of muscularity of leg	0.279	0.015	***	0.021	***	0.02	NS	0.002
Index of muscularity of back	0.061	0.004	***	0.005	***	0.005	NS	–0.002
Compactness								
Leg compactness	64.6	2.549	***	3.647	***	2.758	NS	–0.218
Carcass compactness	36.6	1.485	***	1.507	***	1.556	†	–0.286
Weight								
Carcass, kg	18.37	0.642	***	0.540	***	0.707	***	–0.252
Shoulder, g	1,603	72.95	***	65.31	***	62.96	*	–18.5
Lumbar, g	1,916	170.5	***	175.6	NS	47.88	*	–52.5
Leg, g	2,951	156.7	***	125.4	***	211.4	*	–40.0
Malleolar bone thickness[e]	3.03	0.183	NS	0.014	NS	0.046	NS	0.014

[a]NS = $P > 0.10$; †$P < 0.10$; *$P < 0.05$; ***$P < 0.001$.
[b]Polygenic breed effect corresponding to the substitution of 25% of genes from Texel origin by 25% of genes from Romanov origin. BC = backcross.
[c]A positive value for TT – RR corresponds to an additive increase due to the Belgian Texel QTL. T = Texel, R = Romanov.
[d]A negative value for TR – (TT + RR)/2 corresponds to a QTL recessive effect.
[e]Variables with superscript are included in principal component analysis.

In summary, the polygenic Texel effect and the single QTL effect independently resulted in an improvement of conformation and muscularity and in an increase of carcass yield, but the characteristics involved were different. The Texel polygenic environment improved conformation mainly through changes in skeletal frame shape: bone weight was lower and segments were shorter. Consequently, muscles were more compact, shorter, and thicker. Muscle mass and fatness were slightly higher in Texel. The relative contribution of loin joint to carcass weight was higher. The single QTL affected muscle development. Thickness and weight of muscles were increased. Differences of skeleton frame morphology between the three genotypes of the single QTL were small, except the enlargement of back at hind limb and shoulder level. Considering the low effect of the Texel QTL on skeletal structures, this difference probably expresses more an increase of thickness of muscles covering pelvis and shoulder. Fat content was lower with Texel QTL. The relative contribution of hind limb to carcass weight was increased with Texel QTL. These characteristics of development attributed to the QTL are comparable to those described in "double-muscled" cattle presenting a mutation on the gene coding for myostatin (Dumont, 1980; Ménissier, 1980). In lambs carrying of the Belgian Texel QTL and also in "double-muscled" cattle, composition in myosin changed toward an increase of fast contractile type. In the present case, consequences on sensory traits are unknown, but in many species selected for muscle development, an increase of fast contractile type is most often accompanied by an increase of the glycolytic metabolism and a decrease of oxidative metabolism. This change has no direct effect on meat sensorial qualities, but these contractile characteristics are related to pigments, fat, and proteolytic enzymes rates that have a direct effect on color, flavor, juiciness, and texture of meat (Calkins et al., 1981; Totland et al., 1988; Monin and Ouali, 1991; Koohmaraie et al., 1995). In addition, increased muscularity is accompanied by a less compact and thinner collagen network and, consequently, more tender raw meat (Bailey et al., 1980; Dumont, 1980).

