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RESEARCH ARTICLE

Sensory quality of meat from eight different types of cattle in relation with their biochemical characteristics

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Abstract

The present study compared eight breeds of cattle differing in gender (heifers, bulls and steers) to determine associations between muscle characteristics and meat sensory qualities of the *Longissimus thoracis* muscle. Animal types differed in all the muscle characteristics and sensory qualities. Many correlations among muscle characteristics and among sensory qualities were consistent for most animal types. Isocitrate dehydrogenase (ICDH) activities allowed discrimination of muscles with respect to myosin heavy chain (MyHC)-I proportions for all animal types. Lactate dehydrogenase (LDH) and phosphofructokinase (PFK) activities were positively correlated for most animal types. Overall liking was correlated with beef flavour and abnormal flavour in all animal types and with global tenderness for all animal types except for Charolais cross breed steers. For all animal types except for Angus×Friesian heifers, beef flavour and abnormal flavour were negatively correlated. Overall liking was not correlated with juiciness. PFK, ICDH and citrate synthase (CS) activities were strongly associated with tenderness, beef flavour and overall liking when average values for all animal types were used. However, associations between muscle characteristics and sensory qualities within animal types were weak and inconsistent.

Keywords: cattle, muscle characteristics, meat sensory qualities, gender, breed, prediction

1. Introduction

Meat quality attributes (colour, tenderness, flavour and juiciness) have major effects on the satisfaction of the consumer (Dransfield *et al.* 2003). These attributes are influenced by muscle characteristics of the animal and post-mortem biochemical reactions (Ouali 1990; Dransfield *et al.* 2003; Jurie *et al.* 2007). Muscle characteristics are influenced

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[#] Deceased. We would like to dedicate this work to the memory of Didier Micol.

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by management factors such as breed, age, sex and diet (Cuvelier *et al.* 2006; Jurie *et al.* 2006). They depend on the contractile and metabolic properties of the different categories of the myofibres (type I, type IIa, type IIx and/or type IIb) that compose the bovine skeletal muscles (Picard and Cassar-Malek 2009) and on the attachment of these fibres to the intramuscular connective tissues (IMCT) of which collagen is the major protein component (Nishimura 2010; Dubost *et al.* 2013). Muscle fibre composition is known to influence colour, tenderness and ultimate pH (Muchenje *et al.* 2009; Wu *et al.* 2014; Gagaoua *et al.* 2015a) and intramuscular fat (IMF) content is believed to influence tenderness and juiciness (Mandell *et al.* 1997; Scollan *et al.* 2001; Gagaoua *et al.* 2014).

The mechanisms underlying the relationships between muscle fibre type composition and sensory qualities are complex and results are inconsistent across studies. In a study on young Charolais bulls, Renand *et al*. (2001) explained 25 to 35% of the variability in global tenderness by collagen characteristics and metabolic properties. In a study combining seven breeds and cross-breeds from different experiments, *Longissimus thoracis* muscles with lower collagen contents and increased contractile and metabolic activities had greater tenderness, but each correlation explained at most 4% of the variability between animals (Chriki *et al.* 2012a). In other studies, muscle characteristics could predict sensory qualities across, but not within muscles and with varying precision (Keith *et al.* 1985; Bonny *et al.* 2015).

Little or no information is available on the existence of consistent relationships between various traits in different muscles or animal types. The present study aims to compare relationships between muscle characteristics (fibre type, collagen, intramuscular fat contents and enzyme activities) and meat sensory qualities in *Longissimus thoracis* muscle between different types of cattle. The main objective was to determine whether consistent relationships exist between sensory qualities and muscle characteristics, independently of gender and breed or rearing site. The study is a part of the European ProSafeBeef project (www.prosafebeef.eu).

2. Materials and methods

2.1. Animals

The study used 265 beef cattle of comparable chronological age (less than two years old) and different genders of four different experiments of the European ProSafeBeef project. The eight animal types included young bulls (B), i.e, 25 Limousin (Li), 25 Blond d'Aquitaine (BA) and 24 Angus (AA) reared in France (FR) and 25 Holstein (Ho) reared in Germany (DE); steers (S), i.e., 40 Belgian-Blue×Holstein (BH) and 32 Charolais×Friesian (CF) reared in Wales (UK); and heifers (H), i.e., 47 Belgian-Blue×Friesian (BF) and 47 Angus×Friesian (AF) reared in Ireland (IE). Hence each experiment corresponded to a different gender of cattle, and young bulls were reared in two experiments. The aim of the study was not to compare genders or breeds, but to evaluate differences and similarities between different animal types.

2.2. Management, slaughtering and sampling

During the finishing period (90 to 110 days), the animals were housed in groups of four animals of a same breed in 4 m×4 m pens with *ad libitum* access to high energy feed in the four experimental farms. The diets of the animals consisted of pasture, grass silage or concentrates, supplemented with lipids and/or antioxidant from plants additives according to the ProSafeBeef project. Details concerning the feeding regimens are as described in the ProSafeBeef project (www.prosafebeef.eu) and synthesised in the following sections.

The experiment in France was performed with 74 young bulls varying in their earliness of puberty. Bulls were fed, for a 100 days finishing period, rations composed of a 80% concentrate and 20% straw, supplemented with 1.3% Na bicarbonate and 0.75% vitamins and minerals. Within each breed, 25% of the animals received the control regime in which the concentrate contained 17% wheat, 34% maize, 25% beetroot pulp, 15% soybean meal and 8% alfalfa. For 75% of the animals, maize was removed and the regime was supplemented with unsaturated fatty acids. Hence the concentrate was composed of 15% wheat, 10% wheat middlings, 15% wheat bran, 25% beetroot pulp, 4% sunflower meal, 5% rapeseed meal and 25% extruded linseed.

The experiment in Germany used 30 Holstein young bulls assigned to two dietary treatments. Half of the animals received concentrate based on 40% crushed wheat, 10% maize, 41% soybean meal, 5% minerals, 2% molasses and 2% straw. The experimental group received grass silage with concentrate containing 58% crushed wheat, 20% crushed maize, 12% rapeseed cake, 3% linseed oil, 5% minerals, and 2% molasses.

