Fine mapping of quantitative trait loci underlying sensory meat quality traits in three French beef cattle breeds[1]

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ABSTRACT: Improving the traits that underlie meat quality is a major challenge in the beef industry. The objective of this paper was to detect QTL linked to sensory meat quality traits in 3 French beef cattle breeds. We genotyped 1,059, 1,219, and 947 young bulls and their sires belonging to the Charolais, Limousin, and Blonde d'Aquitaine breeds, respectively, using the Illumina BovineSNP50 BeadChip (Illumina Inc., San Diego, CA). After estimating relevant genetic parameters using VCE software, we performed a linkage disequilibrium and linkage analysis on 4 meat traits: intramuscular fat content, muscle lightness, shear force, and tenderness score. Heritability coefficients largely ranged between 0.10 and 0.24; however, they reached a maximum of 0.44 and 0.50 for intramuscular fat content and tenderness score, respectively, in the Charolais breed. The 2 meat texture traits, shear force and tenderness score, were strongly genetically correlated (–0.91 in the Charolais and Limousin breed and –0.86 in the Blonde d'Aquitaine breed), indicating that they are 2 different measures of approximately the same trait. The genetic correlation between tenderness and intramuscular fat content differed across breeds. Using a significance threshold of 5×10^{-4} for QTL detection, we found more than 200 significant positions across the 29 autosomal chromosomes for the 4 traits in the Charolais and Blonde d'Aquitaine breeds; in contrast, there were only 78 significant positions in the Limousin breed. Few QTL were common across breeds. We detected QTL for intramuscular fat content located near the *myostatin* gene in the Charolais and Blonde d'Aquitaine breeds. No mutation in this gene has been reported for the Blonde d'Aquitaine breed; therefore, it suggests that an unknown mutation could be segregating in this breed. We confirmed that, in certain breeds, markers in the *calpastatin* and *calpain 1* gene regions affect tenderness. We also found new QTL as several QTL on chromosome 3 that are significantly associated with meat tenderness in the Blonde d'Aquitaine breed. Overall, these results greatly contribute to the goal of building a panel of markers that can be used to select animals of high meat quality.

Key words: beef cattle, fine mapping, meat quality, quantitative trait loci

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INTRODUCTION

For decades, breeding companies have used AI and selection programs to improve the growth and carcass quality traits of young bulls of French beef cattle breeds (Bouquet et al., 2010).

Because consumers are increasingly demanding consistent meat quality, improving quality-related traits is now a major challenge in the French beef industry. Consequently, the Qualvigène research program was started in France to study genetic and genomic contributions to meat quality in French beef cattle breeds.

When it comes to beef, the most important sensory quality characteristics for consumers are meat tenderness, marbling, and color (reviewed by Geay et al., 2001).

Without routine measurement of these traits when the animals are slaughtered, selection efforts could potentially take advantage of QTL. Many candidate genes have already been identified (Barendse, 1999, 2002, 2007, 2008; Haegeman et al., 2000; Grisart et al., 2002; Page et al., 2002; Bernard et al., 2007; Cho et al., 2008; Allais et al., 2010; Reardon et al., 2010; etc.). However, in a previous study (Allais et al., 2011), we showed that QTL detected in 1 breed do not necessarily have generalized significance across all the *Bos taurus* breeds. In particular, this is true for the *calpastatin* and *calpain 1* genes, which each affect tenderness in a single breed: the Blonde d'Aquitaine and the Charolais, respectively.

Thanks to the advent of BeadChip technology, we can now access the dense information that is present throughout the whole genome. Therefore, we performed a whole genome scan to detect QTL linked to sensory meat quality attributes in 3 French breeds: Charolais, Limousin and Blonde d'Aquitaine. We studied 4 traits in particular: intramuscular fat content, muscle lightness, shear force, and tenderness score.

MATERIAL AND METHODS

The animals used in this study were slaughtered by certified slaughterhouses in accordance with French animal protection regulations (Code Rural, Articles R214-64 to R214-71; Legifrance, 2011).

The Qualvigène program, which is described in detail elsewhere (Allais et al., 2010), was a collaborative French research program involving AI companies, the INRA, and the Institut de l'Elevage (the French Livestock Institute). It was initiated to study the degree to which traits related to sensory meat quality are genetically determined using France's 3 main beef cattle breeds. This study formed an integral part of the Qualvigène program.

Animals

The Qualvigène program used progeny tests conducted over 3 successive years. The population used in this study is described in Allais et al. (2010). Briefly, purebred young bulls (the progeny of 48, 36, and 30 sires from the Charolais, Limousin, and Blonde d'Aquitaine breeds, respectively) were randomly mated to generally unrelated dams in a large number of herds. The young bulls were humanely slaughtered in a commercial slaughterhouse when they reached an average live weight of 730 kg (±15 kg) for the Charolais bulls or an average age of 479 (±3 d) or 417 d (±4 d) for the Limousin or Blonde d'Aquitaine bulls, respectively. A total of 1,114 Charolais, 1,254 Limousin, and 981 Blonde d'Aquitaine purebred young bulls were used in this study.

Phenotypic Data

The longissimus thoracis (**LT**) muscle was removed from the seventh to ninth ribs on the right side of the carcass and sliced into 3 steaks. The first steak was divided into small samples that were immediately frozen for use in later biochemical analyses. The other 2 steaks were vacuum packaged and left to age for 14 d at 4°C before being frozen. Muscle lightness (**ML**; L*) was measured using the freshly cut LT muscle section and using a Minolta spectrophotometer (CM 2002; Minolta France SA, Carrières sur Seine, France). Intramuscular fat content (**IMF**; %) was measured using LT samples from the seventh rib by using the Soxhlet method and a Soxtherm apparatus (Gerhardt France SARL, Les Essarts Le Roi, France).

The LT steaks from the eighth rib were thawed at 4°C for 24 h and then cooked on an electric grill until they reached an internal temperature of 55°C (rare); the cooking equipment, cooking temperature, and cooking time were kept consistent. Cooked steaks were cooled to room temperature before 10 core samples (parallelepiped in form) were obtained; they were cut with their fibers running parallel to the long axis. Mean Warner-Bratzler shear force (**WBSF**; N/cm^2) was estimated using the 10 core samples.

Tenderness was evaluated by 3 test panels composed of 12 trained panelists; there was 1 panel for each breed. Most of the panelists remained on the panel for the 3 yr of the study. The same cooking procedure as described above was applied to the ninth rib LT steaks, and the cooked steaks were immediately served to panelists. The Limousin and Blonde d'Aquitaine test panels had to evaluate 12 samples during each session. The Charolais test panel had to evaluate 15 samples. Panelists scored tenderness (tenderness score [**TS**]) using an ordinal 100-point scale: from 1 (extremely tough) to 100 (extremely tender). The panelists' scores were averaged to obtain a mean for each animal.

Genotyping Data

Purebred young bulls and their sires were genotyped using the BovineSNP50 v1 and v2 DNA Analysis BeadChip by Illumina, Inc. (San Diego, CA). Some of the Blonde d'Aquitaine animals (117) were genotyped at the Centre National de Génotypage (National Center for Genotyping; Evry, France). The others (971 animals) and all of the Limousin and Charolais animals were genotyped at the Labogena laboratory (Jouy-en-Josas, France).

