Meat and Muscle Biology™

Meat Tenderness: Underlying Mechanisms, Instrumental Measurement, and Sensory Assessment

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Abstract: Meat tenderness is a quality trait critical to consumer acceptance and determines satisfaction, repeat purchase, and willingness to pay premium prices. The aim of this review was to explore instrumental and sensory methods for assessing meat tenderness in relation to underlying mechanisms and to identify limitations of existing methods, as well as opportunities for global standardization. To achieve this, tenderness is defined, and the main instrumental methods for tenderness are presented, including their historical development and standardization. The significant determinants of meat tenderness are presented, encompassing connective tissue and cross-links, myofibrillar integrity, sarcomere length, intramuscular fat, and protein denaturation during cooking. The development of sensory methods for assessing meat is presented as well as the link between objective measures of texture and consumer tenderness scores. Recent advances in statistical methods for sensory data are discussed, and considerations for future research are outlined.

Key words: tenderness, Warner-Bratzler shear force, sensory, cooking, denaturation, degradation
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Introduction

Tenderness is an important and characteristic trait of meat quality and includes instrumental measures and consumer and trained panel sensory assessments, which determine satisfaction, repeat purchase, and willingness to pay premium prices (Sasaki et al., 2010). Meat texture is used to describe meat tenderness, although this term also describes the firmness or coarseness of a meat surface (Purchas, 2014). In this review, the term "tenderness" generally refers to instrumental measures, such as Warner-Bratzler shear force (WBSF), or sensory assessments. In the literature, the term tenderness is often used interchangeably with "sensory-tenderness" and objective tenderness measurements.

Research over the last 70 y has been pivotal in understanding the mechanisms determining meat texture and tenderness and industry advances in quality assurance. These industry advances and understanding of mechanisms, including biology, biochemistry, and biophysics of meat tenderness, have occurred throughout the meat supply chain and have been extensively reviewed. A history of research on meat

tenderness is presented in this review, encompassing the primary determinants of meat tenderness: connective tissue and cross-links, myofibrillar integrity, sarcomere length, protein denaturation, and intramuscular fat (IMF). The development of sensory methods for assessing meat is presented with the link between objective measures of tenderness and consumer tenderness scores as well as recent advances in statistical and biometrical methods.

The aim of this review was to explore instrumental and sensory methods for assessing meat tenderness in relation to underlying mechanisms and to identify limitations of existing methods, as well as potential for global standardization.

Defining the Term "Tenderness," a Unique Characteristic of Meat

Tenderness, in relation to food texture, is a term often used to describe meat. For example, a "tenderizer" is defined as "something to make meat tender" and "tenderize" "to make food tender, especially meat" (Oxford English online dictionary; www.oed.com; accessed 5 October 2020). Yet although meat scientists are familiar with the term, consumers are not always clear what is meant by tenderness, particularly in countries where English is not the spoken language. In this review, meat texture is a term used to describe meat tenderness, whereas texture can also be used to describe the firmness or coarseness of a meat surface (Purchas, 2014).

In meat science literature, the term tenderness is often used interchangeably with "sensory-tenderness" and objective tenderness measurements. Furthermore, some references refer to instrumental measurements as "texture" (Claus, 1995; Solomon et al., 2008), and other references only use the term tenderness when referring to trained or consumer sensory panels. Bourne, who is recognized for his seminal contributions to understanding food texture, explains that "texture, unlike the aroma, color or taste, cannot be created from a bottle, and the most distinctive textures are created by nature" (Bourne, 2002c). When in the intact rather than minced or comminuted form, meat can be described as having a unique texture, which has not been successfully replicated. In addition, minced or ground meat retains some structural integrity, and the resulting texture is difficult to replicate.

