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# Metabolic Properties of Fibers and Connective Tissue of Four Muscles from Bovine Carcasses

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## Abstract

**Meat-grain-size (MGS) assessment is an empirical method for the early prediction of meat quality, a larger grain being synonymous with higher meat tenderness. The objective was to characterize 4 muscles (*longissimus thoracis* LT; *rectus abdominis* RA; *longus colli* LC; *diaphragma* D) of 5 coarse and 5 fine carcasses in terms of MGS in order to establish a link between muscular physicochemical properties and carcass MGS score. All comparisons were made of samples with similar fat content. The broiled sample hardness (shear force) was significantly higher for the coarse group than for the fine group (7.20 vs 5.89 kg; RA). Higher collagen content (27.94 vs 24.87 mg/g of dry matter in LT muscle; 15.86 vs 13.13 mg/g of dry matter in D muscle), higher oxidative metabolism (cytochrome-c oxidase; LT and D) but also higher glycolytic metabolism (lactate dehydrogenase; LT) were also observed in the coarse groups. Not all the muscles react in a similar way depending on the MGS group. Nevertheless, significant results are constant from one muscle to another, the RA being the only muscle for which the difference in hardness between the two groups is significant.**

## Keywords

**Meat Grain, Tenderness, Muscles, Collagen, Bovine**

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## 1. Introduction

Beef wholesalers and butchers are very interested in predicting meat quality traits in order to evaluate consumer acceptance of beef. The method involving consumers or trained panels is time-consuming, expensive and impossible on a large scale. Moreover, it is useful to have early knowledge of the meat quality traits of carcasses and this method cannot be used early enough. Early knowledge allows professionals to direct carcasses to the various markets (butchers, mass retailing, hard-discount, etc.) in the most appropriate way. For this reason, the beef industry is currently attempting to distinguish between standard and high-quality beef products sold by both supermarkets and butchers mainly on the basis of tenderness rather than flavor and taste. This is partly founded on the assumption that butchers possess a know-how which allows them to classify the carcasses according to their expected quality early on.

Carcass classifications of meat quality are integrated into many French specifications so that carcasses can be approved or rejected depending on their expected quality. This is all the more important since many surveys have already shown that the lack of consistency in meat quality is the principal reason for consumers to stop purchasing beef [1]. On the other hand, it seems that many consumers may be ready to pay more for beef if the meat quality, especially tenderness, can be guaranteed [2]. Some butchers have know-how that is founded on subjective criteria used to judge the expected tenderness of carcasses. This know-how calls on a property of the meat which is called "grain of meat". Previously, Hammond [3] indicated that there was no correlation between grain size and tenderness, but that coarse grain size led to less palatable and "stringy" meat. A preliminary ethnological study [4] based on the analysis of expert opinions revealed that the notion of "meat grain" was positive and had become confused with that of tenderness.

Meat grain size corresponds to the observable network on a cross section of muscle and also includes the distribution of the perimysium, the diameter of the muscular fibers and the extra-cellular matrix which surrounds them [5] [6]. According to Purslow [6], the "grain of meat" is easily discerned by the eye, and is described as the division of muscles into fascicles. This notion of "grain of meat" was included in a review of the history of sensory evaluation of meat by Szczesniak [7] and had also been used in the USDA grading scheme for beef for many decades with fine grain being a requirement for the top grades. Nevertheless, much of the work on muscle grain and meat texture cited in the literature is 40 - 70 years old and therefore did not appear in modern databases.