The experiment in Ireland used 96 heifers of two genotypes (BF and AF) on pasture as described in Dunne *et al.* (2010). Briefly, at four months of age, within each breed one-third of the animals were assigned to a standard grass-based production system only, one-third were assigned to this system but supplemented with a sunflower oil containing concentrate and one-third were assigned to this system but supplemented with a ruminally protected fish oil containing concentrate (920 g dry matter kg^{-1}, 302 g lipid kg^{-1} DM, 3.47 g EPA (20:5n-3)/100 g^{-1} and 5.74 g DHA (22:6n-3)/100 g^{-1}). Supplements were designed to enhance conjugated linoleic acid (CLA) or n-3 polyunsaturated fatty acid (PUFA) depo-

sition in muscle. The cattle were housed in a slatted floor shed during winter. They were slaughtered at the end of the second grazing season or after a second winter indoors.

The experiment in the United Kingdom used 72 steers initially housed and fed *ad libitum* on first cut perennial ryegrass silage. Feeding regimes were based on the addition of plant extracts (PX): a PUFA-rich luzerne based plant extract obtained from the liquid fraction extracted from fresh luzerne (*Medicago sativa* L.), and then heat-treated and dried. The first group of 40 Belgian-Blue×Holstein was allocated to one of five dietary treatments: 1) Grass silage only, 2) grass silage plus 75 kg PX/DM intake, 3) grass silage plus 150 kg PX/DM intake, 4) straw plus control concentrate and 5) straw plus PX-supplemented concentrate and vitamin E (~300 mg kg^{-1}). The second group of 32 Charolais×Friesian were housed indoors and fed on *ad libitum* grass silage and a conventional commercial concentrate at 70:30 forage:concentrate ratio on a DM basis, for a 30 day finishing period. After this period, eight animals were allocated at random to one of four dietary treatments: 1) grass silage, 2) grass silage plus 1.5% Echium oil/silage dry matter intake, 3) grass silage plus 3.0% Echium oil/silage DMI and 4) grass silage plus 3.0% linseed oil/silage DMI. Approximately 1 kg of sugar beet pulp and higher level of vitamin E (300 IU kg^{-1}) was also offered to all animals. However, results presented in the present study were not influenced by feed composition.

The 265 beef animals were slaughtered when they achieved the fat class 3 on the EUROP grid of carcass classification (European Economic Community (EEC) Regulations No. 1208/81). Each research group slaughtered approximately equal numbers of cattle from each nutritional diet/animal type combination on each slaughtering day. They were all slaughtered under standard conditions in either commercial or experimental slaughterhouses, depending on the facilities of each country. Before slaughter, all animals were food deprived for 24 hours and had free access to water. Slaughtering was performed in compliance with the welfare regulations of each country and respecting EU regulations (Council Regulation (EC) No. 1099/2009). All animals were stunned using a penetrative captive bolt, prior to exsanguination. The carcasses were not electrically stimulated and they were chilled and stored at 4°C until 24 h *post-mortem*. Ultimate pH was recorded between the 6th and 7th rib using a pH meter equipped with a glass electrode 24 or 48 h *post-mortem* (Gagaoua *et al.* 2015a).

The *Longissimus thoracis* muscle (LT, fast oxido-glycolytic) was excised from the right side of the carcass 24 h after slaughter. The epimysium was carefully dissected and about 400 g of muscle was taken between the 6th and 11th ribs of the LT muscle. Muscle cuts were divided into 3 parts, one for sensory evaluation and two for biochemical analysis. Part of the sample was frozen in liquid nitrogen and kept at –80°C until analysed for determination of enzyme activities, protein extraction and myosin heavy chain (MyHC) quantification. Another part of the sample was cut in pieces (1–2 cm cross-section), vacuum packed and stored at –20°C until analysed for collagen and intramuscular fat content. Samples for sensory evaluation were cut into steaks and placed in sealed plastic bags under vacuum and kept between 2–4°C for 14 days (bulls from France and Germany and heifers from Ireland) or 10 days (steers from UK) of ageing. Each loin sample was then frozen and stored at –20°C until sensory evaluation. All evaluations of muscle characteristics, intramuscular fat content excepted (using the same protocol), were conducted by the same laboratory (INRA, France).

2.3. Enzyme activities measurement

Glycolytic enzyme activities (phosphofructokinase (PFK; EC 2.7.1.11); lactate dehydrogenase (LDH; EC 1.1.1.27)) and oxidative enzyme activities (isocitrate dehydrogenase (ICDH; EC 1.1.1.42), citrate synthase (CS; EC 4.1.3.7) and cytochrome *c* oxidase (COX; EC 1.9.3.1)) were quantified as described by Jurie *et al.* (2006). These different enzymes representative of different steps of the glycolytic and oxidative pathways are currently used for the characterization of the metabolic types of muscles in beef (Sudre *et al.* 2005; Jurie *et al.* 2006), poultry (Eadmusik *et al.* 2011), pig (Demars *et al.* 2007), sheep (Mascio *et al.* 2005) and camel (Abdelhadi *et al.* 2012; Al-Owaimer *et al.* 2014). For each of the 265 animals, 200 mg of frozen muscle was thawed, ground and homogenized with a Polytron for 15 s in a 5% (w/v) solution buffer of 10 mmol L^{-1} Trizma-Base (pH 8.0), 250 mmol L^{-1} sucrose and 2 mmol L^{-1} EDTA. One aliquot of homogenate was centrifuged at 6 000×g for 15 min at 4°C for determination of PFK, LDH and ICDH activities. The rest of the homogenate was freeze thawed and sonicated for determination of CS and COX activities before centrifugation for the determination of CS activity. Enzyme activities (means of triplicate) were measured at 25 or 28°C using an automatic spectrophotometer (Uvikon 860, Kontron Instruments, Milan, Italy). The results were expressed as units per gram of wet muscle.

2.4. Intramuscular connective tissue measurement

Lyophilized muscle powder was prepared for collagen determination as described by Jurie *et al.* (2007). Briefly, frozen muscle was homogenized in a household cutter, freeze-dried for 48 h, pulverized in a horizontal blade mill and stored at 4°C until analysed. To estimate total and insoluble collagen, the amount of total hydroxyproline (OH-prol) content was

measured.

Total collagen content was determined after overnight hydrolysis of 50 mg of lyophilized muscle powder with 10 mL HCl 6 N at 105°C according to the method of Listrat *et al.* (1999). Insoluble collagen was determined in triplicate according to a procedure adapted from Hill (1966). Lyophilised muscle powder (100 mg) was rehydrated for 1 h in 10 mL of buffer (0.23 mol L^{-1} NaCl, 25 mmol L^{-1} Trizma, pH 7.4) before being heated in a water bath at 75°C for 1 h. After centrifugation at 4 000×g for 15 min at 20°C, the pellets were evaporated for 4 h to dryness at 45°C. After this, they were hydrolysed with 10 mL of HCl 6 N and treated as for total collagen. The data (means of triplicates) are expressed in μg of OH-prol per mg of dried matter for both total and insoluble collagen.