Table 2. Means of carcass and dissection measurements and genetic effects

			Population		QTL effect			
Measurements	Mean	SD	Test[a]	F_2 – BC[b]	Test[a]	TT – RR[c]	Test[a]	TR – (TT + RR)/2[d]
Yield, %								
Carcass	50.9	1.769	***	1.472	***	1.934	***	–0.711
Shoulder	8.70	0.337	NS	–0.016	NS	0.002	NS	0.004
Lumbar	10.41	0.854	***	0.519	NS	–0.148	NS	–0.133
Leg	32.3	1.025	NS	–0.103	***	0.811	NS	–0.087
Shoulder dissection								
Muscle weight, g	1,182	64.11	***	63.91	***	99.63	*	–18.6
Bone weight, g	275	19.24	***	–15.9	*	–7.34	†	–3.85
Fat weight, g	145	36.54	***	15.94	***	–29.5	NS	3.202
Muscle, %	73.6	2.232	***	1.024	***	3.202	NS	–0.308
Bone, %	17.1	1.125	***	–1.64	***	–1.07	NS	–0.072
Fat, %	9.2	2.228	NS	0.543	***	–2.15	NS	0.338
Muscle:bone ratio	4.34	0.352	***	0.505	***	0.477	NS	–0.015
Fatness								
Fat score	5.94	0.789	***	0.392	***	–0.514	NS	–0.05
Kidney fat weight, g	352	87.25	*	20.67	***	–47.2	NS	6.894
Back fat thickness, mm	3.1	1.1	***	0.6	***	–7.33	NS	0.856

[a]NS = $P > 0.10$; †$P < 0.10$; *$P < 0.05$; ***$P < 0.001$.
[b]Polygenic breed effect corresponding to the substitution of 25% of genes from Texel origin by 25% of genes from Romanov origin. BC = backcross.
[c]A positive value for TT – RR corresponds to an additive increase due to the Belgian Texel QTL. T = Texel, R = Romanov.
[d]A negative value for TR – (TT + RR)/2 corresponds to a QTL recessive effect.

The QTL had an important effect on carcass traits, but this effect was relatively small considering differences between Texel and Romanov breeds. For example, the QTL effect on the conformation score, which summarizes the different carcass traits, was equal to 1.2 units of residual standard deviation (table 1). This effect corresponded to 2.4 units of additive genetic standard deviation, assuming a heritability of 0.25 (Bibé et al., 2002). This important difference was relatively low in comparison with the difference of 5.6 (4 × 1.4) units of residual standard deviation between the two pure breeds. Thus, according to the hypothesis of additivity of the effects, the polygenic differences between pure breeds should be four times the difference between F_2 and BC (1.4 units of residual standard deviation).

Table 3. Means of semimembranosus (Sm) and vastus lateralis (Vl) muscle typing and genetic effects

			Population		QTL effect			
Muscle type	Mean	SD	Test[a]	F_2 – BC[b]	Test[a]	TT – RR[c]	Test[a]	TR – (TT + RR)/2[d]
Myosin IIb, %								
Sm IIb outer	83.5	4.748	NS	1.085	***	3.215	NS	–0.816
Sm IIb inner	73.6	7.201	NS	–0.052	***	5.461	NS	–0.822
Vl IIb outer	84.1	4.920	NS	0.148	***	3.265	NS	–0.573
Vl IIb inner	72.8	6.713	***	3.335	***	5.235	NS	–0.479
Myosin IIa, %								
Sm IIa outer	10.3	2.985	NS	–0.573	***	–2.03	†	0.713
Sm IIa inner	13.9	4.301	*	–1.49	***	–2.94	NS	0.296
Vl IIa outer	9.8	3.300	NS	–0.236	***	–2.06	NS	0.343
Vl IIa inner	12.8	4.235	***	–2.24	***	–3.4	NS	0.490
Myosin I, %								
Sm I outer	6.2	2.876	NS	–0.513	*	–1.19	NS	0.103
Sm I inner	12.5	4.656	†	1.544	***	–2.53	NS	0.525
Vl I outer	6.15	3.149	NS	0.089	*	–1.21	NS	0.230
Vl I inner	14.4	5.390	NS	–1.09	†	–1.83	NS	–0.011

[a]NS = $P > 0.10$; †$P < 0.10$; *$P < 0.05$; ***$P < 0.001$.
[b]Polygenic breed effect corresponding to the substitution of 25% of genes from Texel origin by 25% of genes from Romanov origin. BC = backcross.
[c]A positive value for TT – RR corresponds to an additive increase due to the Belgian Texel QTL.
[d]A negative value for TR – (TT + RR)/2 corresponds to a QTL recessive effect.