Genotypes were obtained for 1,059, 1,219, and 947 young bulls and 47, 34, and 29 sires belonging to the Charolais, Limousin, and Blonde d'Aquitaine breeds, respectively. All of the Blonde d'Aquitaine animals as well as 76 Limousin and 17 Charolais animals were genotyped using a Bovine SNP50 v1 BeadChip (54,001 SNP; Illumina, Inc.). The others were genotyped using a Bovine SNP50 v2 BeadChip (54,609 SNP; Illumina, Inc.). The X and Y chromosomes were not included in the analyses. For the Blonde d'Aquitaine breed, of the 54,001 SNP included on the chip, we used the 37,556 SNP that occur in the Btau 4.0 (www.hgsc.bcm.edu//other-mammals/bovine-genome-project) assembly of the 29 autosomal chromosomes and that have a minor allele frequency of greater than 0.05 and a Hardy-Weinberg equilibrium *P*-value of greater than 10^{-4}. In the other 2 breeds, because of the mix of genotypes on the 2 chips, only the common SNP were studied. Consequently, 37,581 and 36,919 markers were used for the Charolais and Limousin breeds, respectively.

Methods

Estimation of Genetic Parameters. Heritability and phenotypic and genetic correlations were estimated using VCE software (Groeneveld et al., 2010); a maximum of 5 generations were taken into account. The Charolais, Limousin, and Blonde d'Aquitaine relationship matrices included 4,295, 6,366, and 3,854 animals, respectively.

Quantitative Trait Loci Detection. First, we used a hidden Markov model method to reconstruct the haplotypes. This method uses population information (linkage disequilibrium) and familial information (Mendelian segregation and linkage) and was applied using PHASEBOOK (Druet and Georges, 2010).

Second, the presence of a QTL at a given position was determined using the following mixed model (as per Meuwissen and Goddard, 2000, and Druet et al., 2008): $\mathbf{y^*} = \mathbf{1_n}\mu + \mathbf{Wh} + \mathbf{Zu} + \mathbf{e}$, in which $\mathbf{y^*}$ is a vector of performances corrected based on fixed effects (slaughtering group or date of sensory tests); $\mathbf{h}$ is a vector of haplotype effects, where $\mathbf{h} \sim N(0,\mathbf{G}\sigma^2_g)$; $\mathbf{u}$ is a vector of random individual polygenic effects, where $\mathbf{u} \sim N(0,\mathbf{A}\sigma^2_a)$; and $\mathbf{e}$ is a vector of residual effects, where $\mathbf{e} \sim N(0,\mathbf{I}\sigma^2_e)$. Here $\mathbf{G}$ is a matrix of identical by descent (Meuwissen and Goddard, 2001) and transmission probabilities, constructed in every test using a window of 6 flanking markers, and $\mathbf{A}$ is the pedigree relationship matrix. The matrices $\mathbf{W}$ and $\mathbf{Z}$ are the design matrices that link phenotypes to corresponding haplotype clusters and animal effects, respectively. The variances σ^2_g, σ^2_a, and σ^2_e are the variances of gamete effects, individual polygenic effects, and residual effects, respectively. The variance associated with the QTL effect is twice σ^2_g; consequently, the proportion of total genetic variance due to the QTL is equal to $2\sigma^2_g/(2\sigma^2_g + \sigma^2_a)$.

Model variances were estimated using restricted maximum likelihood implemented in a program developed by Druet et al. (2008) that was based on BLUPF90 software (Misztal et al., 2002).

The presence of a QTL at each SNP position in the genome was examined using the following likelihood ratio test (**LRT**): LRT = –2 ln[L(H0)/L(H1)], in which L(H0) and L(H1) are the maximum values of the likelihood functions under polygenic models in which no QTL has been fitted and in which a QTL is present, respectively.

The distribution of the statistical test was an equally weighted mixture $[(1/2)\chi^2_0 + (1/2)\chi^2_1]$ of a Dirac distribution (probability mass of 1) with 0 df (usually denoted as χ^2_0) and of the more typical χ^2 distribution with 1 df (χ^2_1). This resulted in a *P*-value that was half that of the χ^2_1 distribution, that is, *P*-value = $(1/2)\Pr[\chi^2_1 > \Delta(-2L)_{obs}]$ (Visscher, 2006).

When many chromosomal segments are tested, a number of null hypotheses will be rejected (the *P*-value of statistical test will be below a predetermined level) by chance only. To deal with multiple tests, we applied stringent significance thresholds (*P*-values of 5×10^{-4}, 5×10^{-5}, and 5×10^{-6}, as per Teyssèdre et al., 2012). The most stringent threshold was chosen because it represented an approximation of 10,000 independent tests corrected with the Bonferroni (1936) method. The threshold of 5×10^{-5} signaled moderate evidence of association (The Welcome Trust Case Control Consortium, 2007), and the threshold of 5×10^{-4} was used to describe and compare QTL among traits and breeds. The LRT corresponding to the *P*-values of 5×10^{-6}, 5×10^{-5}, and 5×10^{-4} were 19.5, 15.1, and 10.8, respectively.

RESULTS AND DISCUSSION

Phenotypic Information

The number of records, means, and phenotypic SD (**RSD**) for the 4 sensory meat quality traits (IMF, ML, WBSF, and TS) for the Charolais, Limousin, and Blonde d'Aquitaine breeds are described in Table 1. It was not possible to compare mean breed values since the bulls were slaughtered at different times and sensory test panels differed for the different breeds. The coefficients of variation were much higher for IMF (CV > 40%) than for

Table 1. Number of observations, means, and phenotypic SD (RSD[1]) for the phenotypes studied in the Charolais, Limousin, and Blonde d'Aquitaine breeds

		Charolais			Limousin			Blonde d'Aquitaine		
Trait	Abbreviation	*n*	Mean	RSD	*n*	Mean	RSD	*n*	Mean	RSD
Intramuscular fat content, %	IMF	1,114	1.53	0.84	1,254	1.18	0.49	981	0.56	0.37
Muscle lightness, L*	ML	1,114	34.75	3.58	1,253	32.79	3.55	979	33.08	3.84
Warner-Bratzler shear force, N/cm^2	WBSF	1,114	38.09	7.32	1,252	40.98	7.47	977	40.54	10.41
Tenderness score, /100	TS	1,113	62.42	7.87	1,241	58.74	7.25	970	61.4	10.72

[1]RSD is the root mean square error from the simple model that included only the fixed effect for the contemporary groups.

tenderness score (CV ≈ 15%) or ML (CV = 10%). Shear force demonstrated an intermediate level of variability (CV ranged from 18 to 26%). The within-breed analysis of variances used to estimate the polygenic and QTL effects on traits in each breed may provide valuable information for comparing genetic determinism across breeds.

The values of the genetic parameters for the Charolais, Limousin, and Blonde d'Aquitaine breeds are provided in Tables 2, 3, and 4, respectively. Most of the heritability coefficients ranged from 0.10 to 0.24, except for those for IMF and tenderness score in the Charolais breed; they were as high as 0.44 and 0.50, respectively. The heritability coefficients for ML (L*) were slightly lower (0.10 to 0.23) than the few estimates (0.17 to 0.32) reported in the literature (Aass, 1996, Johnston et al., 2003; Boukha et al., 2011). Past results (review by Marshall, 1999; Johnston et al., 2003; Riley et al., 2003) have shown that the heritability of IMF can be highly variable; it ranged from 0.17 to 0.54. Marshall (1999) and Burrow et al. (2001) found that shear force and tenderness score were moderately heritable (0.22 to 0.25, on average); however, Riley et al. (2003), Boukha et al. (2011), and Zwambag et al. (2013) all found lower values. The estimates obtained in this study encompass these literature values and reveal that the traits underlying meat quality are generally moderately heritable. The 2 meat texture traits, shear force and TS, were strongly genetically correlated, indicating they are 2 different measures of approximately the same underlying trait. The relationship between tenderness and IMF differed among breeds; Charolais and Blonde d'Aquitaine animals with fattier muscles also had slightly more tender meat. In contrast, the opposite result was observed in the Limousin breed. Most previous studies have found a positive relationship between LM lipid content or marbling and tenderness (Burrow et al., 2001).