2.5. Intramuscular fat content measurement

Steaks (20 mm thick) of LT muscle were taken as described by Scollan *et al.* (2001) for the analysis of fatty acid (FA) composition. Briefly, total intramuscular fat content from a tissue powder were extracted with chloroform-methanol (2:1, v/v) according to the method of Folch *et al.* (1957) by homogenisation at room temperature. The lipid contents were determined by gas liquid chromatography (GLC) on CP Sil 88 glass capillary column. Muscle total lipids are reported as g of fatty acid per 100 g wet tissue.

2.6. Protein content quantification

The protein concentrations of the samples were determined according to the Bradford method (Bradford 1976) using the Bio-Rad Protein Assay. Bovine serum albumin (BSA) at a concentration of 1 mg mL^{-1} was used as standard.

2.7. Electrophoresis and quantification of MyHC

Myofibrillar proteins from the LT muscles were extracted on ice as described by Picard *et al.* (1994). Briefly, 100 mg of frozen muscle were ground in 5 mL of extraction buffer solution containing 0.5 mol L^{-1} NaCl, 20 mmol L^{-1} Na pyrophosphate, 50 mmol L^{-1} Tris, 1 mmol L^{-1} EDTA and 1 mmol L^{-1} dithiothreitol. After 10 min at 4°C on ice, the sample was centrifuged for 5 min at 5 000×g. Following centrifugation, the supernatant was diluted 1:1 (v/w) with glycerol at 87% and stored at –20°C until used. The samples were then mixed with an equal volume of loading buffer containing 4% SDS (w/v), 125 mmol L^{-1} Tris, pH 6.8, 20% glycerol (v/v), 10% β-mercatptoethanol (v/v) and 0.02% pyronin Y (w/v). The proteins were separated by SDS-PAGE electrophoresis according to Picard *et al.* (2011) using 9.2% polyacrylamide gels which were made in the Bio-Rad mini-Protean II Dual Slab Cell System. After staining, the gels were scanned and the proportions of the different MyHC bands were quantified by densitometry with ImageQuant software 5500 (Amersham Biosciences/GE Healthcare).

The quantification of the bands revealed the existence of MyHC-IIb isoform (Picard & Cassar-Malek 2009) in only 22 of the 265 animals (BH (8); BA (6); CH (5); AA (2); and Li (1)) with a maximal percentage of 5.5%. Consequently MyHC-IIb percentages were totalled with those of MyHC-IIx creating a new variable “MyHC-IIx+b” (fast glycolytic fibres).

2.8. Sensory analysis

The panellists were trained in accordance with the ISO standards ISO/TC 34 (ISO_8586 2012) and the accuracy and precision of the panellists were verified before sensory analysis. Sensory analysis was performed at Bristol University in the United Kingdom on the LT muscle taken 24 h after slaughter as previously described by Karamichou *et al.* (2007) and Gagaoua *et al.* (2013). Each loin sample was aged 14 days (bulls from France and Germany and heifers from Ireland) or 10 days (steers from the United Kingdom). Approximately 40 h before sensory assessment, samples were thawed, without stacking or overlapping, at 4–5°C. The morning of the analysis, the meat samples were cut into two 1.9 cm thick steaks and cooked under domestic grills, turning every 2 min until the temperature of 74°C (typical in the UK) was reached as measured in the geometric centre of the steak (measured by a thermocouple probe). After grilling, each steak was cut into 3 cm×2 cm×2 cm portions which were immediately presented to 10 panellists trained in beef meat sensory analysis. Each tasting booth was equipped with computer terminals linked to a fileserver also running a sensory software programme (FIZZ ver. 2.20h, Biosystemes, Couternon, France) that facilitated the direct entry of assessor ratings on a 0 to 10 unstructured scale to evaluate the following attributes: global tenderness (0, extremely tough; 10, extremely tender), juiciness (0, extremely dry; 10, extremely juicy), beef flavour intensity (0, extremely weak; 10, extremely strong), abnormal flavour intensity (0, extremely weak; 10, extremely strong) and overall liking (0, dislike very much; 10, like very much). All sensory assessments were completed under red light in a purpose built sensory analysis room.

2.9. Statistical analysis

The SAS software (ver. 9.1, 2002; SAS Institute Inc., Cary, North Carolina, USA) was used to verify the normality of the data and to conduct ANOVA and principal component

analyses (PCA). Pearson correlations, ANCOVA and regression analyses were carried out using XlStat (ver. 2009.1.01, Addinsoft®, New York, NY, USA). Data were normally distributed (Shapiro-Wilk test). ANOVA was used to compare animal types. For these comparisons, the general linear model (GLM) procedure fitting animal type as fixed effect, and Tukey test were used to compare LSmeans (SAS ver. 9.1, 2002; SAS Institute Inc.). PCA (Pearson) was conducted on all variables using all animal types to produce graphs to illustrate visually the different characteristics of the animal types. An overall Kaiser's measure of sampling adequacy (MSA) was calculated using PROC FACTOR of SAS. Variables with low MSA (<0.5) were removed from the final PCA (Gagaoua *et al.* 2015a). ANOVA was carried out to compare the individual PCA scores on the first and second axis between breeds.

Pearson correlations were calculated across animal types using average values to determine which muscle characteristics and sensory qualities were associated at the level of animal types. Pearson correlations were further calculated within animal types, to determine consistency of relationships among muscle characteristics and sensory qualities across animal types. Results are reported in figures referred to as "correlation networks". ANCOVA was used to determine relationships among sensory qualities and muscle characteristics within genders while taking into account breed.

The ANCOVA model used was $y_{ij}=\mu+\alpha_i+\beta(x_{ij}-\overline{x})+\varepsilon_{ij}$

Where,

y_{ij} is the value of the dependent variable for the jth observation in the ith animal type.

μ is the overall (constant) mean value of the dependent variable.

α_i is the effect of the ith animal breed on the dependent variable.

β is the pooled regression slope of the dependent variable with the explicative variable for each breed.

x_{ij} is the value of the explicative variable for the jth observation from the ith breed.

$\overline{x}$ is the common mean of x of all samples,

ε_{ij} is the random or unexplained error associated with the jth observation in the ith animal type group not explained by the animal type of the explicative variable.