Consumers may have their own criteria to judge meat tenderness because consumers are neither selected nor trained like an expert sensory panel (Sasaki et al., 2014). The textural properties of meat are perceived in the mouth upon consumption, and plant-based analogs of meat have attempted to replicate this consumer experience, with varying success (Dekker et al., 2018). Muscle is composed of fibrous proteins, which are a part of the sensory experience in the mouth when meat is being chewed. The sensorially appraised in-mouth texture attributes of meat can be divided into first-bite properties, mastication properties, and after-feeling properties. These can be described by compressibility, cohesiveness, chewiness, fibrousness, fiber coarseness, connective tissue, and mealiness (Purchas, 2014). Interestingly, the terms adhesiveness, cohesiveness, and chewiness are also terms used in objective measurements using texture profile analysis (TPA) (Bourne, 2002b; Purchas, 2014).

Meat scientists often use the word "tenderness," but it is not always clear what is meant when this term is used. According to Sasaki et al. (2010), the meaning of tenderness is not at all well-defined in meat science literature. They suggest using the International Organization for Standardization (ISO; www.iso.org) 5492:1992 standards, which are an internationally established vocabulary for sensory analysis and methods. Using this terminology, they discovered that the term "hardness," defined as the force required to achieve a given deformation, was encompassed by the ISO5492:1992 trained panel qualitative terms "soft," "firm," and "hard." Conversely, the term "chewiness," defined as the length of time required to masticate a product into a state for swallowing, was encompassed by the ISO5492:1992 trained panel qualitative terms "tender," "chewy," and "tough." In subsequent research, Sasaki et al. (2014) recommended the use of ISO11036:1994 terminology as these standards provide detailed sensory scales for "chewiness" and "hardness" with definitions and reference materials (www.iso.org). ISO11036:1994 was replaced with ISO11035:2020 in May 2020 (www.iso.org). The terms chewiness and hardness are related to WBSF values and also TPA hardness and chewiness values (Sasaki et al., 2010, 2014).

Instrumental Measurement of Tenderness

Early work developed a series of empirical devices to quantify some physical property that was associated either with sensory evaluation of tenderness or established palatability grades. These included devices

measuring the force required to break a meat sample by axially opposed blades intended to simulate a biting action (Lehman, 1907; Volodkevich, 1938; Winkler, 1939; Macfarlane and Marer, 1966) and those measuring the force required to break a sample by blades or bars passing by each other in close proximity, involving so-called shearing of the sample (Warner, 1929; Bratzler, 1932; Kramer et al., 1951). Szczesniak and Torgeson (1965) recognized that it was extremely difficult to state precisely what forces and deformations were applied to the structure of meat in these tests, and therefore which basic mechanical properties of the tissues were being assessed. This remains true today. The WBSF test, or some variation of it, continues to be widely used today. Szczesniak and Torgeson (1965) listed 51 publications showing correlations between WBSF and sensory evaluations of tenderness ranging from very high to very low, with correlation coefficients ranging from −0.914 to −0.001, respectively. Those authors suggested that the sensory panels' poor performance could be one reason for the observed low correlation. Still, they also highlighted the problem that the properties measured by WBSF might not align fully with those evaluated in sensory tests. This topic is explored more fully in the next section.

What Warner-Bratzler shear force measures

Application of shear devices, such as the WBSF test, involves tensile, compression, and shear stresses and consists of both force and deformation. Therefore, these shear tests measure a multitude of properties (Voisey, 1976; Bourne, 2002b). Using modified Warner-Bratzler equipment comprising a rectangular-shaped blade and rectangular sample block rather than a circular core, Bouton et al. (1975a) showed that the shear force-deformation curve could be analyzed for 2 components: (1) the force at initial yield, which represents the force required to compress and shear the myofibrillar structures, and (2) the peak force minus initial yield, which appeared to be an indication of the strength of the connective tissue. But under different conditions such as muscles varying in connective tissue content or comparing cold-shortened and stretched muscles, these relationships are not constant (Bouton et al., 1976). Bouton et al. (1975b) stated that no single parameter from the WBSF test had been shown to have a reliable predictive value for taste panel tenderness when meats of widely different structural properties were tested. Shackelford et al. (1995) found that shear force did not accurately measure the differences in tenderness, measured by a trained panel, among 10 different muscles in the beef carcass. Møller (1981) used an analysis of the force-deformation curve to show that connective tissue is the principal contributor to the WBSF at 60°C, whereas at 80°C, myofibrillar strength is the dominant contributor, which helps explain the variation between muscles in WBSF with differing connective tissue content. For these reasons, the American Meat Science Association (AMSA) (2016) recommends that the WBSF test not be used to compare between muscles, due to the variation in the sensitivity of the method to connective tissue, depending on endpoint cooking temperature.