With regard to knowledge and know-how, a preliminary in-depth analysis of beef retailer and butcher discourses on grain of meat expression was conducted [4], and led to a definition of this term and the identification of some "meat markers" that could be used to estimate grain of meat for the entire carcass and after the separation of fore and hindquarters. The ethnological study [4] [8] indicated that "grain-of-meat" evaluation might be obtained by associating various senses such as touch, sight, but also texture evaluation. It is useful to quantify the variability of muscle characteristics in relation to meat quality traits evaluated by scoring the meat grain size of the carcasses. However, it is essential to specify the terms as "fine" grain has previously been associated with different characteristics: texture for Brady [9] or grain size for Hammond [3]. Hammond [3] uses "fine" to describe small grain, *i.e.* small bundle or fascicle size. Five years later, Brady [9] uses the term "fine" to indicate the most desirable texture, the finest texture actually being the largest grain size. So although Brady and Hammond associated "fine texture" with tenderness, they meant opposite things by the word "fine". That was why an in-depth study was carried out further to the ethnological work in order to establish a marking grid for the grain of meat. In this way, some of the markers among those identified in the ethnological study were formalized and integrated into a scale (**Table 1**) and associated with a written and/or a photographic definition. The finest grain was obtained in the well-shaped and well-balanced carcass, with a really round thigh, large muscle thickness, limited marbling, a M. *longissimus thoracis* without nerves and smooth and soft to the touch, in accordance with a statistical analysis of data [10] [11]. According to the operators of the French Charolais beef industry, four muscles can provide information about the meat grain size of a carcass: M. *longissimus thoracis*, *rectus abdominis*, *longus colli* and *diaphragma* [11]. The M. *longissimus thoracis* for which numerous results are available is often considered to be a reference. Its removal is difficult to carry out and brings about significant depreciation whereas M. *rectus abdominis*, *longus colli* and *diaphragma* are easier to sample without excessive depreciation of the value of the carcass. The variability between the contractile and metabolic properties of muscles is high. The permanently active muscles such as M. *diaphragma*, the heart or M. *masseter* have a more oxidative metabolism than less active muscles such as M. *longus colli*. The physicochemical properties of one muscle are difficult to

**Table 1.** Criteria scored for the whole carcass and after the separation of quarters to assess "grain of meat".

| | Score 1* (coarse grain of meat) | Score of 5* (fine grain of meat) |
|---|---|---|
| **Carcass assessment relative to evaluation of the whole carcass** | | |
| Carcass assessment | big and hollow | plump and well conformed |
| Balance between hind and forequarters | bad balance, too much forequarters | good balance, little forequarters |
| Thigh conformation | thigh without round | round and regular thigh |
| Bone development | unrefined, too developed | fine |
| Fat development | thin or very fat carcass | covered carcass |
| Feel of the *diaphragma* | hard and dry fibres | crushing and flexible fibres |
| Feel of the *longus colli* | hard and dry fibres | crushing and flexible fibres |
| **Carcass assessment relative to evaluation after separation of quarters** | | |
| Muscle relative depth | no muscle depth, high fat depth | large muscle depth, light fat depth |
| Inter-muscular fat at the 5$^{th}$ rib level | large amount | limited fat development |
| *Longissimus thoracis* seepage | dry with small pearls | neither very wet, nor very dry |
| *Longissimus thoracis* nerves | many visible nerves | lack of visible nerves |
| *Longissimus thoracis* marbling | visible and poorly distributed marbling | evenly distributed or invisible marbling |
| *Longissimus thoracis* fibres | easily visible to the neck eye | very fine, not visible |
| Evaluation by touching the *longissimus thoracis* and of the *rhomboideus thoracis* | rough and granular | smooth and soft, without harshness |
| **Global "grain of meat" assessment** | **Very rough/granular** | **Smooth, soft, without harshness** |

*Each criterion is scored between 1 and 5; the score of 1 being the least favorable for "grain of meat" and the score of 5 being the most favorable.

extrapolate to another muscles of the carcass. The choice was made to work on the four muscles instead of just one. Although the physicochemical properties of the various muscles of a carcass present a high proportion of similarity (70% similarity between M. *rectus abdominis* and M. *longissimus thoracis*) [12], it is difficult to extrapolate from one muscle to another. M. *diaphragma* and *longus colli* and, to a lesser extent, M. *rectus abdominis* have not been studied often. The primary aim of this project was to characterize the above-mentioned four muscles of the carcass (M. *longissimus thoracis*, *rectus abdominis*, *longus colli* and *diaphragm*) and to establish links between their properties and the meat grain score attributed to the carcass.