If non-significant, breed was removed from the model, i.e., $\alpha_i=0$, and the model became a simple linear regression ($y_{ij}=\mu+\beta(x_{ij}-\overline{x})+\varepsilon_{ij}$).

For ANCOVA and regression analyses, the option "optimal model" was selected. This option produces the model with the highest adjusted r^2 value. The adjusted r^2 value expressed as a percentage will be referred to as the % of variability explained. The maximal number of explanatory variables was fixed at 3. Variables that were significant but contributed less than 2% in terms of explanatory power (r^2) were excluded from the model. The standardised coefficients are reported in the Results section and refer to how many standard deviations the explained variable will change, per standard deviation change in the explanatory variable.

Finally, for all variables Z-scores were calculated, removing animal type effects (Picard *et al.* 2014). This data set was used to determine associations among variables after removal of breed effects. More specifically, breeds showing a significant correlation between two given variables were combined and an overall r-value was calculated using Z-scores and reported in the correlation networks.

3. Results

3.1. Associations among muscle characteristics and sensory qualities at the level of the animal type

Differences between animal types in terms of LT muscle characteristics and sensory qualities are described in Table 1. Correlations based on the means presented in Table 1 indicate that certain traits are strongly associated at the level of the animal type (Table 2-A–C; Fig. 1). For example, animal types with high COX activity had also high ICDH activity but low LDH activity. High COX activity was further associated with high MyHC-I proportions, low MyHC-IIx+b proportions and high ultimate pH. Animal types with higher proportions of MyHC-IIa had higher levels of collagen. Certain correlations did not reach significance due to the low level of degrees of freedom (d*f*=6). Animal types with high tenderness had high beef flavour and overall liking and were characterised by low PFK and high CS activities (Table 2-C). High tenderness was also associated with high IMF (Table 2-C). The PCA plots illustrate visually the relationships between muscle characteristics and sensory qualities (variable loadings: Fig. 2-A) and the similarities and differences between the breeds and genders of the different experiments (average individual scores: Fig. 2-B). The first principal component accounting for 28% of variability was positively correlated with oxidative enzyme activities (ICDH, COX and CS), MyHC-I fibres, tenderness, juiciness, beef flavour and overall liking and negatively correlated with MyHC-IIx+b and the activity of the glycolytic enzymes PFK and LDH. The second principal component accounting for 21.7% of the variability was relatively strongly positively correlated with total and insoluble collagen and negatively with IMF content and the activity of the glycolytic enzyme LDH. Individual scores of the first axis averaged per breed discriminated between nearly all breeds, apart from AF heifers and Ho bulls, who had similar scores, and BF heifers

Table 1 Effect of animal type on muscle characteristics and sensory qualities of *Longissimus thoracis* muscle

Traits[1)]	Gender	Heifers[2)]		Bulls[3)]				Steers[4)]		SEM[5)]	*P*-value	CV (%)
	Breed	AF	BF	Ho	Li	BA	AA	BH	CF			
	(*n*)	(47)	(47)	(25)	(25)	(25)	(24)	(40)	(32)			
Metabolic enzyme activities (μmol min^{-1} g^{-1})												
LDH		1 131 a	1 181 a	921 c	1 007 b	989 b	807 d	877 c	740 e	12.03	***	34.2
PFK		83.3 d	79.8 d	180 a	154 b	159 b	132 c	74 d	64 d	3.38	***	25.4
ICDH		1.28 c	1.24 c	1.62 b	0.96 e,d	0.77 e	1.11 c,d	2.08 a	2.14 a	0.04	***	47.7
COX		14.0 d	13.5 d	18.0 c	16.9 c	14.1 d	20.8 b	20.5 b	25.9 a	0.37	***	51.8
CS		6.54 a	6.84 a	4.54 b	5.33 b	5.11 b	5.20 b	7.21 a	7.27 a	0.09	***	20.0
Collagen contents (μg OH-prol mg^{-1} DM)												
Total collagen		2.84 c	2.95 c	3.74 b	3.33 b,c	3.26 b,c	4.40 a	4.57 a	3.35 b,c	0.07	***	32.1
Insoluble collagen		2.09 c	2.19 b,c	3.03 a	2.49 b,c	2.44 b,c	3.35 a	3.39 a	2.64 b	0.05	***	31.0
Myosin heavy chain (MyHC, %)												
MyHC-I		18.7 d	15.8 d	28.5 b	23.6 c	19.1 d	27.3 b	19.6 d	39.6 a	0.62	***	43.9
MyHC-IIa		34.9 b,c	29.9 c	50.2 a	30.7 c	23.9 d	54.4 a	37.7 b	38.8 b	0.81	***	36.0
MyHC-IIx+b		46.3 b	54.2 a	21.2 c	45.6 b	57.0 a	18.3 c	42.7 b	21.5 c	1.07	***	43.6
Muscle characteristics												
Ultimate pH		5.50 c	5.52 c	5.56 c	5.55 c	5.53 c	5.62 b	5.57 b,c	5.73 a	0.007	***	2.29
Intramuscular fat content (g 100 g^{-1} wet tissue)		5.92 a	3.90 b	2.41 c	1.52 d	1.18 d	3.49 b	2.40 c	3.68 b	0.11	***	57.0
Sensory qualities (0–10 scale)												
Tenderness		5.74 a,b	5.71 a,b	4.20 c	3.79 c,d	3.50 d	4.12 c	5.45 b	6.21 a	0.08	***	25.9
Juiciness		6.60 a	6.54 a	6.76 a	4.78 c	4.30 d	4.65 c	5.53 b	6.75 a	0.06	***	18.1
Beef flavour		5.60 b,c	5.30 c	5.26 c	2.95 e	2.92 e	3.78 d	5.87 b	6.46 a	0.08	***	26.2
Abnormal beef flavour		2.53 c,d	2.82 c	3.99 a	2.57 c,d	2.66 c,d	2.36 d	3.46 b	3.26 b	0.04	***	25.7
Overall liking		4.84 c	4.20 d	3.51 e	3.43 e	3.14 e	3.94 d	5.81 b	7.03 a	0.09	***	31.5

[1)] LDH, lactate dehydrogenase; PFK, phosphofructokinase; ICDH, isocitrate dehydrogenase; COX, cytochrome *c* oxidase; CS, citrate synthase. The same as below.
[2)] Heifers (AF, Aberdeen Angus×Friesian; BF, Belgian-Blue×Friesian).
[3)] Bulls (Ho, Holstein; Li, Limousin; BA, Blond d'Aquitaine; AA, Aberdeen Angus).
[4)] Steers (BH, Belgian-Blue×Holstein; CF, Charolais×Friesian).
[3)] SEM, standard error of mean.
Least square means in the same row for animal type effect not followed by a common letter (a–e) differ significantly, $P<0.05$. ***, $P<0.0001$.

