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Factors influencing the variation in tenderness of seven major beef muscles from three Angus and Brahman breed crosses

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Abstract

Beef carcasses ($n = 30$) from 3/4 Angus (A) × 1/4 Brahman (B), 1/4A × 3/4B, and 1/2A × 1/2B F_1 crosses were used to evaluate breed type, electrical stimulation, and postmortem aging on the *M. semimembranosus* (SM), *M. semitendinosus* (ST), *M. biceps femoris* (BF), *M. vastus lateralis* (VL), *M. gluteus medius* (GM), *M. longissimus dorsi lumborum* (LD), and *M. triceps brachii* (TB). Shear force values decreased with increased postmortem aging to a greater extent in steaks from 3/4A × 1/4B than steaks from the other breed types. Shear force values for steaks from the round (SM, ST, BF, VL) were higher than steaks from the loin (LD, GM) and chuck (TB) for both electrically stimulated and non-electrically stimulated muscles. In the LD muscle, calpastatin activities were similar among breed types. Muscle type played the greatest role in determining tenderness.
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1. Introduction

Although considerable research has been conducted concerning the mechanisms of beef tenderness, a solution to toughness has yet to be fully determined. Morgan et al. (1991) documented problems in beef with tenderness consistency, especially in retail cuts from the round and chuck. In addition, Boleman et al. (1997) indicated that consumers were willing to pay more for meat of known tenderness levels. Because consumers consider tenderness to be one of the most important organoleptic characteristics of meat (Savell et al., 1987, 1989), understanding the mechanisms of beef tenderness is essential to improving overall tenderness and reducing inherent variability. Whereas a significant amount of research has been conducted on mechanisms affecting the tenderness of the longissimus muscle (George, Bendall, & Jones, 1980; Savell, Smith, & Carpenter, 1978), there are insufficient data on the mechanisms of tenderness in other major beef muscles.

The effects of breed type and electrical stimulation on the contractile and degradative state of muscle proteins, the amount and solubility of collagen, and the level of fatness of several beef muscles warrant further investigation. A unique group of cattle of known breeding and genetics became available, and we were given the opportunity to utilize these animals to evaluate the effects of breed type on meat tenderness. In addition, electrical stimulation and postmortem aging also were applied to determine any further impact these strategies might have on inherent tenderness differences.

2. Materials and methods

2.1. Animals

Cattle ($n = 30$; 15 steers and 15 heifers) were obtained from a gene-mapping project conducted at Texas A&M

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University. The cattle selected were 3/4 Angus × 1/4 Brahman ($n = 10$), 1/2 Angus × 1/2 Brahman ($n = 10$), and 1/4 Angus × 3/4 Brahman crosses ($n = 10$). These cattle were harvested at a constant age-point at the Rosenthal Meat Science and Technology Center on the Texas A&M University campus following methods set forth in Savell and Smith (2000).

2.2. Carcasses

Each carcass was split, and the right side was electrically stimulated whereas the opposite side was used as a non-stimulated control. A single electrical probe (approx 0.6 × 12.5 cm) was inserted into the carcass musculature between the scapula and thoracic vertebrae with the rail serving as the electrical ground. Electrical stimulation consisted of 17 impulses of 550 V (AC) and 2–6 A for 1 min. Impulses were of 1.8 s duration with a 1.8 s pause between pulses, and electrical stimulation was administered within 1 h postmortem.

Carcasses were chilled for 48 h at −2 °C with temperature and pH decline monitored in the *M. semimembranosus* (SM), *M. semitendinosus* (ST), *M. biceps femoris* (BF), *M. vastus lateralis* (VL), *M. gluteus medius* (GM), *M. longissimus dorsi lumborum* (LD), and *M. triceps brachii* (TB) muscles of each side. Temperature was monitored at 1, 3, 6, 9, and 21 h postmortem using copper–constantan thermocouples inserted into the approximate geometric center of each muscle, and was collected with an Omega recording thermometer (Model OM 272; Omega Engineering, Inc., Stamford, CT). The pH was determined at 1, 3, 6, 9, and 21 h with a UniFET pH meter (Model UF100-01; UniFET Inc., San Diego, CA) equipped with a stainless steel, solid-state probe, ensuring that the probe was inserted deep into the muscle tissue. Three measurements for each time period and muscle were obtained, and the average of the three readings was recorded. All carcasses were evaluated for USDA (1989) quality and yield grade characteristics by trained carcass evaluators. At 22 h, samples for use in calpastatin activity and sarcomere length quantification were obtained from the anterior portion of each muscle from both sides of all carcasses.

2.3. Muscle removal

At 48 h postmortem, the remainder of each muscle was removed from both sides of each carcass. Immediately following, four 2.54 cm steaks were removed from the anterior end of each muscle, vacuum-packaged in high oxygen barrier bags (B540 bags; Cryovac Sealed Air Corporation, Duncan, SC), and assigned randomly to 2, 14, 28, or 42 d aging. Upon completion of each postmortem aging period, steaks were blast frozen at −34 °C and stored until subsequent shear force analysis. Muscle not cut into steaks was homogenized in a Cuisinart® food processor (Cuisinart®, Inc., Greenwich, CT,) and stored at frozen (−34 °C) until subsequent analysis of collagen and fat.