## 2. Materials and Methods

### 2.1. Animal and Carcass Measurements

The study concerned the M. *rectus abdominis*, *longissimus thoracis*, *longus colli* and *diaphragma* of 10 Charolais heifers. Heifers were slaughtered on average at the age of 35 months with a carcass weight of 405 kg. All the carcasses chosen scored 3 on the European scale of fat development. This study was conducted in an industrial slaughterhouse and required no ethical approval.

The muscles were removed 24 hours post mortem from non-electrically stimulated carcasses. The meat grain size score was recorded just before removal, following a meat grain scale (**Table 1**). The assessment of the whole carcass was carried out by 4 experts who were regular users of this approach at least 24 hours post mortem. Seven criteria were scored between 1 and 5 (with no half-points). The assessment was carried out on the forequarter after separation of quarters, at the level of the 5$^{th}$ rib, 48 hours post mortem. Eight criteria were scored between 1 and 5 (with no half points). For each criterion, the score of 5 was attributed to the modality most favourable to the "grain of meat" according to the experts (**Table 1**). It had previously been confirmed that scores given for each of the 15 criteria were in line with the global score given to "grain of meat" and that the touch evaluation of each of the 4 muscles was equivalent for a given carcass [10] [11]. To select the 10 carcasses with extreme grain of meat scores, a total of 60 heifer carcasses were scored by 4 experts familiar with "grain of meat" evaluation at the commercial slaughterhouse "Charollais Viande" located in Paray-Le-Monial (France). Among these carcasses, we selected the 5 that had the best score and the 5 that had the lowest score for "grain of meat". As no carcasses were scored either 1 out of 5 or 5 out of 5, we constituted two groups consisting of 10 animals, with a score of either 2 or 4 out of 5 in "grain-of-meat" assessment. The 2 groups were called **coarse** and **fine** respectively.

## 2.2. Muscle Characteristics

Muscle characterization was carried out on muscles excised 24 hours after slaughter. All slaughters were performed in the same industrial slaughterhouse in order to standardize slaughtering, chilling and storing procedures. The sampling procedures were standardized for each muscle with a clearly identified sample location. Muscles were removed from the right half-carcass 24 hours post mortem.

The samples of M. *rectus abdominis*, *longissimus thoracis* and *diaphragma* destined for collagen, dry matter and lipid content analysis were vacuum packed, aged at 4˚C for 14 days post mortem and then frozen. After thawing, three trial groups of 10 g of muscle were taken for each of the three analyses of dry matter, collagen content and solubility and lipid content. Dry matter content was measured on ground meat by oven drying at 103˚C for 48 hours. The intramuscular lipid content was determined after hydrolysis with hydrochloric acid and extraction with petroleum ether (boiling point: 35˚C; Soxhlet standard method) [13]. Collagen content was measured by the hydroxyproline content, following the Bergman and Loxley method [14]. Insoluble collagen was determined in accordance with a procedure described by Bonnet and Kopp [15]. Collagen solubility was expressed as a percentage of heat-soluble to total collagen.

The samples of M. *rectus abdominis*, *longissimus thoracis*, *longus colli* and *diaphragma* intended for characterization of the metabolic properties of the muscles were cut into small fragments, frozen in liquid nitrogen and stored at −80˚C before grinding. The metabolic type of the muscles was determined by measuring enzyme activity on 200mg of frozen sample. Anaerobic glycolytic metabolism was assessed by lactate dehydrogenase (LDH) activity [16]. Aerobic oxidative metabolism was assessed by isocitrate dehydrogenase (ICDH) and cytochrome-c oxidase (COX) activities according to Briand *et al*. [17] and Piot *et al*. [18] respectively. To confirm the accuracy of each result, each muscle sample was tested in triplicate for each muscular characteristic.