Table 2 Correlations between means per animal type

A Muscle characteristics

Variables	LDH	PFK	ICDH	COX	CS	Total collagen	Insoluble collagen	MyHC–I	MyHC–IIa	MyHC–IIx/b
PFK	–0.01									
ICDH	–0.52	–0.57								
COX	**–0.92**	–0.28	**0.72**							
CS	0.02	**–0.98**	0.62	0.28						
Total collagen	–0.67	0.09	0.36	0.54	–0.10					
Insoluble collagen	**–0.73**	0.16	0.41	0.60	–0.17	**0.98**				
MyHC–I	**–0.81**	–0.02	0.51	**0.86**	0.00	0.18	0.31			
MyHC–IIa	–0.57	0.16	0.33	0.53	–0.27	0.62	**0.71**	0.50		
MyHC–IIx+b	**0.77**	–0.10	–0.47	**–0.77**	0.18	–0.50	–0.62	**–0.82**	**–0.90**	
Ultimate pH	**–0.87**	–0.28	0.59	**0.95**	0.27	0.32	0.40	**0.91**	0.41	**–0.72**
IMF[1)]	0.26	–0.62	0.21	–0.04	0.48	–0.33	–0.34	–0.01	0.20	–0.13

B Sensory qualities

Attributes	Tenderness	Juiciness	Beef flavour	Abnormal beef flavour
Juiciness	0.76			
Beef flavour	0.90	0.86		
Abnormal beef flavour	0.19	0.54	0.56	
Overall liking	**0.84**	0.50	**0.81**	0.28

C Sensory qualities and muscle characteristics

	LDH	PFK	ICDH	COX	CS	IMF	Insoluble collagen	Total collagen	Ultimate pH
Tenderness	0.04	**–0.92**	0.69	0.29	**0.90**	**0.72**	–0.21	–0.20	0.29
Juiciness	0.14	–0.45	0.61	0.13	0.44	0.62	–0.25	–0.34	0.14
Beef flavour	–0.15	**–0.72**	**0.87**	0.41	**0.71**	0.60	0.05	0.01	0.35
Abnormal beef flavour	–0.31	0.06	0.71	0.35	0.03	–0.21	0.39	0.28	0.22
Overall liking	–0.45	**–0.84**	**0.85**	0.70	**0.85**	0.42	0.12	0.12	0.66

[1)] IMF, intramuscular fat.
Significant correlations (P<0.05) are shown in bold characters.

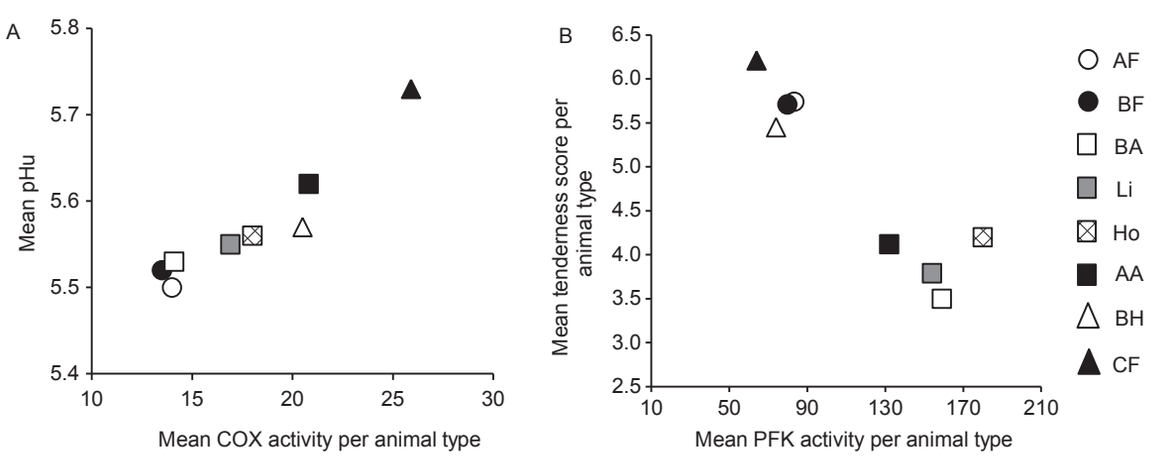

Fig. 1 Correlation graphs to illustrate associations between means per animal type of cytochrome *c* oxidase (COX) activities and ultimate pH (pHu, A) and phosphofructokinase (PFK) activities and tenderness (B). AF, Aberdeen Angus×Friesian; BF, Belgian-Blue×Friesian; BA, Blond d'Aquitaine; Li, Limousin; Ho, Holstein; AA, Aberdeen Angus; BH, Belgian-Blue×Holstein; CF, Charolais×Friesian. The same as below.

and AA bulls, who had also similar scores (Fig. 2-C). Briefly, CF and BH steers were characterised by high activities of oxidative enzymes and MyHC-I and high scores for tenderness, juiciness, beef flavour and overall liking, while for Li