2.4. Warner–Bratzler shear force

Frozen steaks were assigned randomly to day of shear force evaluation so that within a Warner–Bratzler shear day, a steak from each breed type, treatment, muscle, and aging period was evaluated. Steaks were tempered at 4 °C for 24 h, then broiled to an internal temperature of 35 °C, turned, and broiled to a final internal temperature of 70 °C on electric broilers (Model 450N; Farberware Open-hearth Broilers, Kidde, Inc., Bronx, NY). Internal temperature was monitored using copper–constantan thermocouples attached to an Omega recording thermometer (Model RD 4031; Omega Engineering, Inc., Stamford, CT), and cook time was recorded and cooking loss was measured for each steak. Steaks were cooled to room temperature (25 °C), and a minimum of six, 12.75 mm cores were taken from each steak parallel to muscle fiber orientation. Each core was sheared once using a Universal testing machine equipped with a Warner–Bratzler attachment, and the shear force value reported for each steak was the average value for all evaluated cores.

2.5. Sarcomere length

Sarcomere length was determined by the neon-laser diffraction method as described by Cross, West, and Dutson (1981). Samples consisting of 10 g of muscle tissue were homogenized in 50 mL of 0.25 M sucrose solution for 15 s with a VirTis® 45 mechanical homogenizer (The VirTis Co., Inc., Gardiner, NY). A single drop of the resulting homogenate was placed on a microscope slide and covered with a glass cover slip. The neon-laser (Model 155SL; Spectra Physics Inc., Eugene, OR) was operated at 632.8 nm. The lengths of 25 diffraction patterns were measured from each sample, and sarcomere length was determined by averaging these 25 measurements.

2.6. Calpastatin activity

Procedures used to determine calpastatin activity followed those outlined in Shackelford et al. (1994). Unless stated otherwise, all samples and buffers were held at 2–4 °C. Samples (10 g) were homogenized at 24–28 h postmortem in 30 mL of extraction buffer (100 mM Tris, 5 mM EDTA, and 10 mM β-mercaptoethanol at pH 8.3) three times for 30 s using a pre-cooled Waring® blendor (Waring® Commercial, New Hartford, CT) with a 30 s rest between each burst to prevent heating of the sample. The resulting homogenate was centrifuged for at least 1 h at 35,000*g*. The supernatant fraction was decanted and heated in a 95 °C water bath for 15 min, and then chilled in an ice water bath for 15 min. During chilling, the coagulated protein was scrambled with a small glass rod to facilitate separation of the supernate and pellet before samples were centrifuged again at 35,000*g* for 30 min. Following centrifugation, the volume of the supernatant fraction was determined and recorded for subsequent calculation of calpastatin activity.

Samples were assayed as described by Koohmaraie (1990). The assay procedure was initiated by adding 250, 300, 350, and 400 μL of sample into 13 × 100 mm test tubes. Each tube was brought to 500 μL with elution buffer according to Koohmaraie (1990), and EDTA blanks were prepared at each level. Purified calpain was added at a predetermined volume that was established by screening the calpain, and calcium and EDTA were added to respective tubes at 100 μL. Immediately following, tubes were mixed and placed into a 25 °C water bath for 1 h. Following incubation, 2 mL of 5% TCA was added to each tube to terminate the reaction, and tubes were centrifuged at 1500*g* for 30 min. Calcium and EDTA samples then were read on a spectrophotometer at 278 nm against a calcium blank.

2.7. Collagen

Total collagen amount and collagen solubility were determined by isolating hydroxyproline from homogenized steaks as described by Hill (1966). Hydroxyproline was quantified using a color reaction as described by Kolar (1990) and converted to collagen content as defined by Cross, Carpenter, and Smith (1973). Hydroxyproline of both the supernate concentration and residues was converted to collagen by multiplying by a factor of 7.52. Total collagen was calculated by combining the collagen content of the supernates and residues, and percent solubility was calculated using the following equation:

$$\text{Percent collagen solubility} = (\text{supernate collagen}/\text{total collagen}) \times 100.$$

2.8. Chemical lipid

Lipid percentages were determined using the oven-dried method and ether fat extraction procedures outlined by AOAC (1984). Homogenized meat samples were placed into pre-dried (105 °C for 12 h), pre-weighed Whatman #2 filter paper thimbles and then weighed. Samples were dried for at least 12 h at 105 °C, and subsequent dried weights were recorded. Samples then were placed in a soxhlets, and were extracted with petroleum ether for at least 12 h in a distillation apparatus. Percent fat was determined by the difference between the extracted weight and dried weight divided by the wet weight.