## 2.3. Texture Measurements

The samples of M. *rectus abdominis* and *diaphragma* destined for textural measurements on raw and broiled meat were vacuum packed, aged at 4˚C for 14 days post mortem and then frozen. The frozen samples were maintained at 30°C for 20 minutes. Shear force was measured following the Salé method [19] adapted for an MTS Synergie 200 material testing machine. Meat samples were tested raw, or after having being grilled for 1 minute 45 seconds at 300˚C in order to reach a core temperature of 55˚C (as measured with a temperature probe). Every muscle sample was cut into core samples with different thickness. For each sample, 25 measurements were carried out in various thicknesses of muscle core samples of between 0.3 and 1.3 cm. Meat samples were cut perpendicularly to fibers. The force-movement diagram obtained presents a peak which corresponds to the maximum shear measured in kilograms. The final value of the maximum shear was calculated by linear regression for a thickness of 1 cm.

The M. *longus colli* was too thin and too small to evaluate all of the characteristics. Only the enzymatic analyses were performed on it. Likewise, the M. *longissimus thoracis* removed at the 6$^{th}$ rib did not have enough material to evaluate shear force. Shear force evaluation must be performed on muscles cut parallel to fibers, and this is only feasible on M. *longissimus thoracis* by taking 2 or 3 different ribs depending on the thickness of the rib. However, it turned out that sampling 2 or 3 ribs caused too great a carcass depreciation for the slaughterhouse, all the more so since the carcasses are of high quality.

## 2.4. Statistical Analysis

Variance analysis and mean multiple comparisons with one factor (the grain score) were carried out. Multiple comparisons of the adjusted means (LSMEANS) were carried out using the PDIFF option of the GLM procedure. Variance analysis used the GLM procedure (general linear model) from SAS 9.1 [20].

# 3. Results and Discussion

## 3.1. Carcass Characteristics

Carcasses from the **fine** group were found to be plumper and better-shaped ($p = 0.01$), with a rounder and more regular thigh ($p = 0.04$) than those from the **coarse** group (Table 2). This resulted in the hypothesis of there being a positive link between muscle development and grain of meat. For many other criteria muscles of carcasses from the **fine** group obtained better scores than those from the **coarse** group: M. *diaphragma* and *longus colli* of the **fine** group were found to be more crushable and flexible ($p = 0.02$ and 0.002 respectively). Fewer visible nerves (visible connective tissues) were found on M. *longissimus thoracis* ($p = 0.005$). On touch, M. *longissimus thoracis* was considered to be smoother and softer and with less hardness ($p < 0.0001$; Table 2). It is interesting to note that even though carcasses were selected for homogeneous carcass fat development (score of 3 in the EUROP fat development grid), the experts found a significant difference in M. *longissimus thoracis* marbling scores between the **coarse** and the **fine** groups: marbling was found to be more homogeneous on the M. *longissimus thoracis* of the **fine** group ($p = 0.02$). The development of fat deposits is indeed different depending on whether it is subcutaneous, abdominal and intermuscular fat (notation EUROP) or intramuscular fat (marbling evaluation).

## 3.2. Muscle Characteristics

Shear force on raw meat is slightly higher in M. *diaphragma* than in M. *rectus abdominis* (6.88 and 5.73 vs 5.03 and 4.46 kg; Table 3). However, the difference between these two muscles was not found for broiled meat, with averages equal to 6.35 and 6.54 kg respectively. These results are similar to those obtained on broiled muscles by Belew *et al*. [21], who indicated that M. *diaphragma* is one of the most tender muscles of the carcass (Warner-Bratzler Shear Force = 2.03 kg), whereas M. *rectus abdominis* appears to require a higher Warner-Bratzler shear force to be cut (between 3.2 and 3.9 kg). Rheological measurements were not performed on M. *longissimus thoracis* and *longus colli* because of high carcass depreciation and muscle smallness. Nevertheless, it has previously been indicated that the M. *rectus abdominis* is significantly tougher than M. *longissimus* and *semitendinosus* [22]. The difference in raw meat shear force between M. *diaphragma* and M. *rectus abdominis* could be linked to the total collagen content. Indeed, M. *diaphragma* was composed of significantly more collagen (26.4 vs 20.4 mg/g DM on average) with an equivalent solubility to M. *rectus abdominis*. The difference in shear force between raw and broiled muscles in M. *diaphragma* and M. *rectus abdominis* may be linked either to the variation in lipid content between these two muscles or to the way the muscles were cut. The M. *diaphragma* is twice as rich in lipids as M. *rectus abdominis* (32.2% vs 17.2% DM on average) and it could be hypothesized that the shear needed to cut fat is lower when fat is diffuse than when fat is raw and compact. Moreover, the M. *diaphragma* is a muscle in which it is easy to cut homogeneous steaks with cuts parallel to fibers.