It should be noted that Møller (1981) showed that a comprehensive analysis of the full force-deformation curve yielded far more information than just using the peak force. (A reconsideration of this aspect should be contemplated for the global standardization of tenderness measurements). In addition, Figures 1b, 1c, and 2 illustrate that early research (Bouton and Harris, 1972b) as well more recent research (Christensen et al., 2000; Vaskoska et al., 2020a) have shown that, when cooking temperature experiments are conducted, muscles with high connective tissue show a decrease in WBSF values between 50°C and 60°C due to solubilization of collagen. Although many meat scientists accept that the WBSF test is a good indicator of the myofibrillar component of tenderness, the WBSF test—or any other instrumental test—is only as good as the correlation with sensory panels. This aspect is discussed further in the section on sensory analysis.

Variations in the Warner-Bratzler shear force method

The standard WBSF test involves using a Warner-Bratzler triangular, V-shaped blade originally used by Warner (1929) and further developed by Bratzler (1932). There are specifications for the blade thickness, the cutting edge, the V-notch angle, etc. These are described in Bourne (2002b) and AMSA (2016). These specifications are important because the shear force values are very much affected by variations in these parameters (Voisey and Larmond, 1974). In addition, the cooking method, temperature, sample size, cooking time, etc. can vary, depending on the questions being asked in an experiment, and can also impact shear force results. Variation in shear force application includes use of a straight-edged shear blade, which is used by the CSIRO (Commonwealth Scientific Industrial Research Organization-Australia) (Bouton and Harris, 1972a), and the slice shear force (SSF) method established by Shackelford et al. (1999a, 1999b). The other