Table 2. Heritabilities (**on diagonal**), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for intramuscular fat content (IMF), muscle lightness (ML), Warner-Bratzler shear force (WBSF), and tenderness score (TS) in the Charolais breed (with SE of the genetic parameters in parentheses)

	IMF	ML	WBSF	TS
IMF	**0.44 (0.05)**	–0.12 (0.14)	–0.36 (0.06)	0.27 (0.10)
ML	0.01	**0.15 (0.04)**	–0.22 (0.11)	0.13 (n.e.[1])
WBSF	–0.05	–0.08	**0.24 (0.05)**	–0.91 (0.05)
TS	0.03	0.03	–0.43	**0.5 (0.06)**

[1]n.e. = not estimated.

Probability Distributions

Quantile–quantile plots (**QQplots**) are very useful in verifying that the distribution of *P*-values obtained (on the *y*-axis) is consistent with the distribution expected (*x*-axis) under the null hypothesis. If the 2 distributions are similar, then the QQplot should show a solid series of points that follow the $y = x$ line until the series curves sharply at the upper end; this curve represents the small number of true associations among the thousands of unassociated SNP. Complete deviation from the $y = x$ line may indicate that there is a population stratification problem.

Figure 1 shows the QQplots for shear force in the 3 breeds. The distributions appear to match for the Charolais and Limousin breeds, but the *P*-values seemed to be slightly overestimated in the Blonde d'Aquitaine breed.

Quantitative Trait Loci Detection

We detected over 200 significant positions on the 29 autosomal chromosomes using a threshold of 5×10^{-4} for the 4 traits in the Charolais and Blonde d'Aquitaine breeds; only 78 significant positions were detected in the

Table 3. Heritabilities (**on diagonal**), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for intramuscular fat content (IMF), muscle lightness (ML), Warner-Bratzler shear force (WBSF), and tenderness score (TS) in the Limousin breed (with SE of the genetic parameters in parentheses)

	IMF	ML	WBSF	TS
IMF	**0.23 (0.05)**	0.04 (0.17)	0.50 (0.16)	–0.24 (0.22)
ML	0.08	**0.10 (0.03)**	0.35 (0.19)	–0.06 (0.21)
WBSF	–0.05	–0.04	**0.22 (0.05)**	–0.91 (0.07)
TS	0.00	0.00	–0.34	**0.12 (0.03)**

Table 4. Heritabilities (**on diagonal**), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for intramuscular fat content (IMF), muscle lightness (ML), Warner-Bratzler shear force (WBSF) and tenderness score (TS) in the Blonde d'Aquitaine breed (with SE of the genetic parameters in parentheses)

	IMF	ML	WBSF	TS
IMF	**0.19 (0.04)**	0.16 (0.12)	–0.61 (0.08)	0.38 (0.14)
ML	0.08	**0.23 (0.05)**	–0.13 (0.11)	0.34 (0.09)
WBSF	–0.03	–0.20	**0.23 (0.05)**	–0.86 (n.e.[1])
TS	0.00	0.12	–0.36	**0.21 (0.05)**

[1]n.e. = not estimated.

Table 5. Number of positions detected using a significance threshold of 5×10^{-4} for the 3 breeds[1]

Breed	IMF	ML	WBSF	TS	Total
Charolais	25	69	33	86	213
Limousin	14	14	39	11	78
Blonde d'Aquitaine	21	30	120	69	240

[1]IMF = intramuscular fat content; ML = muscle lightness; WBSF = Warner-Bratzler shear force; TS = tenderness score.

Limousin breed (Table 5). Considering the overestimation of the *P*-values in the Blonde d'Aquitaine breed, the higher number of QTL in this breed could be explained by a higher number of false positive tests. Consequently the QTL detected slightly over the threshold (5×10^{-4}) should be used with caution.

Using a threshold of 5×10^{-5}, about 50 of these QTL were still significant in the Charolais and Blonde d'Aquitaine breeds; only 10 remained significant in the Limousin breed (Table 6). The number of QTL was drastically reduced when a very stringent threshold of 5×10^{-6} was used; it dropped to 0 in the Limousin breed (Table 7).

Regardless of the threshold used, several QTL for the same trait were detected within very narrow regions. This leads to the question: are they associated with the same causal polymorphism? Therefore, in Table 8, only the QTL that were separated by at least 4 cM are reported for each characteristic; we considered that if 2 markers occurred within a 4 cM region, then they were likely to be associated with the same causal polymorphism. The value of 4 cM was arbitrarily chosen to limit the number of QTL defined within the same region. Using this separation threshold and a significance threshold of 5×10^{-4}, we found 44, 34, and 64 significant QTL for the 4 traits in the Charolais, Limousin, and Blonde d'Aquitaine breeds, respectively. Each QTL explained about 20% of the genetic variance in a given trait; this value was high because the variance explained by a QTL may be overestimated if a 1-QTL model is used.

We compared the positions of the most significant QTL with those of candidate genes identified in other studies (Table 9).

Only a few QTL occurred across the 3 breeds. We observed that 2 QTL for IMF occurred in close proximity to each other, at 5.9 and 6.1 cM on chromosome 2, in the Charolais and Blonde d'Aquitaine breeds (Fig. 2). These QTL were located near the *myostatin* or *growth differentiation factor 8 gene* (***GDF8***; 6.5 cM; Table 9), which is responsible for double muscling in homozygous mutants (Grobet et al., 1997; Kambadur et al., 1997; McPherron and Lee, 1997). In a previous study, the myostatin Q204X mutation was found to segregate in the same Charolais population (17% of young bulls carried a copy of this Q204X mutation) and to have a significant effect on IMF (–0.47 SD; Allais et al., 2010). Both the effect and the frequency of this mutation clearly underlie the very high significance level of

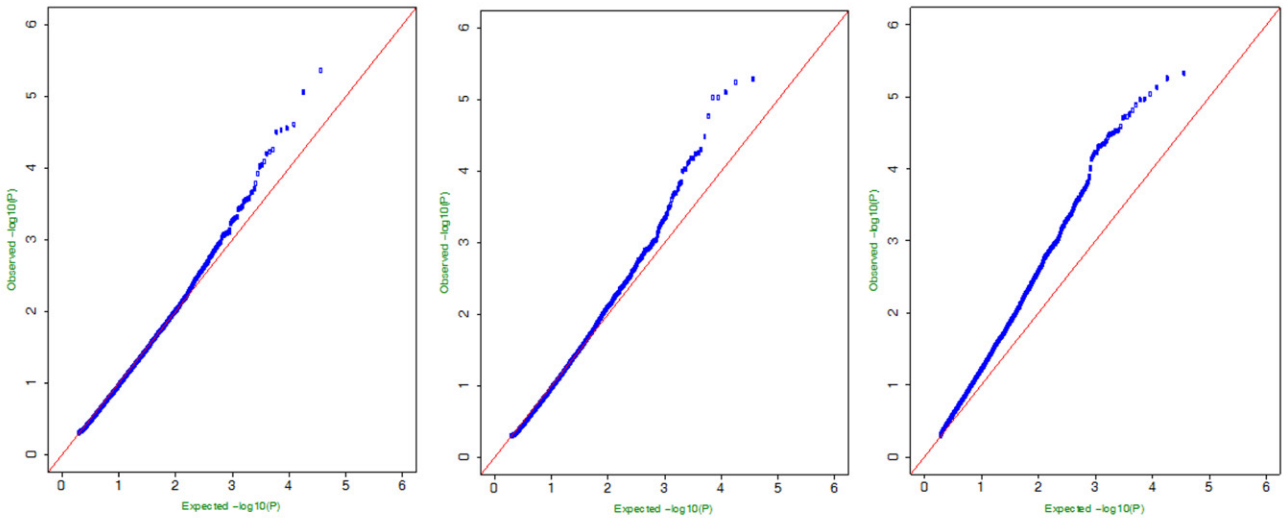

Figure 1. Quantile–quantile plots for shear force in the Charolais, Limousin, and Blonde d'Aquitaine breeds. See online version for figure in color.