**Table 2.** Scores out of 5 given by the experts for various carcass characteristic for the "grain-of-meat" group.

| Criteria for grain of meat evaluation (scores on 5) Meat "grain" size | coarse | fine | *p* |
|---|---|---|---|
| **Carcass appreciation**<br>(big and hollow: 1/5; plump and well conformed: 5/5) | 2.5 ± 0.5[(1)] | 3.3 ± 0.3 | **0.01** |
| **Thigh conformation**<br>(thigh without roundness: 1/5; round and regular thigh: 5/5) | 2.8 ± 0.6 | 3.6 ± 0.4 | **0.04** |
| **Assessment by touching the M. *diaphragma***<br>(hard and dry fibers: 1/5; crushing and flexible fibers: 5/5) | 2.1 ± 0.2 | 3.0 ± 0.6 | **0.02** |
| **Evaluation by touching the M. *longus colli***<br>(hard and dry fibers: 1/5; crushable and flexible fibers: 5/5) | 2.3 ± 0.4 | 3.5 ± 0.4 | **0.002** |
| **Evaluation of the M. *longissimus thoracis* nerves**<br>(many visible nerves: 1/5; lack of visible nerves: 5/5) | 2.7 ± 0.4 | 3.8 ± 0.4 | **0.005** |
| **Evaluation of the M. *longissimus thoracis* marbling**<br>(visible and badly distributed marbling: 1/5; homogeneously distributed or invisible marbling: 5/5) | 2.7 ± 0.3 | 3.6 ± 0.7 | **0.02** |
| **Evaluation by touching the M. *longissimus thoracis***<br>(rough and granular: 1/5; smooth and soft, without hardness: 5/5) | 2.1 ± 0.2 | 3.8 ± 0.4 | **0.0001** |

**Table 3.** Effect of "grain of meat" score (G) and muscle (M) of the carcass on muscular characteristics in M. rectus abdominis, diaphragma and longissimus thoracis.

| Muscle (M) | M. *rectus abdominis* | | M. *diaphragma* | | M. *longissimus thoracis* | | *p* | | |
|---|---|---|---|---|---|---|---|---|---|
| Score of Grain (G) | Coarse | Fine | Coarse | Fine | Coarse | Fine | Muscle effect (M) | Grain score effect (G) | Inter-action (MxG) |
| Shear force on raw meat (kg) | 5.03 ± 0.64[(1)]aB | 4.46 ± 0.71aA | 6.88 ± 0.72bB | 5.73 ± 0.66bA | - | - | <0.0001 | 0.0026 | 0.5955 |
| Shear force on broiled meat (kg) | 7.20 ± 1.07 | 5.89 ± 0.53 | 6.02 ± 0.50 | 6.70 ± 1.95 | - | - | 0.7184 | 0.5561 | 0.0754 |
| Dry matter (%) | 26.82 ± 0.97a | 26.50 ± 1.43a | 31.78 ±2.32b | 30.48 ± 3.24b | 27.28 ± 0.49a | 27.39 ± 1.20a | <0.0001 | 0.4748 | 0.7041 |
| Fat content (% Dry Matter) | 17.13 ± 2.81b | 17.23 ± 5.56b | 34.85 ± 5.70c | 29.47 ± 11.15c | 12.71 ± 2.78a | 12.62 ± 3.91a | <0.0001 | 0.4242 | 0.5242 |
| Total collagen content (mg/g Dry Matter) | 20.80 ± 2.72b | 19.93 ± 2.76b | 27.94 ± 3.53c | 24.87 ± 3.97c | 15.86 ± 1.50a | 13.13 ± 1.30a | <0.0001 | 0.0655 | 0.6991 |
| Soluble collagen (% total) | 13.76 ± 5.5 | 17.00 ± 2.94 | 15.62 ± 4.32 | 13.80 ± 5.59 | 16.04 ± 5.09 | 19.09 ± 1.52 | 0.3297 | 0.3608 | 0.3581 |