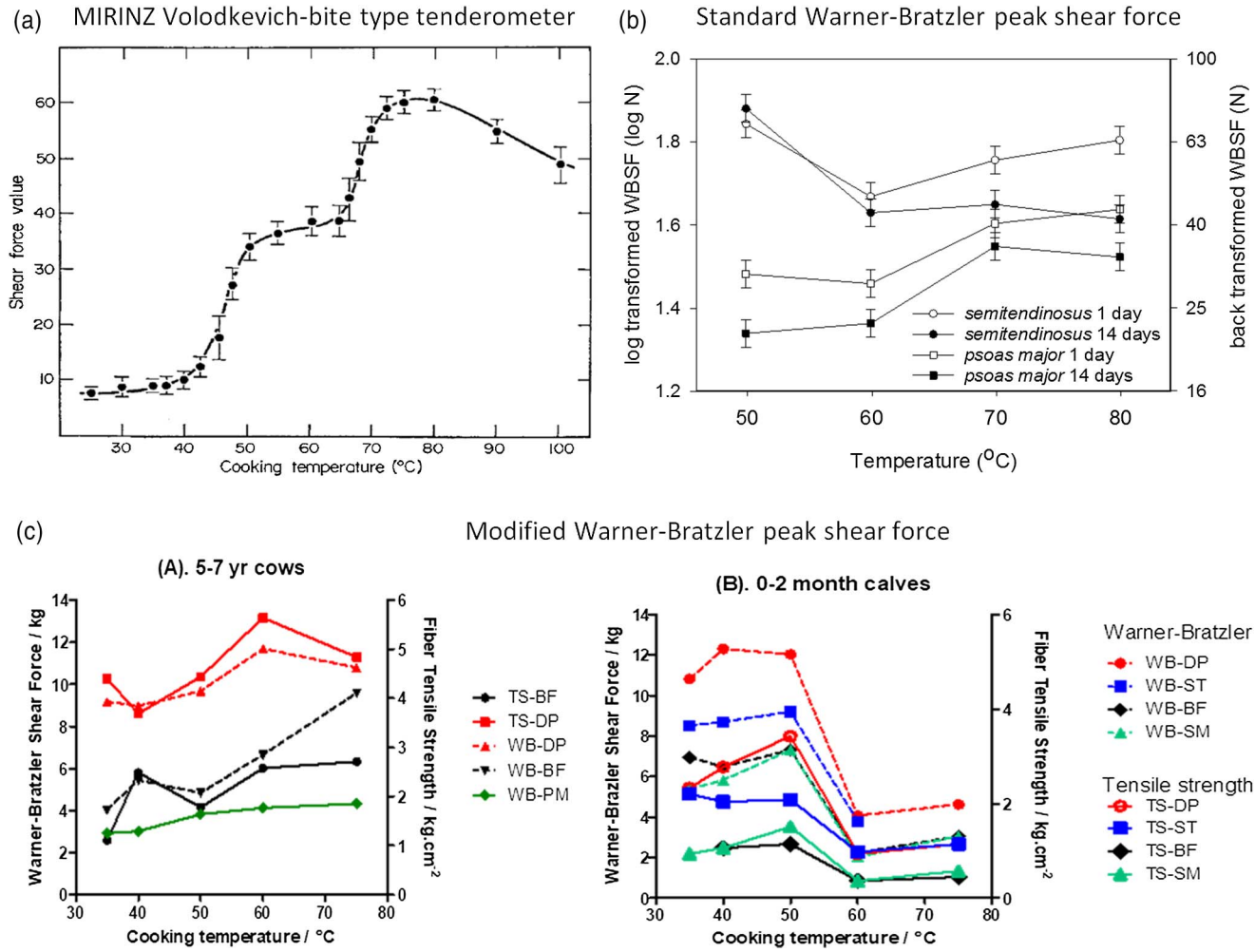

Figure 1. Effect of cooking temperature on the shear force results with different machines and different sample treatment conditions; (a) effect of cooking temperature on shear force value (Newtons; convert to kg by dividing by 9.8) of beef *sternomandibularis* using a Meat Industry Research Institute New Zealand (MIRINZ) tenderometer, from Davey and Gilbert (1974); (b) effect of bovine muscle and ageing (1 or 14 d) on Warner-Bratzler peak shear force (back-transformed WBSF) with cooking temperature using the standard method, adapted from Vaskoska et al. (2020a); (c) effect of muscle (deep *pectoralis* [DP], *biceps femoris* [BF], *semimembranosus* [SM], *semitendinosus* [ST]) and age (A) 5- to 7-year-old cows, (B) 0- to 2-month-old calves, on Warner-Bratzler peak shear force (kg) with cooking temperature using a modified jig, adapted from Bouton and Harris (1972b). All figures are with permission.

major variation is the shape and size of the meat sample. The original WBSF method (AMSA, 2016) used in North America utilizes a 1.27-cm-diameter round "core" sample. However, a rectangular 1-cm^2 block is used in Europe (Møller, 1981; Hildrum et al., 2009) and has been used exclusively in Australia since the 1970s (Bouton and Harris, 1972a; Perry and Thompson, 2005; Pearce, 2009; Warner et al., 2010). Although AMSA (2016) recommends using the 1.27-cm core sample for WBSF, Silva et al. (2017) reported that the 1-cm^2 sample block produced more precise and more repeatable results, and sample collection is easier to perform than the round core sample. Likewise, the SSF test developed by Shackelford et al. (1999a, 1999b) is reported to be a more rapid, easier, more repeatable sampling method with a higher correlation to sensory tenderness than WBSF (Shackelford et al., 1999a). Others have reported that the SSF test is less efficient in classifying samples into consumer sensory tenderness groups, and also more variable, relative to the WBSF test (Battaglia et al., 2019). Furthermore, removing samples from muscles with varying fiber orientation or small muscles is more difficult using a core sampler than cutting a rectangular block with 1-cm^2 area and 3–5 cm length. As these sampling strategies are a large point of difference between different laboratories around the world, it will require discussion and consensus if a global standard is to be achieved.