Table 4. Correlation of carcass measurements with the three first components of principal component analysis (PCA)

Variables	Component 1 (20% of variability)	Component 2 (13% of variability)	Component 3 (11% of variability)
Included variables:[a]			
Back width at pelvis	**0.46**[c]	–0.12	**0.44**
Back width at thorax	0.03	**–0.59**	**–0.53**
Back width at shoulder	**0.40**	**–0.53**	**0.39**
Carcass length	**–0.19**	**0.45**	**0.33**
Thoracic deepness	0.01	**0.48**	**–0.36**
Leg length at symphysis	**–0.25**	**0.63**	**0.36**
Leg length at perineum	**–0.35**	**0.30**	**0.54**
Vertical leg length	**–0.37**	**0.30**	**0.52**
Angle leg plumpness	**0.49**	**0.27**	**–0.35**
Thigh medial surface	**0.60**	0.11	0.05
Thigh lateral surface	**0.61**	0.001	**0.14**
Thigh anterior surface	**0.21**	**0.16**	**0.37**
Longissimus surface	**0.82**	**0.28**	–0.03
Longissimus thickness	**0.68**	**0.18**	–0.008
Longissimus width	**0.59**	**0.43**	**–0.13**
Maleolar bone thickness	**0.16**	**0.23**	**0.41**
Excluded variables:[b]			
Carcass weight	**0.58**	–0.04	**0.13**
Leg weight	**0.64**	0.11	**0.19**
Shoulder weight	**0.46**	0.08	**0.13**
Lumbar weight	0.11	**–0.17**	0.01
Carcass yield	**0.58**	–0.04	**0.12**
Leg yield	**0.26**	**0.23**	**0.14**
Shoulder yield	–0.004	**0.16**	0.05
Lumbar yield	**–0.12**	**–0.16**	–0.01
Muscle weight	**0.58**	0.07	0.07
Bone weight	0.02	**0.30**	**0.18**
Fat weight	**–0.17**	**–0.12**	0.03
Muscle percent	**0.42**	0.02	–0.05
Bone percent	**–0.32**	**0.26**	0.09
Fat percent	**–0.27**	**–0.13**	–0.02
Conformation	**0.44**	**–0.18**	–0.06

[a]Variables are used in the PCA calculation.
[b]Variables are not used in the PCA calculation.
[c]Correlation values in bold are significant $P < 0.05$.

Relationships between Morphological Traits and Carcass Quality

The PCA was used to describe variability of carcass morphological traits and to examine their relationships with the conformation score and other carcass quality variables (yields, weights). The three first components explained 46% of the measured variability. Correlation coefficients of measurements with the three first components are presented in Table 4.

The first axis explained 20% of the total variation. This component was chiefly determined by variables expressing muscle development. Correlations of the first component with transversal sections and the thickness of LM, the transversal section of the medial and lateral thigh muscles, and the angular measure of plumpness were the highest (0.82, 0.68, 0.60, 0.61, 0.49, respectively). Next, the first axis was determined by the broadness of back at pelvic and shoulder levels (0.46, 0.40). Lengths of the back and hind limb were opposed to previous measurements but had a lower contribution (–0.19, –0.25, –0.35) to the axis. This first component was strongly related to the weights of carcass, leg, and shoulder (0.58, 0.64, 0.46), the weight and yield of muscle (0.58, 0.52), and also to conformation score (0.44). Weight of fat was negatively correlated (–0.17).

The second axis expressed 13% of variability. This component was best represented by skeletal frame development. Values of dorso-ventral development of thoracic wall, back, and hind limb length, bone thickness, and bone weight (0.48, 0.45, 0.63, 0.23, 0.30) determined the positive aspect of this axis and were opposed to measures of lateral broadness of thoracic wall and shoulder (–0.59, –0.52). The conformation score and measure of plumpness had a low correlation to this component (–0.18 and 0.27). Muscle transversal sections were lowly related to this component, except for longissimus width, which was positively related to the component (0.43).