Table 6. Number of positions detected using a significance threshold of 5×10^{-5} for the 3 breeds[1]

Breed	IMF	ML	WBSF	TS	Total
Charolais	7	16	6	29	58
Limousin	2	0	8	0	10
Blonde d'Aquitaine	6	0	35	7	48

[1]IMF = intramuscular fat content; ML = muscle lightness; WBSF = Warner-Bratzler shear force; TS = tenderness score.

Table 7. Number of positions detected using a significance threshold of 5×10^{-6} for the 3 breeds[1]

Breed	IMF	ML	WBSF	TS	Total
Charolais	3	3	1	12	19
Limousin	0	0	0	0	0
Blonde d'Aquitaine	0	0	4	0	4

[1]IMF = intramuscular fat content; ML = muscle lightness; WBSF = Warner-Bratzler shear force; TS = tenderness score.

the QTL (LRT = 22.9; *P*-value < 5×10^{-6}) in the Charolais breed. In the Blonde d'Aquitaine population, in contrast, only 10 young bulls were carrying 1 of the mutated alleles (Q204X or nt821; Allais et al., 2010). Consequently, these 2 mutations cannot be responsible for the QTL detected in this region because their frequencies were far too low. We suspect that this QTL may be attributable to an original mutation of the *GDF8* gene that is segregating in the Blonde d'Aquitaine breed. However, this hypothesis remains to be tested. In the same genomic region in the Charolais breed, we found an LRT peak for ML (8.4 cM). This result is consistent with results from a previous study (Allais et al., 2010), which showed that 1 copy of the Q204X allele could affect ML in the same Charolais population (if we consider that *GDF8* underlies the detected QTL). In contrast, no QTL was detected in this region in the Limousin breed. A Jersey–Limousin backcross experiment showed that the *GDF8* F94L mutation originated in the Limousin breed and had a significant, moderate effect on IMF (Esmailizadeh et al., 2008). A small sample of French Limousin cattle were found to be homozygous for the *GDF8* F94L mutation (Dunner et al., 2003), while Limousin cattle from the same population (which was also the one used in this study) had a low frequency of the *GDF8* alleles Q204X (0.6%) and nt821 (2.7%; Allais et al., 2010). The lack of QTL detected in the *GDF8* region may result from the fact that the frequency of alleles other than the F94L mutation is too low in this Limousin population.

Several LRT peaks were found for tenderness between 42 and 52 cM on chromosome 29 in the Blonde d'Aquitaine and Charolais breeds (Fig. 3). These QTL occurred near the *calpain 1* gene (***CAPN1***; 45.2 cM; Table 9). The QTL for shear force and TS were significant at a threshold of 5×10^{-6} in the Charolais breed (LRT = 19.9 and 37.7, respectively). In a previous study (Allais et al., 2011), 2 *calpain 1* gene haplotypes were associated with either tougher or more tender meat in the Charolais breed; the *calpain 1* gene haplotypes also had a significant effect on shear force but not on tenderness score in the Blonde d'Aquitaine breed. This result is consistent with the fact that we detected a QTL for shear force at 42.5 and 51.6 cM in this breed. We also detected, on chromosome 7, a QTL for TS at 26.5 and 33.6 cM in the Blonde d'Aquitaine breed and a QTL for shear force at 24.9 cM in the Charolais breed (Fig. 4). These positions are located on either side of the *lysyl-oxidase* gene (***LOX***; 30.5 cM; Table 9), which Barendse (2002) identified as a candidate gene for meat tenderness. At another position (98.4 cM) on the same chromosome, we found a significant QTL for TS in the Blonde d'Aquitaine breed using a threshold of 5×10^{-5}. This LRT peak was at the same location as the *calpastatin* gene (***CAST***; 97.5 cM; Table 9). In a previous study (Allais et al., 2011), a haplotype of this gene was found to have a negative effect on TS and a positive effect on shear force in the Blonde d'Aquitaine breed. In the present study, we found a weak LRT peak (9.8) for shear force, but it was not significant any more with the correction for the multiple tests. In the Charolais and Limousin breeds, neither the previously used candidate gene approach (using markers in the *CAST* gene) nor the fine mapping approach used in this study revealed whether a polymorphism in the *CAST* gene region was related to tenderness.

Several QTL for tenderness (shear force and TS) were found between 111 and 124 cM on chromosome 1 and between 92 and 120 cM on chromosome 6 in the 3 breeds, but no candidate genes have been identified in these genomic regions.

On chromosome 3, we found a QTL for shear force at 15.7 and 31.8 cM in the Charolais breed and the Limousin breed, respectively. In the Blonde d'Aquitaine breed, we found several QTL for shear force or TS around 18 to 28 cM and 40 to 55 cM on the same chromosome (Fig. 5). The QTL in the Blonde d'Aquitaine and Limousin breeds were highly significant (*P*-values < 5×10^{-6}). The wide spread of different QTL on chromosome 3 is surprising. Furthermore, these QTL do not appear to correspond to any candidate genes for meat tenderness in the literature.

Because of the very high level of genetic correlation between shear force and tenderness score in the 3 breeds, we expected that the QTL for these 2 traits would be the same. However, the results were not so simple. One explanation could be that shear force only partially accounts for tenderness.

Only a few QTL for IMF were detected in each breed. In the Limousin breed, we found 2 LRT peaks, at 15.5 and 19.6 cM, on chromosome 23. No candidate genes have been identified in this region. In the Blonde d'Aquitaine breed, a QTL was detected at about 29.1 cM on chromosome 20, which is near the *growth hormone*

Table 8. Positions and proportions of the genetic variance explained by the QTL detected for the 4 meat quality traits in the 3 breeds using a significance threshold of 5×10^{-4}; the positions had to be separated by at least 4 cM