Standardization

The peak load, or peak force, obtained from the Warner-Bratzler force-deformation curve has been generally found to be the best predictor of sensory

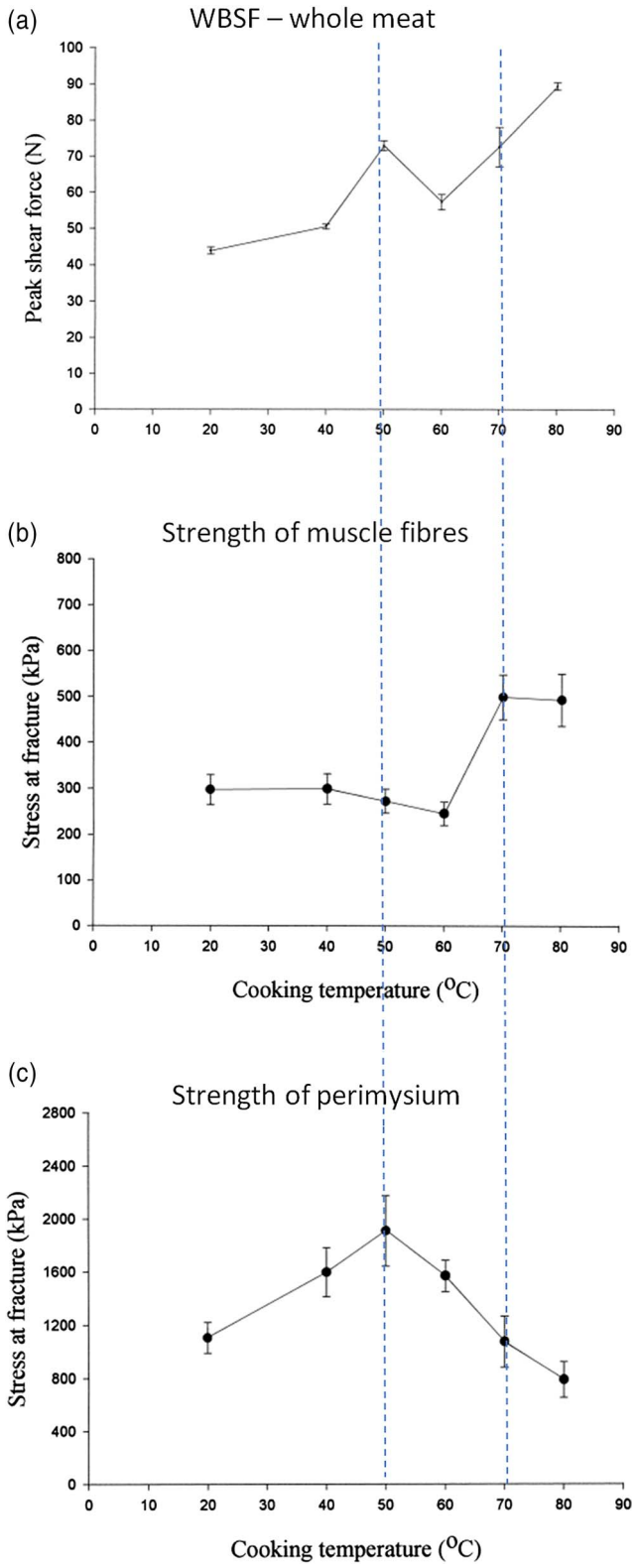

Figure 2. Comparison of (a) WBSF of whole cooked meat (top) with (b) the strength of individual muscle fibers (middle) and (c) the strength of isolated perimysium strands versus cooking temperature. Dotted lines show that the peak in WBSF at 50°C coincides with the peak in perimysial strength and that a rise in WBSF at 70°C and above coincides with an increasing muscle fiber strength above 70°C. From Christensen et al. (2000) with permission. WBSF, Warner-Bratzler shear force.