[(1)]Values are mean ± standard deviation. [(2)]Different lowercase letters indicate a significant difference ($p \leq 0.05$) for the muscle. Different capital letters indicate a significant difference ($p \leq 0.05$) for the grain score.

On the contrary, in the M. *rectus abdominis*, cutting is harder to perform and fibers have to be cut on the bias to achieve homogenous thickness. Thus, it could be hypothesized that the way in which fibers are cut has a significant impact on muscle shrinkage during cooking, leading to excessive hardening of M. *rectus abdominis* in comparison to M. *diaphragma*.

These two hypotheses could explain why shear force increases with cooking in M. *rectus abdominis* and decreases in M. *diaphragma* but this needs to be confirmed by further analysis. As previously indicated [12], M. *longissimus thoracis* was composed of significantly less collagen than M. *rectus abdominis* (14.5 vs 20.4 mg/g DM on average). The solubility of this collagen was slightly higher in M. *longissimus thoracis*, but the difference was not significant. M. *longissimus thoracis* contained slightly less intramuscular fat (12.7% vs 17.2% DM on average) than M. *rectus abdominis*, as previously indicated by Brackebush *et al*. [23]. However in the present work, the difference between M. *rectus abdominis* and *longissimus thoracis* intramuscular fat was not significant. Indeed, lipid content was extremely heterogeneous in the muscles tested, with the M. *diaphragma* having practically twice the lipid content as M. *longissimus thoracis* (1.8 times more) and M. *rectus abdominis* (2.5 times more).

For enzyme activity, M. *longissimus thoracis* and *rectus abdominis* appeared more glycolytic than M. *diaphragma* and *longus colli* (573 and 549 vs 306 and 357 µmol/min/g; **Table 4**) but the difference was not significant. Nevertheless, it could be hypothesized that the difference might appear significant on a larger number of samples. On the other hand, M. *longissimus thoracis* and *rectus abdominis* appeared less oxidative (COX and ICDH activities) than M. *diaphragma*; M. *longus colli* being in an intermediate position (**Table 4**). The difference in activities between M. *longissimus thoracis* and M. *rectus abdominis* was not significant but we confirmed previous results indicating that M. *rectus abdominis* is less glycolytic and more oxidative than M. *longissimus thoracis* [22] [24] [25]. In the present work, the differences in enzyme activities are not significant, probably because of the small cell sizes that may have limited the present results. It was previously indicated that gene encoding proteins involved in fast contraction and in glycolytic metabolism are under-expressed in M. *rectus abdominis* in comparison to other muscles [26]. This could explain why higher oxidative and lower glycolytic metabolisms are noted in the present work for M. *rectus abdominis* than for M. *longissimus thoracis* even though the difference is not significant.

### 3.3. Relationship between Grain Score and Muscle Characteristics

It was previously indicated that all of the 10 carcasses were given a score of 3 for the EUROP fat grid and that the high variability of fat content between carcasses (**Table 2**) led to a non significant difference in intramuscular fat between the two grain-of-meat groups in any muscle ($p > 0.10$). This lack of difference makes it possible to compare all samples at equivalent lipid content levels (**Table 3**). When considering M. *rectus abdominis* and M. *diaphragma* together, the shear force needed to cut broiled meat was equivalent for samples from the **coarse** group and for those from the **fine** group (6.61 vs 6.29 kg; $p = 0.5561$). A significant difference was noted in raw meat with high differences between both grain groups (5.96 vs 5.10 kg; $p = 0.0026$). This result confirmed the hypothesis that experts are able to assess different levels of hardness when scoring the carcasses for "grain of meat" [4] [8] [10]. Nevertheless, when evaluating results muscle by muscle, it appears that only shear force in broiled M. *rectus abdominis* is significantly different between the two groups ($p = 0.04$; **Table 3**). No significant difference was noted in M. *diaphragma* ($p = 0.47$). Thus, it appeared that muscle properties could not be extrapolated from one muscle of a carcass to another.