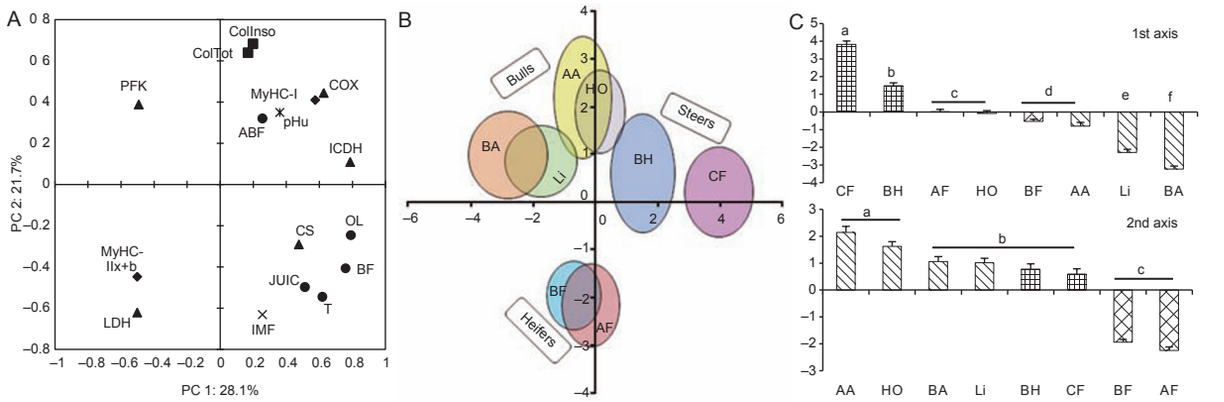

Fig. 2 Principal component (PC) analysis using all studied variables related to beef quality and muscle characteristics. A, loadings on the first two principal axes: ■, collagen characteristics; ●, sensory quality attributes; ▲, metabolic characteristics as indicated by glycolytic and oxidative enzymes; ♦, MyHC isoforms; x, intramuscular fat content; and Ж, pHu. B, individual scores averaged per animal type (breed×gender/site) for the first two axes. The width and height of each oval represent the standard error of the mean for the first and second axis, respectively. C, mean scores per animal type on the 1st (top) and 2nd (bottom) axis of the PCA. An overall MSA (Kaiser's Measure of Sampling Adequacy) of 0.75 was obtained after removal of the variable MyHC-IIa which had the lowest MSA value (MSA=0.32). ColTot, total collagen; ColIns, insoluble collagen; PFK, phosphofructokinase; LDH, lactate dehydrogenase; ICDH, isocitrate dehydrogenase; COX, cytochrome c oxidase; CS, citrate synthase; MyHC-, myosin heavy chain-I, and -IIx+b; IMF, intramuscular fat content; T, tenderness; JUIC, juiciness; BF, beef flavour; ABF, abnormal beef flavour; OL, overall liking for m. *Longissimus thoracis* samples. The same as below.

and BA bulls this was the opposite. BF heifers and AA bulls had the same profile as the latter group, but less extreme. AF heifers and Ho bulls had intermediate profiles. Individual scores of the second axis averaged per breed formed 3 groups that differed significantly (Fig. 2-C). The AA and Ho bulls scored relatively high for collagen and PFK and low for LDH and MyHC-IIx+b while BF and AF heifers scored the opposite. The BA and Li bulls and BH and CF steers had intermediate levels. In conclusion, the eight groups differed on at least one of the two first principal axes.

3.2. Correlations among muscle characteristics within animal types

Correlations calculated per animal type using Z-scores (Fig. 3-A) found that MyHC-IIx+b proportions were negatively correlated with MyHC-I and MyHC-IIa proportions for nearly all animal types. LDH and PFK activities were weakly positively correlated for all breeds apart from BA and Ho. ICDH, COX and CS were positively correlated for at least half of the animal types. ICDH and LDH, and MyHC-I and LDH were negatively correlated for four animal types. These correlations were not gender specific, as the three genders were represented in each of the correlations. Total collagen content was strongly correlated with insoluble collagen for all animal types, as expected. In addition to the figure, for BH heifers LDH activity was negatively correlated (r=–0.44; P<0.05) with COX activity, and for AA bulls, with CS activity (r=–0.44; P<0.05).

3.3. Correlations among sensory qualities within animal types

With respect to sensory qualities, for all animal types, overall liking was positively correlated with beef flavour and negatively with abnormal flavour. For all animal types except for AF heifers, beef flavour and abnormal flavour were negatively correlated (Fig. 3-B). Overall liking was further correlated with global tenderness for all animal types except for CF steers. These correlations were again not gender specific, as the three genders were represented in each of the correlations found. In addition, global tenderness was positively correlated with juiciness for three of the animal types and with beef flavour, also for three animal types (Fig. 3-B). None of the animal types showed a correlation between juiciness and beef flavour (r between –0.20 and 0.28; NS).

3.4. Correlations between sensory qualities and muscle characteristics within animal types

It was not possible to establish a coherent correlation network for correlations between sensory qualities and muscle characteristics as only one significant (P<0.05) correlation was found that showed some consistency across animal types. Tenderness was correlated with CS content for Li bulls (r=0.43), AF heifers (r=0.34) and BH steers (r=0.39). For these animal types, the overall r-value (on Z-scores) was 0.38 (P<0.0001). In addition, fourteen more correlations

Table 3 Regression analyses (optimal models) per gender between sensory qualities and muscle characteristics including within-gender breed effects

Constant	μ	Equation terms (SD)[1)]			Partial adjusted *R*-square (%)^{Significance}			Total adjusted *R*-square (%)
		1st term	2nd term	3rd term	1st term	2nd term	3rd term	
Tenderness								
Heifers	8.5	–2.39 (0.28) LDH	–	–	6.6**	–	–	6.6**
Bulls	3.2	+0.02 (0.23) MyHC–IIa	–	–	4.6*	–	–	4.6*
Steers	14.1	–1.02 (0.54) BH Breed	–1.88 (0.30) pHu	+0.40 (0.31) CS	14.9***	6.9**	6*	27.8***
Z-scores all animal types[2)]		**+0.16 CS**	**+0.13 MyHC–IIa**	**+0.13 IMF**	**2.1***	**1.4***	**1.3***	**4.8****
Overall liking								
Heifers	5.0	+0.61 (0.37) AF Breed	–0.27 (0.25) Total collagen	–	13.8***	5.4**	–	19.2***
Bulls	3.0	+0.24 (0.24) IMF	–	–	9.0**	–	–	9**
Steers	7.6	–1.02 (0.54) BH Breed	–0.17 (0.24) Total collagen	–	35.5***	4.0*	–	39.5***
Z-scores all animal types		**–0.17 (0.24) Total collagen**	**+0.13 IMF**	–	**4.8****	**2.4****	–	**7.2****

[1)] Maximal number of variables allowed was set at three, minimal explanatory power was set at 2% apart from the global models using Z-scores.
[2)] A global model based on Z-scores is presented in bold letters.
*, P<0.05; **, P<0.01, ***, P<0.001