tenderness (Bourne, 2002b), although exceptions have been found (Møller, 1981). Although shear force values can vary among institutions using the same methods and with variation in sampling, cooking, and coring methods (Wheeler et al., 1997; Hopkins et al., 2010), it remains the instrumental method of choice for tenderness measurement, and attention to global standardization is warranted. Standardization has been recently described within the USA (AMSA, 2016) and previously across Europe, Australia, and New Zealand (Chrystall et al., 1994; Honikel, 1998), as well as for extensive studies of thousands of carcasses in the Australian beef Cooperative Research Centre (CRC) (Perry et al., 2001a) and sheep CRC (Pearce, 2009; Mortimer et al., 2010). As these standards have some differences in the shape of the blade, the shape of the sample, and cooking temperature and conditions, an agreed level of global standardization would be useful. See below for further discussion.

Alternatives to Warner-Bratzler shear force

Although the WBSF test remains in use today, several other instrumental measures have been developed, in addition to the variations in the WBSF test described earlier. Instruments used for texture analysis generally measure meat's resistance to shearing, compression, or penetration. The Volodkevich bite tenderometer (Volodkevich, 1938), referred to earlier, was not further developed or adopted (Solomon et al., 2008). However, a Volodkevich-style bite wedge was developed by Macfarlane and Marer (1966), which became the basis of the Meat Industry Research Institute New Zealand (MIRINZ) tenderometer. Notably, the MIRINZ tenderometer device has a "biting" action and is a combination of shearing and compression (Bourne, 2002b), although it is often described as a shearing force. Also, the MIRINZ tenderometer differs from other methods in that it employs a constant rate of increase of force, rather than a constant rate of blade movement (Vincent and Lillford, 1991). The results from the MIRINZ tenderometer are, to some extent, comparable to the WBSF (Solomon et al., 2008), although the values are generally higher (Graafhuis et al., 1991). Although Bourne (2002b) grouped the Warner-Bratzler test and the Volodkevich-type "bite" wedge test together as being shear tests, both Claus (1995) and Purchas (2014) considered shearing devices such as the WBSF test and Allo-Kramer shear test to be different than "biting" devices such as the Volodkevich and MIRINZ tenderometer. Further comparison of these devices is available in Vincent and Lillford (1991).

TPA, wherein a compressing action occurs when a plunger is pushed into the sample, was invented in 1963 by the General Foods Corporation and was modified for use on the Instron Universal Testing machine by Bourne (1968). TPA has been used extensively in processed meats to quantify texture parameters, including hardness, springiness, adhesiveness, and cohesiveness (Bourne, 2002a, 2002b). TPA has also been used in fresh cooked meat as it is thought to reflect the connective tissue contribution to tenderness to a greater extent than shear or biting tests (Purchas, 2014). Hence, a beef genetics program in Australia utilizing data from 3,350 beef carcasses included "compression" (calculated from the hardness and cohesiveness parameters from the TPA data) as a phenotype, enabling heritability to be quantified (Johnston et al., 2003). More details about compression testing for meat and meat products are available in reviews (Claus, 1995; Bourne, 2002a, 2002b; Purchas, 2014) and are not discussed further.

Underlying Mechanisms for Meat Tenderness

To understand the relationship between instrumental and sensory measures of tenderness, we first examine 5 fundamental mechanisms; connective tissue and cross-linking, myofibrillar integrity, sarcomere length, IMF, and protein denaturation during cooking, which together determine the majority of variations in meat tenderness.

Connective tissue content and cross-linking

Early work focused on the amount of connective tissue as a cause of variations in tenderness between muscles, starting with Lehman's work (1907). Some early investigations histologically measured the amount and distribution of intramuscular connective tissue (Ramsbottom et al., 1945; Strandine et al., 1949; Carpenter et al., 1963) and related this to variations in tenderness. Analysis of collagen content by sodium hydroxide extraction of all muscle components, except for collagen and elastin (Mitchell et al., 1927), and subsequent methods involving the measurement of hydroxyproline content of various muscles (Loyd and Hiner, 1959) provided a consensus that variations in tenderness among different muscles were largely due to the collagen content of their intramuscular connective tissue. However, as demonstrated by a comparison of 18 beef muscles by Dransfield (1977), the total amount of collagen in a muscle is only able to explain part of the variation in tenderness between muscles; 45% of the overall variation in toughness when the meat is heated to 60°C for 1 h, 34% when heated to 75°C for 1 h, and only 18% when heated to 90°C for 1 h.