2.9. Statistical analysis

The GLM procedure of SAS was utilized to fit the appropriate linear models and construct analyses of variance. Non-significant effects ($P > 0.15$) for each model were pooled into the error term, and the resulting model was used for analysis of variance. Carcass trait data were analyzed separately in a one-way analysis of variance with breed type defined as the main effect and residual error used to determine significance. Calpastatin, sarcomere length, collagen, percentage collagen solubility, pH and temperature at each time period, fat, cook time, and cooking loss were analyzed as a split-plot design. The whole plot included breed type, and the error term was defined as animal within breed type. In the split-plot, main effects of muscle and electrical stimulation were defined. Two- and three-way interactions were tested in the split-plot. The residual error was the error term defined. Warner–Bratzler shear force was analyzed as a split–split plot where postmortem aging and two- and three-way interactions were tested in the split–split plot. The residual error was the error term defined. Significance level was set at $P < 0.05$. For main effects and interactions that were significant ($P < 0.05$), least-squares means were reported and Bonferroni's mean separation test at $P < 0.05$ was used to determine differences.

3. Results and discussion

3.1. Carcass traits

Carcass traits are provided to characterize the samples in this investigation. Least-squares means and residual standard deviations for live animal weights and carcass traits are provided in Table 1. There were no differences ($P > 0.05$) in hot carcass weight, fat thickness, and USDA yield and quality grades among breed crosses (Table 1), possibly due to a relatively limited sample size. In contrast, past research has shown that *Bos taurus* cattle had higher actual and adjusted fat thicknesses, USDA yield grades, and marbling scores than their *Bos indicus* counterparts (Crouse, Cundiff, Koch, & Koohmaraie, 1989; Shackelford, Koohmaraie, Miller, Crouse, & Reagan, 1991).

3.2. Warner–Bratzler shear force

Warner–Bratzler shear force was affected by breed type, electrical stimulation, muscle, and postmortem aging time. There also were breed × postmortem aging time (Fig. 1), electrical stimulation x muscle (Fig. 2), and muscle × postmortem aging time (Fig. 3) interactions for WBS. Steaks from 1/2A × 1/2B cattle had higher WBS than steaks from the other breed types after 2 d postmortem aging (Fig. 1).

Table 1
Least squares means for carcass traits as affected by breed

Trait	3/4A[a]	1/2A	1/4A	RSD[b]
Hot carcass wt. (kg)	334.8	302.2	320.1	42.3
Fat thickness (cm)	1.09	1.04	1.32	0.07
USDA yield grade[c]	2.99	3.11	3.45	0.64
USDA quality grade[c]	Choice$^-$	Choice$^-$	Choice$^-$	53.40

[a] 3/4A = 3/4 Angus × 1/4 Brahman, 1/2A = 1/2 Angus × 1/2 Brahman, 1/4A = 1/4 Angus × 3/4 Brahman.
[b] RSD, residual standard deviation.
[c] Official United States standards for grades of carcass beef (USDA, 1989).

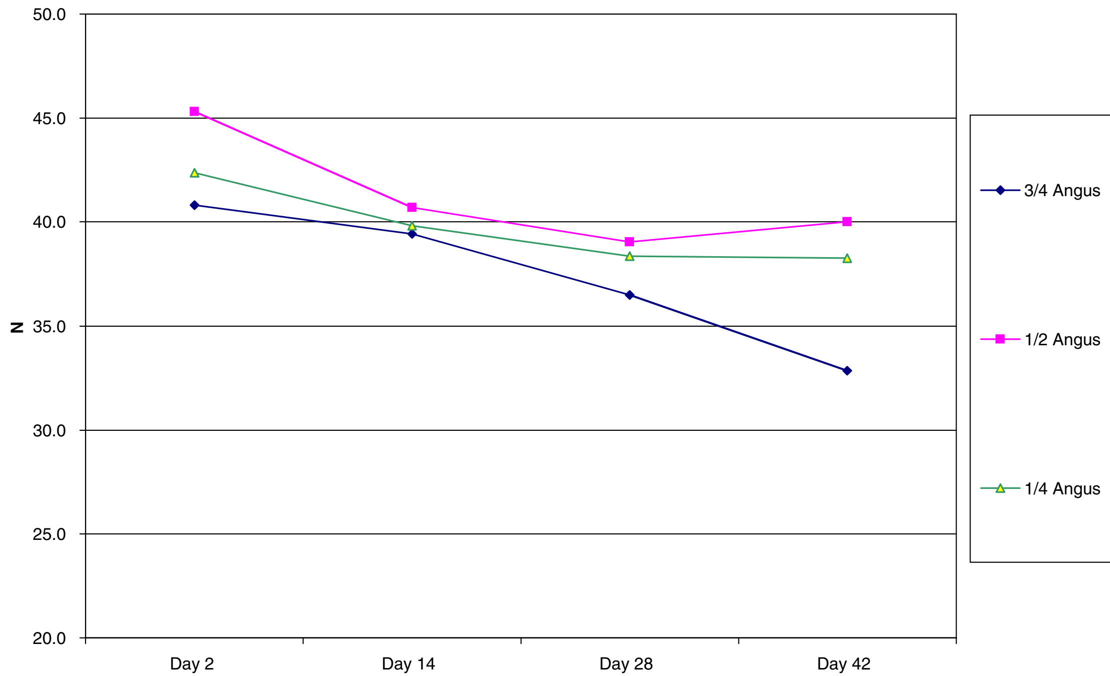

Fig. 1. Least squares means for Warner–Bratzler shear force (N) for breed × aging time interaction.