The third axis explained 11% of variability. It was also mainly represented by skeletal traits. The positive aspect of this axis was characterized by back and hind

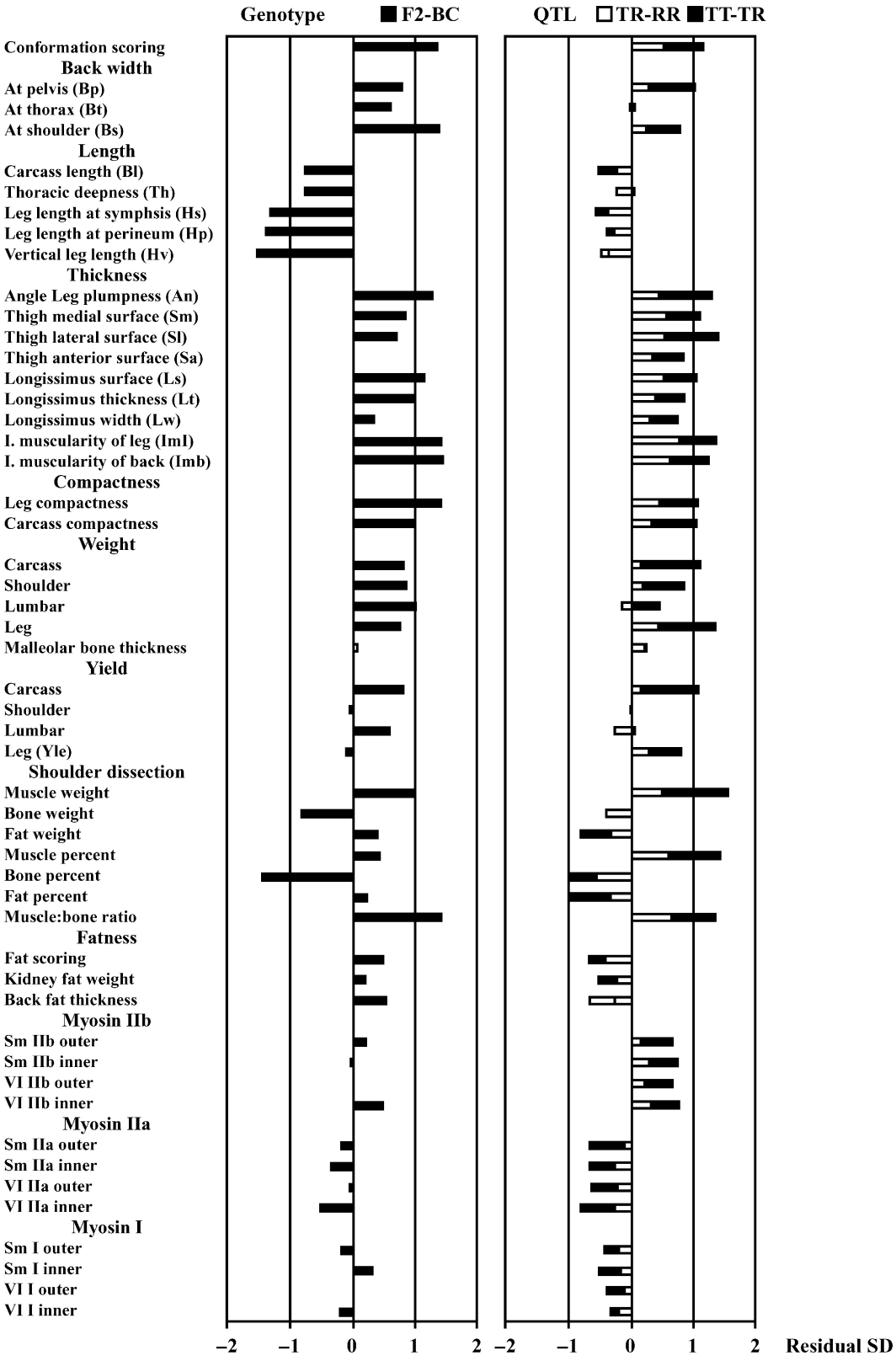

Figure 5. Genetic differences that can be attributed to a single QTL effect (TR – RR and TT – TR) or to the polygenic breed effect (F_2 – BC). Results are expressed in residual standard error.