This difference between M. *rectus abdominis* and *diaphragma* could be due to muscle variability between the carcasses. It has been shown that there are large differences in primary fascicle size, perimysium thickness and the degree of associated adipose tissue among muscles [6].

The difference in shear force, all muscles taken together, may be linked to a slightly higher total collagen content (21.52 vs 19.31 mg/g DM; $p = 0.0655$) for the **coarse** group (**Table 3**). Nevertheless, the difference in collagen content was not significant in M. *rectus abdominis*, but this hypothesis might be supported by significant differences in collagen content both in M. *diaphragma* (27.94 vs 24.87 mg/g DM; $p = 0.02$) and *longissimus thoracis* (15.86 vs 13.13 mg/g DM; $p = 0.03$). The lower collagen content in M. *longissimus thoracis* of the **fine** group confirms the scores given by the experts when evaluating the lack of visible nerves on this muscle ($p = 0.005$; **Table 2**). Indeed, as previously indicated [11], the presence of nerves may be related to connective tissue content (correlation: −0.21) and collagen solubility (correlation: −0.36). Moreover, this result could be linked to

**Table 4.** Effect of "grain of meat" score (G) and muscle (M) of the carcass on metabolic enzyme activities in M. *rectus abdominis*, *diaphragma*, *longissimus thoracis* and *longus colli*.

| Muscle (M) | M. *rectus abdominis* | | M. *diaphragma* | | M. *longissimus thoracis* | | M. *longus colli* | | *p* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Score of Grain (G) | Coarse | Fine | Coarse | Fine | Coarse | Fine | Coarse | Fine | Muscle effect (M) | Grain score effect (G) | Inter-action (MxG) |
| Isocitrate Dehydrogenase activity ($\mu mol \cdot min^{-1} \cdot g^{-1}$) | 1.64 ± 0.42aA | 1.85 ± 0.79aB | 8.09 ± 1.49cA | 11.63 ± 3.52cB | 1.48 ± 0.68aA | 1.58 ± 0.29aA | 3.27 ± 0.63bA | 3.91 ± 1.31bB | <0.0001 | 0.0248 | 0.0482 |
| Lactate Dehydrogenase activity ($\mu mol \cdot min^{-1} \cdot g^{-1}$) | 589 ± 86c | 509 ± 52c | 288 ± 66a | 325 ± 22a | 627 ± 46c | 519 ± 82c | 337 ± 74b | 378 ± 40b | <0.0001 | 0.1668 | 0.0167 |
| Cytochrome−c Oxydase activity ($\mu mol \cdot min^{-1} \cdot g^{-1}$) | 15.45 ± 4.22aA | 15.01 ± 2.7aA | 45.89 ± 5.01cB | 38.80 ± 3.06cA | 14.01 ± 3.12aB | 10.33 ± 1.29aA | 22.26 ± 4.16bA | 21.42 ± 3.09bA | <0.0001 | 0.0104 | 0.1436 |

(1)Values are mean ± standard deviation. (2) Different lowercase letters indicate a significant difference ($p \le 0.05$) for the muscle. Different capital letters indicate a significant difference ($p \le 0.05$) for the grain score.

the conclusions of experts concerning the **fine** samples of M. *longissimus thoracis* which were found to be smoother and softer, with less hardness than those of the **coarse** group ($p < 0.0001$; **Table 2**). The experts also noted a difference in the fiber types of M. *longus colli*: those from the **fine** group were more crushable and flexible ($p = 0.02$ and 0.002 respectively) than those from the **coarse** group. The same difference was recorded by experts for fibers from M. *diaphragma* and *longissimus thoracis*, muscles from the **fine** group being both more crushable and more flexible than those from the **coarse** group.