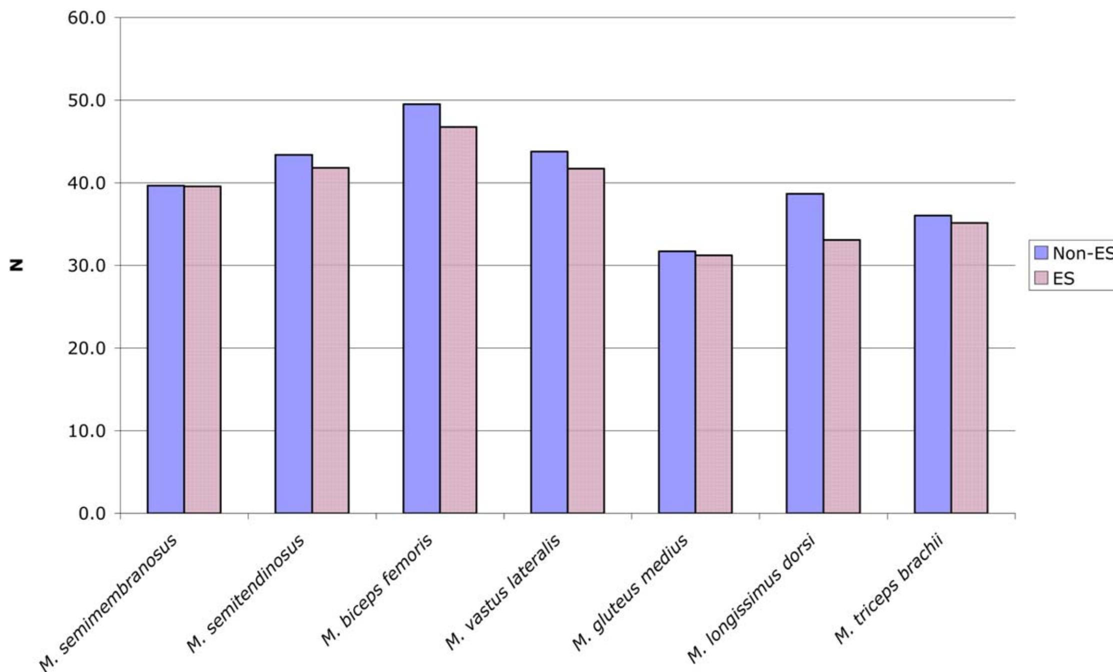

Fig. 2. Least squares means for Warner–Bratzler shear force (N) for electrical stimulation × muscle interaction.

At 14 d postmortem aging, WBS decreased and no WBS differences were observed among breed types.

Steaks from 1/2A × 1/2B and 1/4A × 3/4B cattle decreased ($P < 0.05$) in shear force from 2 to 14 d, then shear force reached a plateau and did not continually decrease ($P > 0.05$) with increased postmortem aging. In contrast, steaks from 3/4A × 1/4B cattle decreased ($P < 0.05$) in shear force between 14 and 28 d and 28 and 42 d postmortem aging indicating that degradation did occur after 28 d postmortem in 3/4 Angus cattle. This supports the results of Johnson, Huffman, Williams, and Hargrove (1990), who showed that loin steaks from purebred Angus and 3/4 Angus × 1/4 Brahman carcasses showed a greater response to postmortem aging than did loin steaks from carcasses from 1/2 and 3/4 Brahman cattle. These results imply that regardless of breed type, postmortem