Trait	BTA[1]	Illumina marker[2]	Position, cM	LRT[3]	*P*-value	$\sigma^2_{QTL}/\sigma^2_g$[4]	Breed[5]
Intramuscular fat content	1	BTA-123503-no-rs	5.2	11.1	4.3×10^{-4}	0.04	CH
Muscle lightness	1	Hapmap33466-BTA-107178	18.5	11.0	4.6×10^{-4}	0.15	BA
Intramuscular fat content	1	BTB-01967977	48.5	12.7	1.8×10^{-4}	0.15	LI
Shear force	1	ARS-BFGL-NGS-111283	70.8	10.8	5.0×10^{-4}	0.19	LI
Muscle lightness	1	ARS-BFGL-BAC-34664	78.6	11.5	3.5×10^{-4}	0.21	BA
Shear force	1	BTB-01568935	111.1	12.2	2.4×10^{-4}	0.36	LI
Tenderness score	1	Hapmap41730-BTA-102454	111.9	18.1	1.0×10^{-5}	0.23	BA
Tenderness score	1	BTB-00054470	124.1	12.8	1.7×10^{-4}	0.12	BA
Tenderness score	1	BTB-01382680	124.3	12.3	2.3×10^{-4}	0.06	CH
Intramuscular fat content	1	Hapmap26724-BTA-152272	126.3	15.9	3.3×10^{-5}	0.2	LI
Muscle lightness	2	BTA-10744-no-rs	1.1	22.2	1.2×10^{-6}	0.37	CH
Intramuscular fat content	2	ARS-BFGL-NGS-18261	1.9	15.6	3.9×10^{-5}	0.08	CH
Muscle lightness	2	Hapmap53000-ss46526222	4.7	13.2	1.4×10^{-4}	0.58	LI
Intramuscular fat content	2	Hapmap44381-BTA-47399	5.9	22.9	8.5×10^{-7}	0.09	CH
Intramuscular fat content	2	ARS-BFGL-NGS-6033	6.1	18.5	8.5×10^{-6}	0.35	BA
Muscle lightness	2	Hapmap38635-BTA-85702	8.4	20.6	2.8×10^{-6}	0.37	CH
Tenderness score	2	ARS-BFGL-NGS-38727	40.3	11.6	3.3×10^{-4}	0.08	CH
Shear force	2	ARS-BFGL-NGS-103501	100.7	14.4	7.4×10^{-5}	0.14	LI
Shear force	3	Hapmap39890-BTA-117039	11.2	12.6	1.9×10^{-4}	0.17	BA
Shear force	3	Hapmap43906-BTA-66658	15.7	16.1	3.0×10^{-5}	0.16	CH
Shear force	3	ARS-BFGL-NGS-1718	18.1	17.7	1.3×10^{-5}	0.23	BA
Shear force	3	ARS-BFGL-NGS-105811	24.5	19.7	4.5×10^{-6}	0.2	BA
Tenderness score	3	ARS-BFGL-NGS-105811	24.5	12.0	2.7×10^{-4}	0.21	BA
Tenderness score	3	UA-IFASA-9337	28.5	11.9	2.8×10^{-4}	0.16	BA
Muscle lightness	3	ARS-BFGL-NGS-105342	29	11.0	4.6×10^{-4}	0.24	LI
Shear force	3	ARS-BFGL-NGS-104159	31.8	19.5	5.0×10^{-6}	0.25	LI
Muscle lightness	3	ARS-BFGL-NGS-42736	35.9	11.6	3.3×10^{-4}	0.28	CH
Shear force	3	BTA-67581-no-rs	39.7	16.2	2.8×10^{-5}	0.12	BA
Shear force	3	ARS-BFGL-NGS-102970	46.2	18.1	1.0×10^{-5}	0.16	BA
Shear force	3	INRA-681	50	17.0	1.9×10^{-5}	0.16	BA
Shear force	3	Hapmap60328-rs29027404	55.5	17.0	1.9×10^{-5}	0.17	BA
Muscle lightness	3	ARS-BFGL-NGS-84153	71.4	13.0	1.6×10^{-4}	0.22	LI
Intramuscular fat content	3	Hapmap39877-BTA-99831	85.1	11.2	4.1×10^{-4}	0.1	LI
Tenderness score	3	BTB-00143051	95.2	11.5	3.5×10^{-4}	0.24	LI
Intramuscular fat content	4	BTB-01186280	27.1	11.3	3.9×10^{-4}	0.08	CH
Shear force	4	BTB-00203584	97.8	10.8	5.0×10^{-4}	0.19	CH
Tenderness score	4	ARS-BFGL-NGS-118785	122.2	11.3	3.9×10^{-4}	0.25	BA
Shear force	5	ARS-BFGL-NGS-90377	78.2	17.2	1.7×10^{-5}	0.33	LI
Shear force	5	BTB-01445745	82.4	18.3	9.4×10^{-6}	0.98	LI
Intramuscular fat content	6	BTA-94737-no-rs	2.5	13.8	1.0×10^{-4}	0.16	BA
Intramuscular fat content	6	Hapmap41082-BTA-76030	7.8	14.8	6.0×10^{-5}	0.15	BA
Shear force	6	Hapmap51979-BTA-43275	61.2	11.0	4.6×10^{-4}	0.12	LI
Shear force	6	Hapmap31190-BTA-161167	64.7	14.0	9.1×10^{-5}	0.14	LI
Tenderness score	6	BTA-121763-no-rs	85.9	11.1	4.3×10^{-4}	0.05	CH
Tenderness score	6	Hapmap42318-BTA-76987	92.2	14.7	6.3×10^{-5}	0.06	CH
Tenderness score	6	Hapmap23975-BTC-043815	105.1	14.1	8.7×10^{-5}	0.17	LI
Shear force	6	Hapmap53755-rs29023406	115.3	11.2	4.1×10^{-4}	0.13	BA
Shear force	6	ARS-BFGL-NGS-54737	120.6	17.4	1.5×10^{-5}	0.17	BA
Shear force	7	BTB-01956476	24.9	16.6	2.3×10^{-5}	0.18	CH
Tenderness score	7	Hapmap42389-BTA-99482	26.5	11.3	3.9×10^{-4}	0.19	BA
Tenderness score	7	Hapmap60838-rs29022006	33.6	13.4	1.3×10^{-4}	0.27	BA
Tenderness score	7	ARS-BFGL-NGS-60914	65	11.7	3.1×10^{-4}	0.27	LI
Intramuscular fat content	7	BTB-01273634	78.7	11.4	3.7×10^{-4}	0.1	BA
Muscle lightness	7	BTB-01514268	81.8	11.0	4.6×10^{-4}	0.2	CH

continued

Table 8. (cont.)