limb length, bone thickness (0.33, 0.37, 0.54, 0.41) associated to the thickness of anterior muscles of thigh (0.37), and the broadness of three levels of back width (0.44, 0.49, 0.39). These characteristics were opposed to dorso-ventral development of thoracic wall (–0.36) and to angular measure of thigh plumpness (–0.35).

Table 5. Objective measurements retained by forward stepwise regression analysis for conformation prediction

Variable	R^2	*F*	Probability
Angle leg plumpness	0.179	57.91	<0.001
Back width at pelvis	0.234	19.08	<0.001
Vertical leg length	0.284	18.44	<0.001
Thigh: medial surface	0.313	11.17	<0.001
Shoulder yield	0.328	5.73	0.017
Thigh: Anterior surface	0.340	4.71	0.031
Longissimus width	0.348	3.20	0.074
Muscle weight	0.360	4.95	0.027

Note that conformation was not related to this axis (0.06).

In summary, conformation scoring and carcass quality traits had a high positive correlation to the first component, which expressed muscle development. Conformation score was negatively but lowly (r = –0.18) correlated to the second component, which reflected length of skeleton. This result can be interpreted by a positive influence of back broadness and a negative influence of back and leg lengthening on conformation scoring independent of muscle development.

Relationships between Conformation Scoring and Carcass Measurements

Regression analysis was used to determine carcass traits that were mainly involved in the conformation score. The four first variables included in the regression equation described the shape of the hind limb, particularly the posterior surface: thigh plumpness, broadness of back at pelvis, leg length, and section of posterior region of the thigh (R^2 = 0.313; Table 5). All components of muscle development (length, thickness, and shape) were represented except muscle weight. The next three variables expressed muscular development of other joints: yield of shoulder and transversal section of lumbar joints, the section of anterior region of the thigh, and muscle weight. These variables made a minor contribution to conformation score explanation (R^2 = 0.360). The conformation score had a relatively high correlation to the objective carcass measurements (r = 0.6). However, back and shoulder muscle development, which largely contributed to variability of muscularity as observed in the first component of the PCA, had a low level of contribution to the conformation score. These parts of carcasses were supposed to be assessed by conformation scoring. Therefore, it seems necessary to assess independently joints of economic importance, such as the back for the chops and the shoulder, which is often deboned and prepared as roast.

Implications

In the current study, two sources of muscularity improvement were evaluated. The first was variation due to skeletal frame morphology (Texel polygenic influence), and the second was variation due to muscle hypertrophy (Belgian Texel quantitative trait locus). The single quantitative trait locus modified contractile properties of muscle. It would be interesting to compare the two effects on meat quality characteristics. In this study, conformation scoring was influenced mainly by leg muscularity. Measurements of different parts of the carcass in a three-dimensional system should provide a more reliable assessment than conformation scoring. The gene and causal mutation have not been identified, but studies are in process. Nonetheless, the quantitative trait locus is already interesting for different purposes. It constitutes a model for studies on muscle development and relationships to meat quality. The presence of relatively close genetic markers allows introgression experiments in ovine populations.

Literature Cited

Bailey, A. J., M. B. Enser, E. Dransfield. D. J. Restall, and N. C. Avery. 1980. Muscle and adipose tissue from normal and double muscled cattle: Collagen types, muscle fibre diameter, fat cell size and fatty acid composition and organoleptic properties. Page 178 in Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production. 16th ed. J. W. B. King and F. Ménissier ed. M. Nijhoff, The Hague, The Netherlands.