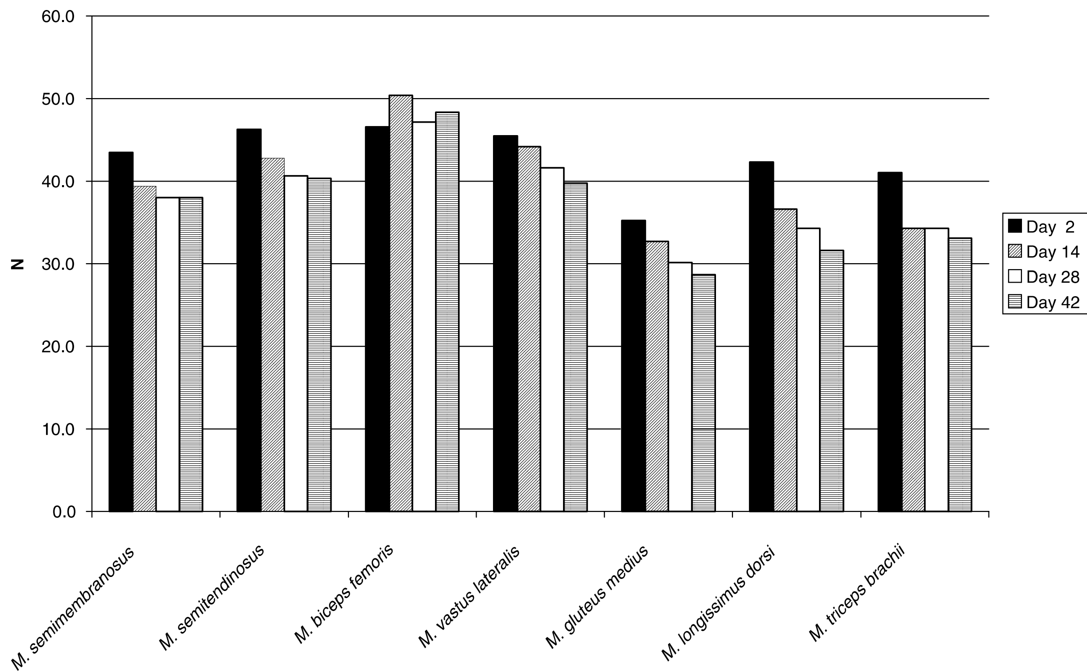

Fig. 3. Least squares means for Warner–Bratzler shear force (N) for muscle × aging time interaction.

aging can improve WBS values up to 14 d; however, postmortem aging beyond 14 d may not be effective in improving WBS force of steaks from cattle with large *Bos indicus* influence.

Effect of electrical stimulation on tenderness was muscle dependent. The non-electrically stimulated muscles were ranked from most tender to least tender according to WBS force values as follows: GM, TB, LD, SM, ST, VL, and BF (Fig. 2). Electrical stimulation improved tenderness in the LD and BF by approximately 5–6 N, but did not significantly improve tenderness in other muscles. The use of electrical stimulation to improve tenderness of the longissimus muscle is well documented (McKeith, Savell, & Smith, 1981; Savell, Smith, Carpenter, & Parrish, 1979, 1977; Smith, Dutson, Carpenter, & Hostetler, 1977), and results of this study concur with those findings. In addition, McKeith et al. (1981) reported that the use of high voltage electrical stimulation reduced shear values for the GM, BF, SM, and LD, but did not reduce shear force values for the ST, VL, and TB (and several other muscles) supporting our findings that across muscles, the tenderness response to electrical stimulation is not the same.

Muscles within this investigation can be grouped into four different aging/tenderness categories: (1) tender with slow but continued response to aging up to 42 d (GM, LD); (2) slightly tender with aging response up to 14 d (SM, TB); (3) slightly tough with slow aging response after 28 d (ST, VL); and (4) tough with no aging response (BF). At 2 d postmortem, the GM had the lowest shear force values followed by the TB, LD, and the SM, while the ST, VL, and BF had the highest shear force values (Fig. 3). The LD, TB, and SM decreased in WBS force from 2 to 14 d. However, WBS force decreased after 28 d for the ST and VL.

An additional decrease in WBS force was observed in the LD from 28 to 42 d. The SM, ST, VL, and GM decreased ($P < 0.05$) in shear force approximately 6–7 N from 2 to 42 d postmortem; whereas the TB decreased in shear force approximately 6 N between 2 and 14 d postmortem. This indicates that the TB responded to aging at a faster rate than the SM, ST, VL, and GM. The LD had the greatest aging response with about a 5 N improvement in shear force from 2 to 14 d, and slow, but significant improvement with additional aging from 14 to 42 d. With increased postmortem aging, shear force values tended not to change for the BF ($P > 0.05$). McKeith, DeVol, Miles, Bechtel, and Carr (1985) showed that muscles from the round (SM, ST, BF, VL) had higher ($P < 0.05$) shear force values than muscles from the loin (LD and GM) and chuck (TB). The same holds true here with muscles from the round having higher ($P < 0.05$) shear force values than muscles from the loin and chuck.

3.3. Sarcomere length

Sarcomere length was not affected by breed type as previously reported by Whipple et al. (1990). There were, however, muscle, electrical stimulation, and muscle × electrical stimulation interactions for sarcomere length. For non-electrically stimulated muscles, the TB had the longest sarcomeres, the SM was intermediate, and the ST, BF, VL, GM, and LD had the shortest sarcomeres (Table 2).

Electrical stimulation did not influence sarcomere length for the SM, BF, VL, GM, and LD, but electrically stimulated ST and TB muscles had longer sarcomeres

Table 2
Least squares means for sarcomere lengths (μm) as influenced by electrical stimulation × muscle interaction

Muscle	NES[a]	ES
M. semimembranosus	1.84cde	1.85bc
M. semitendinosus	1.78f	1.83cd
M. biceps femoris	1.78f	1.76f
M. vastus lateralis	1.78f	1.79ef
M. gluteus medius	1.77f	1.79def
M. longissimus dorsi	1.79def	1.75f
M. triceps brachii	1.90b	2.04a
RSD[b]	0.10	

Least squares means with different letters (a–f) differ significantly ($P < 0.05$).
[a] NES, non-electrically stimulated; ES, electrically stimulated.
[b] RSD, residual standard deviation.

than their non-electrically stimulated counterparts. The placement and action of the TB and ST during electrical stimulation could explain why the process affected their sarcomere lengths. These results are in agreement with Herring, Cassens, and Briskey (1965) and McKeith et al. (1985) who showed that the TB had longer sarcomere lengths than the BF, LD, and GM. In the current study, muscle temperature and pH conditions were not favorable for the occurrence of cold shortening (<10 °C with pH > 6.0; Lochner, Kauffman, & Marsh, 1980), which suggests that tenderness differences between breed types, muscles, and electrical stimulation most likely were not due to cold-induced toughening. The reduced rate of chilling observed in this study could explain why electrical stimulation did not significantly affect sarcomere length for most muscles.