Trait	BTA[1]	Illumina marker[2]	Position, cM	LRT[3]	*P*-value	$\sigma^2_{QTL}/\sigma^2_g$[4]	Breed[5]
Muscle lightness	7	BTA-21118-no-rs	90.5	16.3	2.7×10^{-5}	0.31	CH
Tenderness score	7	Hapmap31128-BTA-148018	93.4	11.8	3.0×10^{-4}	0.17	BA
Tenderness score	7	Hapmap38937-BTA-121815	98.4	15.4	4.3×10^{-5}	0.19	BA
Tenderness score	7	Hapmap49389-BTA-96192	105.1	12.4	2.1×10^{-4}	0.16	BA
Shear force	8	Hapmap53248-rs29027060	53.1	11.1	4.3×10^{-4}	0.18	LI
Tenderness score	9	ARS-BFGL-NGS-36701	37.8	12.1	2.5×10^{-4}	0.17	BA
Intramuscular fat content	9	Hapmap32827-BTA-146530	56.7	14.6	6.6×10^{-5}	0.13	BA
Muscle lightness	9	Hapmap34932-BES2_Contig53	71.8	13.6	1.1×10^{-4}	0.18	CH
Muscle lightness	9	Hapmap50488-BTA-84319	78.4	13.6	1.1×10^{-4}	0.19	CH
Tenderness score	10	ARS-BFGL-NGS-43692	3.5	14.0	9.1×10^{-5}	0.05	CH
Muscle lightness	10	UA-IFASA-7255	13.5	13.3	1.3×10^{-4}	0.18	BA
Shear force	10	ARS-BFGL-NGS-101657	51.7	12.8	1.7×10^{-4}	0.14	LI
Tenderness score	10	BTB-01361961	60.9	15.2	4.8×10^{-5}	0.04	CH
Shear force	10	UA-IFASA-1616	79.7	10.9	4.8×10^{-4}	0.11	BA
Shear force	10	ARS-BFGL-NGS-107149	86.9	14.7	6.3×10^{-5}	0.13	BA
Tenderness score	10	Hapmap57084-ss46526565	88.7	16.2	2.8×10^{-5}	0.14	BA
Tenderness score	10	Hapmap46881-BTA-82468	98.2	12.9	1.6×10^{-4}	0.29	BA
Tenderness score	10	BTA-21035-no-rs	102.8	10.8	5.0×10^{-4}	0.05	CH
Muscle lightness	11	ARS-BFGL-NGS-5463	30.8	11.5	3.5×10^{-4}	0.18	BA
Shear force	11	ARS-BFGL-NGS-18624	38.9	14.9	5.7×10^{-5}	0.15	CH
Shear force	11	Hapmap15326-rs29013300	41.4	14.6	6.6×10^{-5}	0.2	BA
Intramuscular fat content	11	ARS-BFGL-NGS-47330	46.4	19.2	5.9×10^{-6}	0.95	BA
Intramuscular fat content	11	ARS-BFGL-NGS-79604	92	15.4	4.3×10^{-5}	0.2	LI
Shear force	11	Hapmap43778-BTA-117655	103.9	11.6	3.3×10^{-4}	0.11	CH
Muscle lightness	11	ARS-BFGL-NGS-45339	108.9	13.1	1.5×10^{-4}	0.2	BA
Shear force	12	Hapmap54287-ss46526670	15.2	13.4	1.3×10^{-4}	0.15	BA
Muscle lightness	12	ARS-BFGL-NGS-80012	19.9	12.7	1.8×10^{-4}	0.22	BA
Muscle lightness	12	ARS-BFGL-NGS-21636	24.9	11.2	4.1×10^{-4}	0.16	BA
Shear force	12	Hapmap45233-BTA-100751	42.8	15.2	4.8×10^{-5}	0.11	BA
Intramuscular fat content	12	ARS-BFGL-BAC-11215	84.9	11.1	4.3×10^{-4}	0.18	BA
Intramuscular fat content	13	ARS-BFGL-BAC-6788	16.4	13.0	1.6×10^{-4}	0.06	CH
Muscle lightness	13	BTA-07889-rs29027551	82.3	13.6	1.1×10^{-4}	0.23	CH
Shear force	14	UA-IFASA-6545	14.9	12.1	2.5×10^{-4}	0.18	BA
Muscle lightness	14	ARS-BFGL-NGS-31515	19.2	11.1	4.3×10^{-4}	0.26	LI
Tenderness score	14	BTA-13956-no-rs	59.7	11.8	3.0×10^{-4}	0.05	CH
Tenderness score	14	ARS-BFGL-NGS-57639	72.9	14.8	6.0×10^{-5}	0.24	LI
Shear force	15	ARS-BFGL-NGS-77871	35.3	14.7	6.3×10^{-5}	0.19	LI
Shear force	15	Hapmap46538-BTA-88332	41.7	11.6	3.3×10^{-4}	0.11	LI
Shear force	15	BTB-00606070	56	10.9	4.8×10^{-4}	0.11	BA
Intramuscular fat content	15	BTB-01561193	58.8	11.3	3.9×10^{-4}	0.1	CH
Muscle lightness	15	BTB-01280741	62.3	11.5	3.5×10^{-4}	0.2	CH
Shear force	15	ARS-BFGL-NGS-57604	81.9	12.1	2.5×10^{-4}	0.23	CH
Muscle lightness	16	BTB-01346204	64	12.2	2.4×10^{-4}	0.34	LI
Shear force	17	BTB-02009238	1	10.9	4.8×10^{-4}	0.09	CH
Muscle lightness	17	ARS-BFGL-NGS-103975	4.1	12.9	1.6×10^{-4}	0.18	CH
Shear force	17	ARS-BFGL-NGS-87957	16	19.4	5.3×10^{-6}	0.23	BA
Muscle lightness	17	Hapmap61007-rs29024666	22.3	13.4	1.3×10^{-4}	0.36	CH
Shear force	17	Hapmap54587-rs29015138	24.5	11.1	4.3×10^{-4}	0.15	BA
Shear force	17	BTB-00782224	33.8	11.1	4.3×10^{-4}	0.14	LI
Shear force	17	BTB-01308199	35.3	16.2	2.8×10^{-5}	0.18	BA
Shear force	17	ARS-BFGL-NGS-93948	41.5	12.7	1.8×10^{-4}	0.22	BA
Shear force	17	ARS-BFGL-NGS-111789	50.1	13.9	9.6×10^{-5}	0.18	BA
Shear force	17	ARS-BFGL-NGS-111058	56.8	12.6	1.9×10^{-4}	0.15	BA
Shear force	17	BTB-00682446	62.8	11.5	3.5×10^{-4}	0.12	BA
Tenderness score	17	ARS-BFGL-NGS-46768	63.2	11.6	3.3×10^{-4}	0.21	LI

continued

Table 8. (cont.)

Trait	BTA[1]	Illumina marker[2]	Position, cM	LRT[3]	*P*-value	$\sigma^2_{QTL}/\sigma^2_g$[4]	Breed[5]
Muscle lightness	18	BTB-01617999	3.1	14.8	6.0×10^{-5}	0.28	LI
Muscle lightness	18	Hapmap24845-BTA-147038	7.9	11.7	3.1×10^{-4}	0.14	BA
Muscle lightness	18	ARS-BFGL-NGS-2590	17.9	11.7	3.1×10^{-4}	0.12	BA
Shear force	18	ARS-BFGL-BAC-31823	36.6	10.9	4.8×10^{-4}	0.08	CH
Muscle lightness	19	ARS-BFGL-NGS-31404	30.7	12.1	2.5×10^{-4}	0.26	LI
Muscle lightness	20	ARS-BFGL-NGS-70354	9.7	14.3	7.8×10^{-5}	0.17	CH
Muscle lightness	20	Hapmap42340-BTA-84327	17	13.2	1.4×10^{-4}	0.24	CH
Intramuscular fat content	20	BTA-50144-no-rs	29.1	12.5	2.0×10^{-4}	0.06	BA
Muscle lightness	20	Hapmap48202-BTA-118947	32	11.3	3.9×10^{-4}	0.26	LI
Muscle lightness	21	ARS-BFGL-NGS-93930	32.3	11.3	3.9×10^{-4}	0.25	CH
Shear force	22	ARS-BFGL-NGS-44609	13.1	11.6	3.3×10^{-4}	0.14	CH
Tenderness score	22	ARS-BFGL-NGS-52880	18.5	10.8	5.0×10^{-4}	0.07	CH
Intramuscular fat content	23	ARS-BFGL-NGS-34065	15.5	12.4	2.1×10^{-4}	0.15	LI
Tenderness score	23	ARS-BFGL-NGS-23572	16.3	12.7	1.8×10^{-4}	0.13	BA
Intramuscular fat content	23	ARS-BFGL-NGS-33908	19.6	14.3	7.8×10^{-5}	0.11	LI
Muscle lightness	23	ARS-BFGL-NGS-8000	52.2	11.2	4.1×10^{-4}	0.22	BA
Muscle lightness	24	BTA-91299-no-rs	6.6	11.1	4.3×10^{-4}	0.31	LI
Tenderness score	24	Hapmap57059-rs29023291	42	11.5	3.5×10^{-4}	0.06	CH
Muscle lightness	26	Hapmap48021-BTA-61134	31.9	13.0	1.6×10^{-4}	0.11	BA
Tenderness score	26	ARS-BFGL-NGS-27596	51	14.1	8.7×10^{-5}	0.44	BA
Shear force	27	ARS-BFGL-NGS-90721	11.9	11.1	4.3×10^{-4}	0.22	BA
Tenderness score	27	ARS-BFGL-NGS-20681	24.3	14.1	8.7×10^{-5}	0.3	BA
Muscle lightness	27	BTB-00965793	30.2	11.5	3.5×10^{-4}	0.22	BA
Muscle lightness	27	UA-IFASA-1808	37.1	10.9	4.8×10^{-4}	0.32	LI
Tenderness score	28	Hapmap49856-BTA-108815	1.1	13.8	1.0×10^{-4}	0.05	CH
Tenderness score	29	Hapmap51754-BTA-66496	35.1	11.7	3.1×10^{-4}	0.04	CH
Tenderness score	29	ARS-USMARC-Parent-DQ40415	39.4	15.6	3.9×10^{-5}	0.06	CH
Shear force	29	Hapmap43902-BTA-65773	42.5	17.2	1.7×10^{-5}	0.41	BA
Muscle lightness	29	ARS-BFGL-NGS-102787	45.6	11.7	3.1×10^{-4}	0.22	BA
Shear force	29	ARS-BFGL-NGS-113797	45.9	19.9	4.1×10^{-6}	0.21	CH
Tenderness score	29	BTA-66033-no-rs	46.1	37.7	4.1×10^{-10}	0.22	CH
Shear force	29	ARS-BFGL-NGS-31629	51.6	18.8	7.3×10^{-6}	0.28	BA

[1]BTA = Bos Taurus Autosomes.