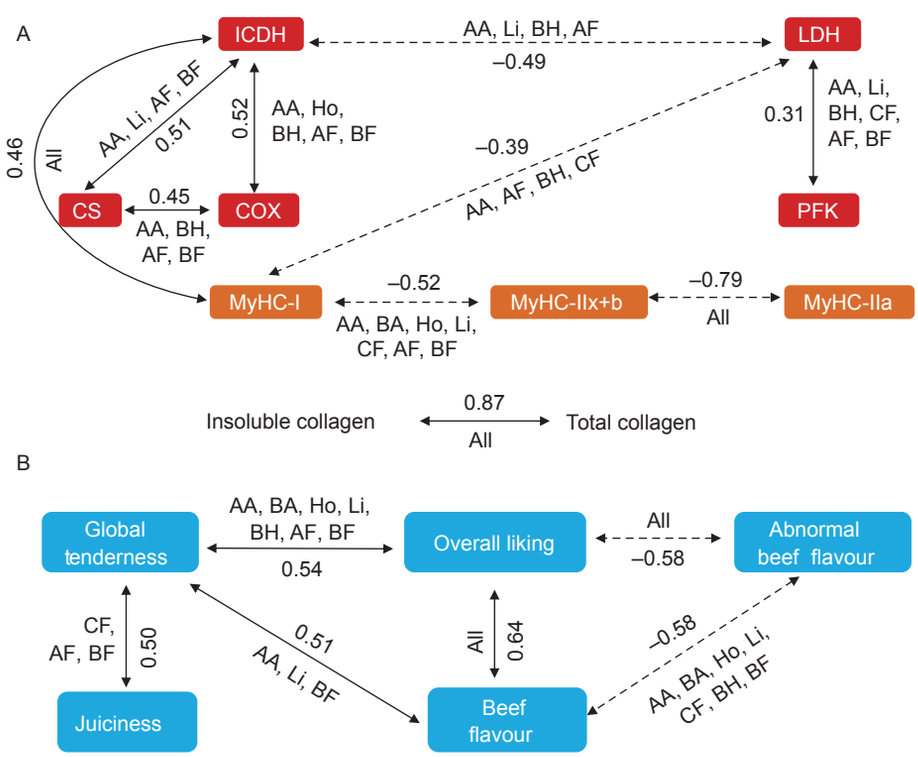

Fig. 3 Correlation network representing consistent correlations between muscle characteristics (A) and sensory qualities (B). Positive correlations are represented by a continuous line; negative correlations are represented by a dotted line. The animal types for which the correlation was significant are indicated next to the arrow. If "all" is indicated, the correlation was significant for all animals. The values next to the arrows represent the regression coefficients calculated using Z-scores including only the animal types for which the correlation was significant.

were found between muscle characteristics and sensory qualities with *r*-values over 0.40 (P<0.05), but showed no consistency across animal types. Most correlations were found for Li bulls: abnormal beef flavour with PFK (r=0.47), beef flavour with MyHC-IIa, MyHC-IIb+x and LDH (r=0.40; –0.47 and –0.52, respectively), overall liking with insoluble

collagen and PFK (r=–0.63 and –043, respectively) and juiciness with ultimate pH (pHu) (r=0.48). For Ho bulls, beef flavour was correlated with MyHC-IIa and COX (r=–0.52 and 0.49, respectively) and juiciness with MyHC-IIa, ICDH and COX (r=–0.50; 0.51 and 0.67, respectively). For AF heifers, juiciness was correlated with insoluble collagen and lipid content (r=–0.40 and 0.55, respectively). Other significant correlations were found for AF and BF heifers and BH steers, but they were relatively weak (r<0.40).

The lack of consistency between animal types explains the weak explanatory power of the regression models subsequently established. When genders were considered separately using raw data of muscle characteristics, the models explained between 4.6 and 39.5% of the variability between animals (Table 3). However, breed explained most of the variability and the contribution of muscle characteristics was weak. The strongest contribution was from IMF, explaining 9% of the variability in overall liking between bulls. LDH activity in heifers, and pHu and CS activity in steers, contributed between 6 and 7% to the varaibility of tenderness.

The explanatory power of regression analyses between Z-scores of sensory qualities and muscle characteristics (Table 3) was also very weak. For tenderness, regression analyses using Z-scores found that CS, MyHC-IIa and IMF explained together 4.8% of the variability between animals. For overall liking, total collagen content and IMF explained together 7.2% of the variability between animals in overall liking.

4. Discussion

The present study compared *Longissimus thoracis* muscle characteristics and sensory qualities to explore consistencies and differences in correlations among muscle characteristics and sensory qualities in eight animal types. The animals were similar in age and had all been subjected to a finishing period of 100 days on average. The animal types differed in breed, gender and rearing site, where each rearing site corresponded to a given gender, breed and rearing environment. Untransformed data were used to compare animal types, and Z-scores, after removing the effects of animal type, were used to describe similarities across animal types.

Across all animal types, the LT muscle had high glycolytic and intermediate oxidative properties. Similarly, Chriki *et al.* (2012b) classified the LT muscle as fast oxido-glycolytic. The animal types differed in all the measured contractile and metabolic muscle characteristics and sensory qualities. The animal types were characterised by significantly different positions along the first principal axes of the PCA indicating that the first two axis had good discriminatory power for the animal types used in the study. Due to the choice of breeds, breed effects were stronger for steers and bulls than for heifers. Overall, the LTs of heifers and steers were more glycolytic and oxidative oriented, respectively, while the LT of bulls was intermediate, as also previously reported by Jurie *et al.* (2009). More specifically, compared to the steers and bulls, the heifers had lower MyHC-I proportions, higher LDH and lower COX activities. The fibre type distribution of the BH steers was close to the distribution observed in the heifers, while CF steers had high MyHC-I proportions.

Sensory analysis also revealed many significant differences between animal types. Steers had the best and bulls the worst scores for sensory qualities, with intermediate levels for heifers. The best scores were obtained for the CF steers. The CF steers and Ho bulls and both heifer breeds scored high for juiciness and Ho bulls scored high for beef flavour compared to the other bulls. These observations agree with earlier results reporting better sensory scores for steers than heifers and for heifers than bulls (Wulf *et al.* 1996; Choat *et al.* 2006; Bureš and Bartoň 2012). Other results found, in contrast, no differences between steers and heifers or between young bulls and heifers (Hoving-Bolink *et al.* 1999) in terms of tenderness. Another study found, also in contrast to our results, higher scores for juiciness and beef flavour for heifers compared to steers (Hennessy and Morris 2003).

Correlations using average values of animal types found coherent associations between fibre type composition and glycolytic and oxidative enzymes. Coherent associations among muscle characteristics were also found within animal types. The correlation network shows that oxidative characteristics (MyHC-I, ICDH, COX and CS) were negatively associated with glycolytic characteristics (MyHC-IIx+b and LDH) for a majority of animal types.