3.4. Rate of pH decline

Postmortem pH decline was affected by electrical stimulation, muscle, and electrical stimulation × muscle interaction at 1, 3, 6, 9, and 21 h (Fig. 4), but was not affected by breed type ($P > 0.05$). There were significant differences in pH decline between electrically and non-electrically stimulated muscles at 1, 3, 6, and 9 h postmortem. Electrical stimulation resulted in approximately a 0.5 pH unit difference between stimulated and non-stimulated muscles at 1, 3, and 6 h (Fig. 4). At 9 h, there was approximately a 0.2 pH unit difference between treatments, and differences between treatments were not observed at 21 h postmortem. For both electrically stimulated and non-electrically stimulated muscles, the TB had the slowest rate of pH decline at all times postmortem, the highest pH at 21 h, and relatively low shear values. The non-electrically stimulated GM demonstrated the fastest rate of pH decline at all times postmortem compared to other non-electrically stimulated muscles, and it also had the lowest shear force values. The rapid pH decline of the GM was most likely due to its anatomical location, slower rate of temperature decline, and excessive work during electrical stimulation. Rate of pH decline did not account for differences in shear force in this study.

3.5. Rate of temperature decline

Muscle temperature and pH conditions were not conducive to the occurrence of cold shortening (<10 °C with pH > 6.0; Lochner et al., 1980). The non-electrically stimulated LD muscles had the lowest temperature at each time

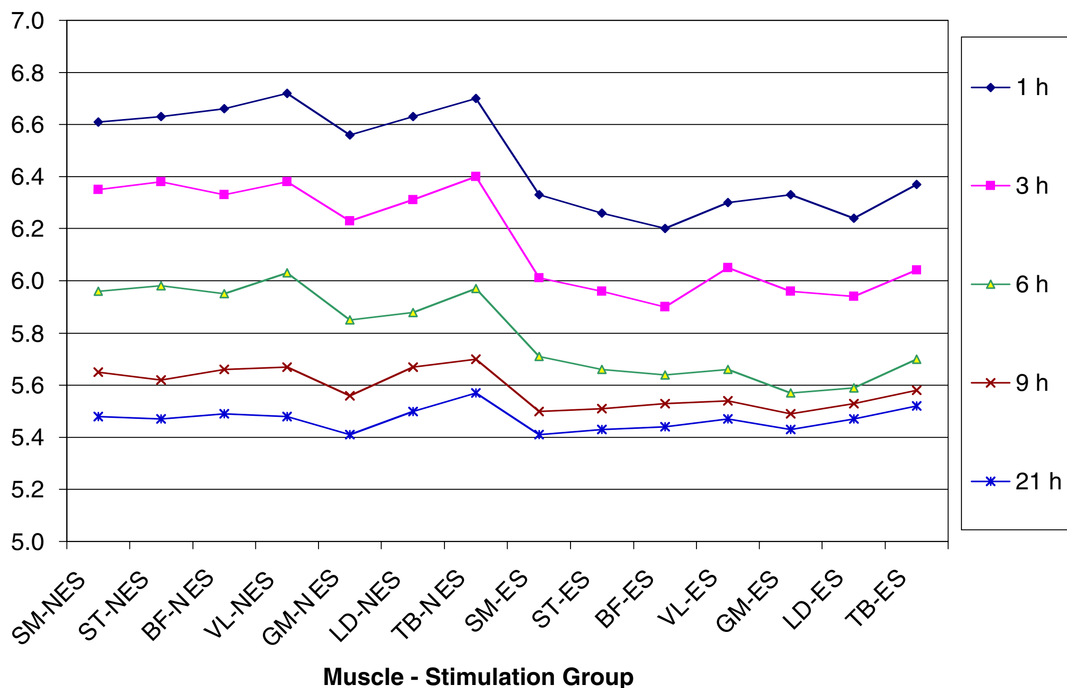

Fig. 4. Least squares means for pH decline across time postmortem as affected by electrical stimulation × muscle interaction.