[2]The marker with the highest LRT, if several positions were significant in the same QTL region.

[3]LRT = likelihood ratio test.

[4]$\sigma^2_{QTL}/\sigma^2_g$ is the proportion of the genetic variance explained by the QTL.

[5]CH = Charolais; LI = Limousin; BA = Blonde d'Aquitaine.

receptor gene (***GHR***; 34 cM; Table 9). We found no significant QTL for IMF on chromosome 14, although many candidate genes for this trait (*DGAT1*, *TG*, *CRH*, and *FABP4*) have been identified in other breeds. A previous study on candidate genes for intramuscular lipid content in the same populations (Renand et al., 2007) also found a lack of QTL on this chromosome. The low number of QTL for intramuscular lipids could be explained by the fact that our French beef cattle breeds have very low levels of IMF compared to many other breeds (Christensen et al., 2011). Intramuscular lipid levels are approximately 1.5, 1.2, and 0.6% in the Charolais, Limousin, and Blonde d'Aquitaine breeds, respectively (Table 1).

We detected a significant QTL for ML at 90.5 cM on chromosome 7 in the Charolais breed using a threshold of 5×10^{-5} (LRT = 16.3; Fig. 6). This QTL may correspond to

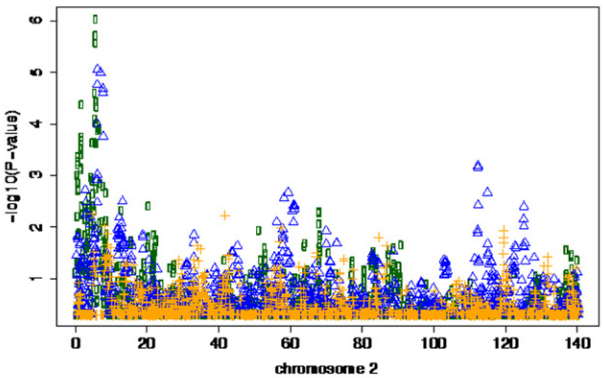

Figure 2. Quantitative trait loci for intramuscular lipids on chromosome 2 in the 3 breeds (Charolais in green circles, Limousin in orange crosses, and Blonde d'Aquitaine in blue triangles). See online version for figure in color.

Table 9. Candidate genes for meat tenderness, intramuscular fat content, and muscle lightness identified in literature

Trait	Candidate gene	Position, bp	Reference
Intramuscular fat content	SST: SomatoSTatin	1: 81,428,283–81,429,731	Morsci et al. (2006)
	GDF8: myostatin	2: 6,532,638–6,539,265	Allais et al. (2010)
	RORC: retinoic acid receptor-related orphan receptor C	3: 20,463,309–20,487,237	Barendse et al. (2007, 2010)
	LEP: leptin	4: 95,677,882–95,694,616	Haegeman et al. (2000); Buchanan et al. (2002); Lagonigro et al. (2003)
	DGAT1: diacylglycerol O-acyltransferase	14: 444,082–446,781	Grisart et al. (2002); Winter et al. (2002); Thaller et al. (2003)
	TG: thyroglobulin	14: 7,658,632–7,894,999	Barendse (1999); Thaller et al. (2003)
	CRH: corticotropin releasing hormone	14: 31,497,511–31,499,127	Wibowo et al. (2007)
	FABP4: fatty acid binding protein 4	14: 41,955,210–41,959,600	Cho et al. (2008)
	GHR: growth hormone receptor	20: 33,896,757–34,206,083	Han et al. (2009)
	ankyrin 1	27: 38,983,949–38,994,492	Aslan et al. (2010)
	IGF2: insulin-like growth factor 2	29: 51,257,937–51,276,553	Schmutz and Goodall (2005)
Muscle lightness	GDF8: myostatin	2: 6,532,638–6,539,265	Allais et al. (2010)
	CAST: calpastatin	7: 97,439,654–97,573,315	Reardon et al. (2010)
	GHR: growth hormone receptor	20: 33,896,757–34,206,083	Reardon et al. (2010)
	SCD: steroyl CoA desaturase delta 9	26: 21,137,945–21,148,317	Reardon et al. (2010)
Tenderness score – shear Force	HGD: homogentisate 1,2 dioxygenase	1: 66,335,194–66,377,628	Zhou et al. (2010)
	GDF8: myostatin	2: 6,532,638–6,539,265	Allais et al. (2010)
	CAST: calpastatin	7: 97,439,654–97,573,315	Barendse (2002)
	LOX: lysyl-oxidase	7: 30,482,478–30,494,584	Barendse (2002)
	DNAJA1 (HSP40)	8: 78,911,498–78,922,166	Bernard et al. (2007)
	CAPN3: calpain 3	10: 37,624,085–37,681,529	Barendse et al. (2008)
	ACAD8: acyl-CoA dehydrogenase family, member 8	15: 84,399,062–84,412,870	Li et al. (2007)
	ankyrin 1 erythrocytic	27: 38,983,949–38,994,492	Aslan et al. (2010)
	CAPN1: calpain 1	29: 45,215,707–45,242,224	Page et al. (2002)

the *CAST* gene, which is located at 98 cM (Table 9). A previous study found that a SNP in the *CAST* gene was highly significantly associated with color in an Irish crossbred cattle breed (Reardon et al., 2010).

The same 3 populations used in this QTL detection study were also used in a functional genomics study that sought to identify differentially expressed genes. Proteomic analysis was conducted on the LT muscles of 2 extreme groups of 10 animals in each of the 3 populations included in the Qualvigene program (Charolais, Limousin, and Blonde d'Aquitaine) to identify new markers for beef tenderness (Table 10; Chaze et al., 2009). Animals were chosen using an index that combined their tenderness and shear force ratings. Differences in gene expression were quantified based on differences in the abundance of marked proteins. In this study, we then compared the genes coding for these proteins with the QTL we detected; we hypothesized that causal mutations could be present in the genes coding for the protein markers (in either