This evaluation might be linked to a difference in collagen content, in favor of the **fine** group samples. Indeed, the negative relationship commonly agreed to exist between collagen content and tenderness [27] [28] argues for a higher tenderness in **fine** group muscles. Therefore, both M. *diaphragma* and *longissimus thoracis* could be used to predict the "grain of meat" score: low collagen content being indicators of **fine** grain of meat. Nevertheless, previous results indicated that for the M. *longissimus thoracis*, no significant relationship exists between grain of meat and either tenderness or shear force, or collagen content and collagen solubility [11]. According to Purslow [6], it appears that tenderness is partly correlated with **fine** grain (small diameters of muscle fascicle), but as is so common in meat science, this single variable is of extremely limited value in predicting the toughness of cooked meat, due to the highly multifactorial nature of texture.

The variability of the enzymatic activities from one muscle to another prevents us from handling the results for all muscles together. No difference was observed between groups for M. *rectus abdominis* and *longus colli* metabolisms either for oxidative or for glycolytic activities. In the M. *diaphragma*, which is well known for being very oxidative, only the Krebs circle enzyme cytochrome-c oxydase was found to be significantly different between groups, the M. *diaphragma* being more oxidative in the **coarse** group (24.40 vs 21.39 µmol/min/g; $p = 0.01$). However, no significant difference appeared in ICDH oxidative enzyme activity, showing a variable reactivity of enzymes depending on their localization (Krebs cycle or respiratory chain). Indeed, ICDH enzyme activity was very variable in M. *diaphragma* (CV: 32 %), leading to a non-significant difference between the two groups. In the M. *longissimus thoracis*, which is both more glycolytic and more oxidative than the 3 other muscles, both oxidative and glycolytic metabolisms were found to be significantly more active in the **coarse** group than in the **fine** one.

According to the literature, in M. *longissimus thoracis*, M. *semitendinosus* and M. *triceps brachii*, tenderness scores increased and shear force on broiled meat decreased with muscle oxidative metabolism (MyHC I proportion and COX activity) [25]. The more oxidative muscles were of higher quality, particularly in terms of tenderness [27]. Moreover, some previous publications have indicated that muscles with a high proportion of slow oxidative fibers or a low proportion of fast glycolytic fibers are more tender [29]-[33]. On the contrary, in M. *longissimus thoracis* from the **fine** group, LDH activity is significantly lower than in the **coarse** group, arguing for a higher tenderness in **fine** group samples, a positive relationship existing between low glycolytic metabolism and high meat quality. Thus, differences in metabolism observed between the **coarse** and **fine** groups could not be used to explain tenderness variations among samples.

## 4. Conclusion

The present results lead us to conclude that it is difficult to identify a single muscle that can be relevant in the prediction of carcass meat quality. Indeed, as already indicated in the literature, the muscles studied did not all evolve in a similar way. Hammond [3], for example, previously found that thigh muscles with the highest rates of post-natal growth were felt to have the largest grain. So, it is undoubtedly utopian to believe that a single muscle can represent the whole carcass. Nevertheless, it should be emphasized that no conflicting conclusions were obtained from one muscle to another and that therefore the choice of a single muscle was feasible, the only possible bias being that not all of the muscles would respond with the same intensity depending on the physicochemical characteristic studied. In the present study, M. *longus colli* was examined in detail and scored by experts even though this muscle was not as easy to sample as the other muscles. Indeed, in many countries, the quartered carcasses are assessed and so the cross-section of the M. *longissimus thoracis* is easily viewed. So, even if the M. *longus colli* is scientifically interesting to study, it does not appear to have any practical application in many countries because it does not represent a sole determinant of a carcass. M. *longissimus thoracis* seems to be too tender as a muscle, and not an appropriate sample to distinguish **fine** and rough grains. It could be hypothesized that broiled M. *rectus abdominis* shear force is the best indicator of "grain of meat" and potential meat tenderness, as samples are tested by rheological analysis in the same way as meat samples are commonly eaten in France.

## Conflicts of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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