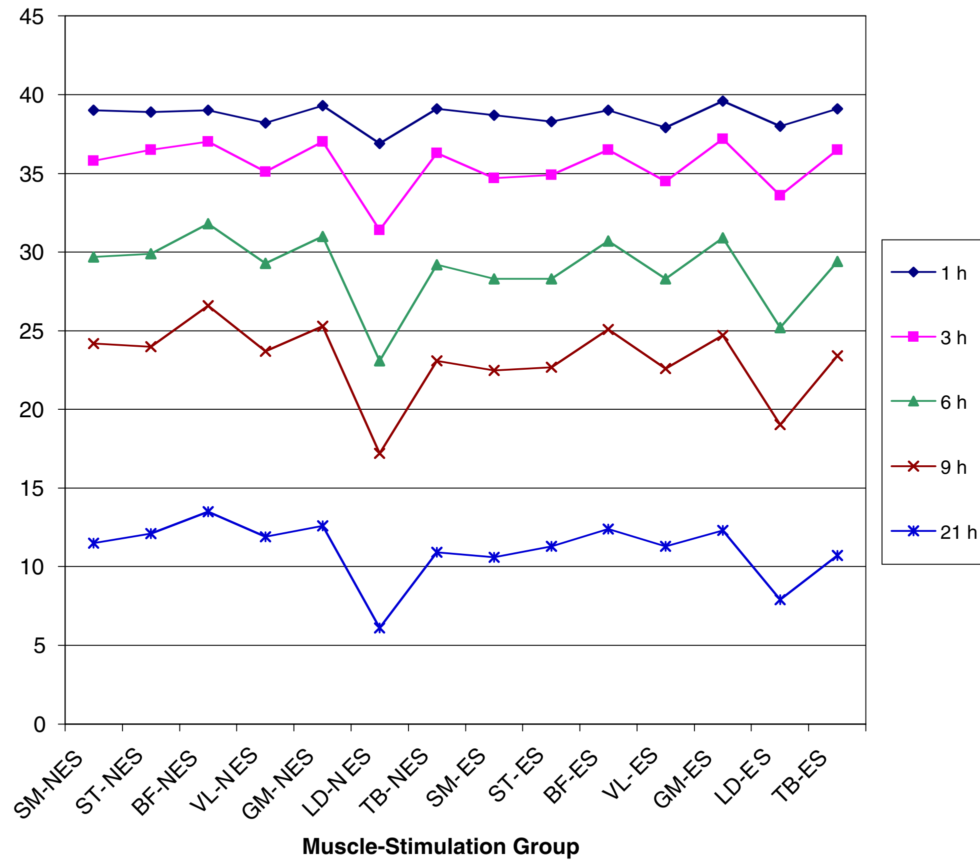

Fig. 5. Least squares means for temperature decline (°C) across time postmortem as affected by electrical stimulation × muscle interaction.

postmortem (Fig. 5). Higher temperatures seen in the electrically stimulated LD were most likely due to the typical increased rate of glycolysis in electrically stimulated muscles that results in a temperature increase immediately postmortem. In addition, the LD had the lowest overall temperature among electrically stimulated and non-electrically stimulated muscles at 3, 6, 9, and 21 h postmortem. This lower temperature could be explained by the location of the LD in relation to the other muscles examined. The BF and GM had higher temperatures ($P < 0.05$) at each time postmortem for both electrically stimulated and non-electrically stimulated muscles, while the SM, ST, VL, and TB maintained similar temperatures throughout the observed time period (Fig. 5).

3.6. Calpastatin activity

Electrical stimulation had no effect ($P > 0.05$) on 24 h calpastatin activity (NES, 2.13 units of activity/g of muscle; ES, 2.12 units of activity/g of muscle); however, there was a breed × muscle interaction for calpastatin activity at this time point (Table 3). In 3/4A × 1/4B cattle, the TB and VL had the highest calpastatin activity, the GM, LD, BF, and SM had the lowest activity, and the ST was intermediate in activity. As percentage *Bos indicus* breeding increased, calpastatin level in the SM and GM increased concurrently. In the ST, VL, LD, and TB muscles, 1/2A × 1/2B cattle displayed higher calpastatin levels than the other breed types.

Table 3
Least squares means for 24 h calpastatin activity as influenced by breed × muscle interaction

Muscle	Calpastatin activity per g		
	3/4A × 1/4B[a]	1/2A × 1/2B	1/4A × 3/4B
M. semimembranosus	1.52fgh	1.93efg	2.20de
M. semitendinosus	2.08def	2.80bc	2.17de
M. biceps femoris	1.53fgh	1.71fgh	1.95ef
M. vastus lateralis	2.18de	2.88b	2.15de
M. gluteus medius	1.44h	1.98efg	2.02ef
M. longissimus dorsi	1.81fegh	2.18de	1.96ef
M. triceps brachii	2.44cd	3.59a	2.17de
RSD[b]	0.70		

Least squares means with different letters (a–h) differ significantly ($P < 0.05$).
[a] 3/4A = 3/4 Angus × 1/4 Brahman, 1/2A = 1/2 Angus × 1/2 Brahman, 1/4A = 1/4 Angus × 3/4 Brahman.
[b] RSD, residual standard deviation.

The LD and TB demonstrated considerable responses to postmortem aging, but had large differences in calpastatin activity (1.98 units of activity/g of muscle and 2.73 units of activity/g of muscle, respectively). Alternatively, the BF and VL displayed large differences in calpastatin activity (1.73 units of activity/g of muscle and 2.40 units of activity/g of muscle, respectively), but had only minimal

response to postmortem aging. This suggests that variation in calpastatin level did not relate to differences in WBS force data or response to aging.