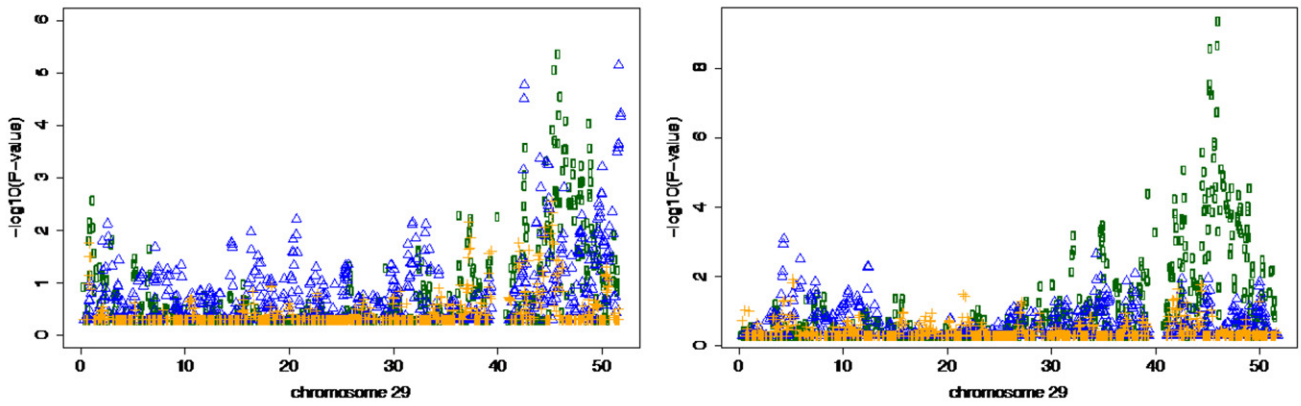

Figure 3. Quantitative trait loci for shear force (on the left) and tenderness score (on the right) on chromosome 29 in the 3 breeds (Charolais in green circles, Limousin in orange crosses, and Blonde d'Aquitaine in blue triangles). See online version for figure in color.

Table 10. Candidate genes for meat tenderness identified using a proteomic analysis of samples obtained from 2 groups of 10 young bulls with extreme tenderness attribute in the 3 breeds (Chaze et al., 2009)

Trait	Candidate gene	Position, bp	CH[1]	LI[1]	BA[1]
Tenderness (index[2])	F-actin capping protein subunit β	2: 137,824,439–137,961,336	x	x	x
	NADH-ubiquinone oxidoreductase 75 kDa subunit	2: 99,538,834–99,568,274			x
	phosphoglucomutase 1 (PGM)	3: 87,921,429–87,987,137	x		
	proteasome subunit β2	3: 117,351,943–117,389,047	x		
	capping protein muscle Z-line α2	4: 53,602,242–53,657,237		x	
	Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	5: 10,853,525–10,857,808		x	
	WD repeat-containing protein 1	6: 109,677,054–109,719,214			x
	geranylgeranyl transferase type2 subunit α	10: 21,172,426–21,178,847		x	
	Rab GDP dissociation inhibitor β	13: 43,225,325–43,253,974		x	
	α crystallin B chain	15: 20,478,751–20,482,075		x	x
	α Enolase	16: 41,637,031–41,650,708		x	
	protein DJ-1	16: 42,542,500–42,559,276	x	x	
	heat shock protein β6 (HSP20)	18: 45,891,747–45,894,274		x	x
	creatine kinase M-type	18: 52,738,345–52,747,755			x
	slow troponin T	18: 62,696,849–62,707,804			x
	14–3-3 protein epsilon	19: 22,605,292–22,640,100			x
	β Enolase	19: 26,813,658–26,818,816		x	x
	myosin light chain 3	22: 53,976,134–53,981,900			x
	myosin regulatory light chain 2	25: 28,385,041–28,387,502	x		x
	actin α	28: 427,012–491,279	x	x	x
	glutathione S-transferase P	29: 47,402,172–47,405,031	x		
	fast troponin T	29: 51,432,267–51,447,730	x		x

[1]CH = Charolais; LI = Limousin; BA = Blonde d'Aquitaine.

[2]The tenderness index was calculated by combining the tenderness score (positive) and the shear force estimate (negative).

the promoter or coding sequences) or that the mutations could locally affect the regulation of these genes.

We found a QTL for tenderness score at 1.1 cM on chromosome 28 in the Charolais breed, which was located in the vicinity of the gene coding for the actin α protein (0.4 cM; Table 10); this gene is more highly expressed in tender meat in the in the Charolais and Blonde d'Aquitaine breeds.. We also found a QTL for shear force and tenderness score (between 45.9 and 46.1 cM) on chromosome 29 in the Charolais breed; this QTL occurred in the same region as the gene coding for glutathione S-transferase P (47 cM; Table 10), which is more highly expressed in tender meat in this breed. The QTL for shear force located at 51.6 cM on chromosome 29 in the Blonde d'Aquitaine breed was in the same position as the gene coding for fast troponin T (51.4 cM; Table 10), which was more highly expressed in tougher meat in the 3 breeds.

We found a limited number of regions that contained both a QTL and a gene coding for a differentially expressed protein related to tenderness. This result suggests that most of the causal mutations likely occur in regulatory elements located farther away; they do not seem to occur close to or in the genes coding for the protein markers.

In conclusion, the 3 breeds shared only a few QTL. The effects of some candidate genes, such as *GDF8*, *CAST*, and *CAPN1*, were confirmed in certain

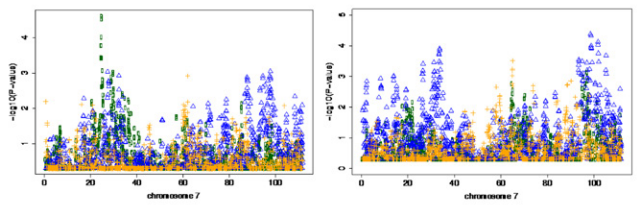

Figure 4. Quantitative trait loci for shear force (on the left) and tenderness score (on the right) on chromosome 7 in the 3 breeds (Charolais in green circles, Limousin in orange crosses, and Blonde d'Aquitaine in blue triangles). See online version for figure in color.

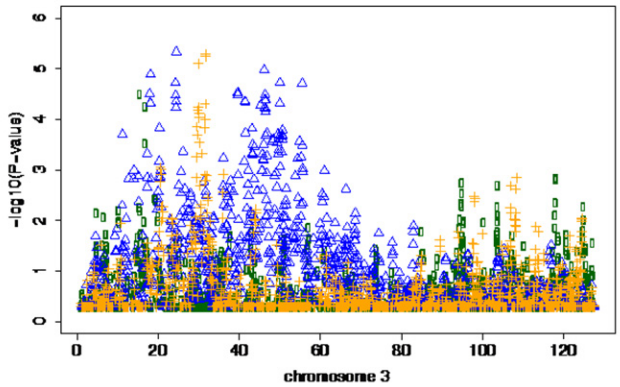

Figure 5. Quantitative trait loci for shear force on chromosome 3 in the 3 breeds (Charolais in green circles, Limousin in orange crosses, and Blonde d'Aquitaine in blue triangles). See online version for figure in color.

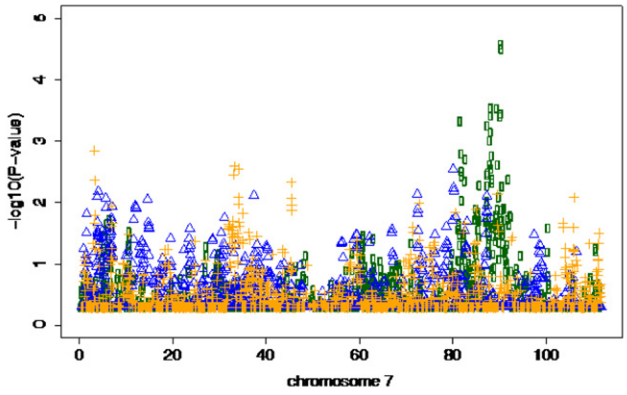

Figure 6. Quantitative trait loci for muscle lightness on chromosome 7 in the 3 breeds (Charolais in green circles, Limousin in orange crosses, and Blonde d'Aquitaine in blue triangles). See online version for figure in color.

breeds. We did not detect very highly significant QTL that explained a high percentage of the genetic variance associated with the meat quality traits examined in this study, but we identified interesting regions as on the chromosome 3. Further analyses are necessary to select a panel of markers for each breed that could be used to identify animals of high meat quality.

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