Bibé, B., J. C. Brunel, Y. Bourdillon, D. Loradoux, M. H. Gordy, J. L. Weisbecker, and J. Bouix. 2002. Genetic parameters of growth and carcass quality of lambs at the French progeny-test Station Berrytest. Pages 335–338 in Proc. 7th World Cong. on Genetic Appl. to Livest. Prod., Montpellier, France.

Calkins, C. R., T. R. Dutson, Z. L. Smith, Z. L. Carpenter, and G. W. Davis. 1981. Relationship of fiber type composition to marbling and tenderness of bovine muscle. J. Food Sci. 46:708–715.

Ch'ang, T. S., and R. Evans. 1985. Heterosis and breed effect on carcass traits of rams. 1. Carcass weight and component trait. Aust. J. Agric. Res. 36:107–117.

De Boer, H., B. L. Dumont, R. W. Pomeroy, and J. H. Weniger. 1974. Reference method for the assessment of carcass characteristics in cattle. Manual on E.A.A.P. Livest. Prod. Sci. 1:151–164.

Dumont, B. L. 1971. Qualité des ovins de boucherie. Pâtre 183:4–12.

Dumont, B. L. 1980. Carcass composition and muscle hypertrophied animals. Page 111 in Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production. 16th ed. J. W. B. King and F. Ménissier ed. M. Nijhoff, The Hague, The Netherlands.

Farid, A. 1989. Direct, maternal and heterosis effects for slaughter and carcass characteristics in three breeds of fat tailed sheep. Livest. Prod. Sci. 23:137–162.

de Gortari, M. J., B. A. Freking, R. P. Cuthbertson, S. M. Kappes, J. W. Keele, R. T. Stone, K. A. Leymaster, K. G. Dodds, A. M. Crawford, and C. W. Beattie. 1998. A second-generation linkage map of the sheep genome. Mamm. Genome 9:204–209.

Klont, R. E., G. Eikelenboom, and L. Brocks. 1998. Muscle fibre type and muscle quality. Page 98 in Proc. 44th Int. Cong. Meat Sci. Technol., Barcelona, Spain.

Koohmaraie, M., S. D. Shackelford, T. L. Wheeler, S. M. Lonergan, and M. E. Doumit. 1995. A muscle hypertrophy condition in lamb (Callipyge): Characterization of effects on muscle growth and meat quality traits. J. Anim. Sci. 73:3596–3607.

Marcq, F., C. Larzul, V. Marot, J. Bouix, F. Eychenne, E. Laville, B. Bibé, P. L. Leroy, M. Georges, and J. M. Elsen. 2002. Preliminary results of a whole-genome scan targeting QTL for carcass traits in Texel × Romanov intercross. Pages 323–326 in Proc. 7th World Cong. on Genetic Appl. Livest. Prod., Montpellier, France.

Ménissier, F. 1980. General survey of the effect of double muscling on cattle performance. Page 23 in Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production. 16th ed. J. W. B. King and F. Ménissier ed. M. Nijhoff, The Hague, The Netherlands.

Monin, G., and A. Ouali. 1991. Muscle differentiation and meat quality. Page 89 in Developments in Meat Science. 5th ed. R. Lawrie, ed., Elsevier Applied Science, London, U.K.

Purchase, R. W., A. S. Davies, and A. Y. Abdullah. 1991. An objective measure of muscularity: Changes with animal growth and differences between genetic lines of southdown sheep. Meat Sci. 30:81–94.

Sayd, T., T. Mera, V. Martin, and E. Laville. 1998. Spatial distribution of myosin heavy chain isoforms and lactate dehydrogenase M4 in the limb musculature of two crossbred lambs. Comp. Biochem. Physiol. Part B. 120:153–163.

Totland, G. K., H. Krivi, and E. Slinde. 1988. Composition of muscle fibre types and connective tissue in bovine M. semitendinosus and its relation to tenderness. Meat Sci. 23:303–315.