3.7. Total collagen amount

The BF and VL had the highest ($P < 0.05$) total amount of collagen as compared to the other muscles while the LD and GM had the lowest ($P < 0.05$) (Table 4). Muscles with relatively higher total collagen amounts (BF, VL, ST, SM) demonstrated the highest WBS force values (Figs. 2 and 3). Furthermore, the GM and LD had the lowest WBS force values (Figs. 2 and 3) and the lowest total collagen amounts (Table 4). Therefore, differences in WBS force between the LD and GM are most likely not due to differences in total collagen amount.

3.8. Percentage collagen solubility

Percentage collagen solubility was affected by muscle and breed type × muscle interaction (Table 5). The LD had the highest ($P < 0.05$) percentage collagen solubility across all breed types, followed by the GM, SM, ST, BF, TB, and VL, respectively. However, ST muscles from 3/4A × 1/4B cattle had a higher ($P < 0.05$) percentage collagen solubility than ST muscles from the other breed types. Muscles with the highest percentage of collagen solubility (LD, GM) had the lowest WBS force values (Figs. 2 and 3). Moreover, the muscles with the lowest collagen solubility (BF, VL, and ST) had the highest WBS force values (Figs. 2 and 3). Therefore, differences in total collagen amount and percentage collagen solubility between muscles seem to explain most of the variation in WBS force between muscles in this study.

Table 4
Least squares means for total collagen amount as influenced by muscle

Muscle	Collagen amount (mg/g)
M. semimembranosus	2.37c
M. semitendinosus	2.68d
M. biceps femoris	2.93a
M. vastus lateralis	2.92a
M. gluteus medius	2.23c
M. longissimus dorsi	2.00d
M. triceps brachii	2.75b
RSD[a]	0.43

Least squares means with different letters (a–d) differ significantly ($P < 0.05$).
[a] RSD, residual standard deviation.

Table 5
Least squares means for percent collagen solubility for breed × muscle interaction

Muscle	3/4A × 1/4B[a]	1/2A × 1/2B	1/4A × 3/4B
M. semimembranosus	16.02bc	15.06c	15.05c
M. semitendinosus	14.06d	12.79ef	12.67efg
M. biceps femoris	12.46efg	12.01fg	12.09fg
M. vastus lateralis	12.19efg	11.78g	12.81ef
M. gluteus medius	16.84ab	16.09b	16.18b
M. longissimus dorsi	17.37a	17.39a	17.21a
M. triceps brachii	12.28efg	13.83d	13.11de
RSD[b]	1.68		

Least squares means with different letters (a–g) differ significantly ($P < 0.05$).
[a] 3/4A = 3/4 Angus × 1/4 Brahman, 1/2A = 1/2 Angus × 1/2 Brahman, 1/4A = 1/4 Angus × 3/4 Brahman.
[b] RSD, residual standard deviation.

Table 6
Least squares means for percent chemical lipid as influenced by breed × muscle interaction

Muscle	3/4A × 1/4B[a]	1/2A × 1/2B	1/4A × 3/4B
M. semimembranosus	2.83hi	3.25fghi	2.76i
M. semitendinosus	3.06ghi	2.99hi	2.94hi
M. biceps femoris	5.26a	4.75ab	4.47bc
M. vastus lateralis	3.40efgh	3.80def	3.44efg
M. gluteus medius	3.36efghi	3.24fghi	3.64efg
M. longissimus dorsi	5.20a	4.35bcd	3.90cde
M. triceps brachii	3.97cde	3.86cdef	3.97cde
RSD[b]	1.06		

Least squares means with different letters (a–i) differ significantly ($P < 0.05$).
[a] 3/4A = 3/4 Angus × 1/4 Brahman, 1/2A = 1/2 Angus × 1/2 Brahman, 1/4A = 1/4 Angus × 3/4 Brahman.
[b] RSD, residual standard deviation.

3.9. Percentage chemical lipid

Percentage chemical lipid was affected by muscle and breed type × muscle interaction (Table 6). In 3/4A × 1/4B cattle, percentage chemical lipid was highest in the LD and BF, intermediate in the TB, and lowest in the SM, ST, VL, and GM. As percentage *Bos indicus* increased, lipid was not affected in the SM, ST, VL, GM, and TB; however, percentage chemical lipid in 1/2A × 1/2B and 1/4 A × 3/4B LD muscles decreased along with 1/4A × 3/4B BF muscles in relation to their 3/4A × 1/4B counterparts. This is in agreement with McKeith et al. (1985), who reported higher percent fat in the LD and BF than the SM, ST, VL, GM, and TB. Though the LD and BF muscles had the highest percentage chemical lipid, these muscles displayed significant differences in WBS force values and postmortem aging responses (Fig. 3). Therefore, percentage chemical lipid (marbling) did not explain significant differences in WBS force between muscles.

4. Conclusions

Muscle appeared to play the greatest role in tenderness differences in this study. Muscles from the round had higher shear force values than muscles from the loin and chuck. Breed type was associated with inherent tenderness differences of muscles, however, this role was limited to rate of postmortem aging and calpastatin activity. Electrical stimulation improved tenderness slightly for most muscles, however, early-postmortem chilling conditions could be a

major determinant of the extent to which electrical stimulation can improve tenderness. Postmortem handling, aging, and cooking conditions that are used for cuts originating from the loin do not have the same effect on cuts originating from the round.

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