For the eight animal types studied, ICDH activity was correlated with the proportion of slow oxidative fibres, MyHC-I. These results are coherent with earlier results showing that MyHC-I proportions may be appropriate to characterise the muscle in terms of oxidative capacity in pigs (Gil *et al.* 2003), cattle (Olivan *et al.* 2004), rabbits (Ramirez *et al.* 2004), and sheep (Sazili *et al.* 2005). Overall, results are coherent with existing knowledge on the associations between metabolic and contractile characteristics of muscle fibres, but apart from the correlation between ICDH activity and MyHC-I proportions, many variations existed within the animal types. The relatively weak explanatory power of muscle characteristics is in accordance with other studies (Keith *et al.* 1985; Chriki *et al.* 2012b; Bonny *et al.* 2015).

The comparison between the analyses within animal types and the analysis on average values of animal types indicates that although overall, similar biological laws operate in the eight animal types, when looked at in details, the

precise balance between enzymes may be regulated differently according to animal type. For example, PFK and CS activities were strongly negatively correlated when average values of animal types were used but this correlation was not found within animal types, suggesting that these enzymes are not directly causally related. The negative association between LDH and ICDH observed in some of the animal types may be explained by the competition relative to the fate of pyruvate, conversion into lactate or entrance into the citric acid cycle. The absence of consistent correlations between two traits may be also related to the fixed effects. For example, PFK and LDH activities were not correlated when average values were used, because bull breeds had much higher PFK activity but similar LDH activity compared to the other breeds.

Correlations between sensory qualities within animal types or using averages per animal type associated high beef flavour, high tenderness and high overall liking. Beef flavour and juiciness were correlated when average values of animal types were used, but not within any of the animal types, suggesting that meat from certain animal types (i.e., heifers, steers and Ho bulls) had more beef flavour and was juicier but that there was no causal link between the two traits. The significant correlations show a strong consistency in the determinism of overall liking across animal types and suggest that flavour may be as important as tenderness in determining overall liking for fresh beef steaks as also previously indicated (Mottram 1998; Monson *et al.* 2005). No relationship was found between overall liking and juiciness. These findings are consistent with a previous study, which found tenderness and flavour to be the most important attributes in beef eating quality by UK consumers while juiciness had a relatively low impact (Glitsch 2000). In contrast, a previous study on bulls found that overall liking was associated with tenderness and flavour, but also with juiciness (Monson *et al.* 2005).

In contrast to overall liking, the determinism of tenderness in terms of other sensory attributes showed little consistency when animal types were considered separately. The only correlation showing some consistency was between tenderness and juiciness: for three animal types, CF steers and AF and BF heifers. Similar results were earlier reported (Serra *et al.* 2008; Oury *et al.* 2009; Gagaoua *et al.* 2013). These animal types had higher tenderness and juiciness scores than the other animal types. Possibly, at higher levels of tenderness and juiciness, the perceptions of tenderness and juiciness reinforce each other mutually. Meat juiciness is considered to arise from moisture released by meat during chewing, and moisture from saliva (Juarez *et al.* 2012).

The negative association between tenderness and abnormal beef flavour observed for bulls may be related to the halo effect, i.e., the perceived level of a sensory quality is influenced by another sensory quality (Gill *et al.* 2010). In bulls, abnormal beef flavour scores were relatively high compared to heifers and steers.

Correlations between muscle characteristics and sensory qualities were weak within and inconsistent across animal types. In contrast, high CS activities, high IMF contents and low PFK activities were very good predictors for good tenderness and overall liking, but only when average values of animal types were used. These correlations were, however, inconsistent with correlations within animal types. Thus, the relationships between high tenderness and overall liking, and high CS activities and IMF contents and low PFK activities were, at least in part, only indirect. The associations found in the regression models were, albeit weak, coherent with earlier studies. For example, tenderness was slightly better in meat from young bulls containing more MyHC-IIa, from steers with higher CS activity and from heifers with lower LDH activity. This is coherent with earlier studies showing positive correlations between LT tenderness and proportions of slow oxidative fibres (Renand *et al.* 2001; Chriki *et al.* 2012a). Zamora *et al.* (1996) found a positive relationship between myofibre resistance and CS activity. However, other studies found negative (Ozawa *et al.* 2000), or little or no correlations (Vestergaard *et al.* 2000).

IMF content was retained in several explanatory models of tenderness and overall liking; the only meaningful contribution of IMF content was to overall liking in the young bulls, where it reached 9%. For comparison, Wheeler *et al.* (1994) who evaluated 1 667 cattle and Bonny *et al.* (2015) who evaluated 6 muscles from 36 cattle found that IMF explained at most 5 to 6% of the variation in palatability traits. Recently, another study conducted by our group found no effect of IMF on the tenderness score in LT muscle of young bulls and cows (Chriki *et al.* 2013).

Total collagen content had a weak negative effect on overall liking both in heifers and steers. Although negative associations between total collagen content and overall liking and tenderness were earlier reported, these associations existed only across but not within muscles, suggesting that in contrast to our study, in these studies, there was no direct causal relationship, but rather an effect of muscle (Schonfeldt and Strydom 2011; Bonny *et al.* 2015).

Finally, pHu was weakly correlated with tenderness in steers. Earlier reports indicated that ultimate pH may influence meat quality including flavour, juiciness and tenderness (Mottram 1998; Calkins and Hodgen 2007; Boudjellal *et al.* 2008). The absence of relationships for heifers and bulls may be related to the narrow range of ultimate pH in these animal groups (5.50 to 5.62).

5. Conclusion

Overall, across animal types, markers of oxidative metabolism and slow contractile fibres, and increased IMF content were strongly associated with higher tenderness and overall liking of the LT muscle. Within animal types or genderss, the biological indicators varied and the associations were much weaker. For example, in heifers, higher tenderness was associated with lower LDH activity and in steers with higher CS activity. These differences and the weak correlations illustrate the multifactorial nature of the determinism of tenderness and overall liking (Renand *et al.* 2001; Purslow 2005; Gagaoua *et al.* 2015b). In addition, associated characteristics may have opposite effects. For example, animal types with higher proportions of oxidative fibres (I and IIa) had higher tenderness but higher proportions of MyHC-IIa were associated with higher total collagen content, which reduced tenderness. Thus, a given characteristic such as high proportions of a given fibre type may produce contrasting effects on sensory qualities. Multiple and partly opposite effects add to the complexity of the determinism of sensory qualities and may explain the relatively strong effects of animal type in the present study.

In conclusion, when considering average values per animal type, the present results show strong associations between increased tenderness and overall liking, and oxidative and slow contracting muscle fibre characteristics of the LT muscle. However, to understand and predict meat quality at the level of the individual animal based on muscle characteristics, the animal characteristics need to be taken into account, including breed, gender and undoubtedly also, age.

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