Meat from veal calves is more tender than meat from older cattle. However, Wilson et al. (1954) showed that there was no increase in intramuscular collagen with animal age. In fact, muscles from older steers and cows contained less intramuscular collagen than the same muscles in calves. Goll et al. (1963) found that *biceps femoris*' collagen content varied only between 1.36% and 1.83% of fresh muscle weight among veal calves, 1- to 2-year-old steers, 5-year-old cows, and 10-year-old cows. In contrast, WBSF values on cooked meat increased significantly with age, from 37.7 lb (17.15 kg) for meat from the veal calves to 56 lb (25.4 kg) for meat from 10-year-old cows. Jackson and Bentley (1960) observed that newly synthesized collagen was the most easily extracted, and rationalized that the degree of stabilization by covalent cross-linking increased with time post synthesis. Hill (1966) and Carmichael and Lawrie (1967) confirmed a decrease in soluble collagen with age. Cross et al. (1973) showed that the percentage of collagen solubilized on heating varied with animal age and was related to sensory evaluations of the connective tissue component of toughness (but not to WBSF in meat cooked to 72°C). Bailey (1972) surmised that increasing meat toughness with animal maturity must be due to intramuscular connective tissue, as actin and myosin are turned over very quickly. Recent measures of the replacement rates of myosin, titin, actin, Z-band components, and thick filament-associated proteins show that all these are replaced in minutes to hours, with replacement being regulated by heat shock protein chaperones (Ojima, 2019). In contrast, collagen's replacement rate is extremely slow and can be measured in months (McAnulty and Laurent, 1987; Rucklidge et al., 1992), allowing time-dependent changes in its covalent cross-linking, which in turn affects its mechanical and thermal stability. Upon synthesis of collagen, specific lysines and hydroxylysines in the nonhelical peptides are converted by lysyl oxidase to allysine and hydroxyallysine, respectively. These aldehydes react with hydroxylysines in the molecule's helical portion to form divalent intermolecular cross-links that stabilize the newly synthesized collagen fibers. The divalent cross-links from the allysine pathway (aldimines) are easily broken down by heat, whereas those from the hydroxyallysine pathway (ketoamines) are heat stable. Shimokomaki et al. (1972) showed that the

concentration of these divalent intermolecular cross-links in 7 different muscles of bovine animals increased up to approximately 1 y after birth but decreased thereafter, suggesting that long residence time of collagen in the body allows for slow condensation reactions to convert these divalent cross-links into more stable, trivalent cross-links.

Fujimoto (1977) first isolated the major forms of mature cross-linking residue on the hydroxyallysine pathway as trivalent, 3-hydroxypyridinium residues. Two forms, hydroxylysylpyridinoline and lysylpyridinoline, have been identified (Eyre, 1987). Bosselmann et al. (1995) showed that lysylpyridinoline and hydroxylysylpyridinoline concentrations in the connective tissue of 3 beef muscles generally increased with age but varied with animal sex and feeding intensity. Another trivalent cross-link from the hydroxyallysine pathway has a pyrrole structure that can react with Ehrlich's reagent (Scott et al., 1983), and so this cross-link is sometimes referred to as Ehrlich chromogen (EC). Horgan et al. (1991) measured both EC and pyridinoline cross-links in goat muscles. They found that, while pyridinoline cross-links increased with animal age, as did the thermal denaturation temperature of the collagen, EC concentrations diminished after 1 y of age. A more comprehensive description of the cross-linking of collagen is given by Yamauchi and Sricholpech (2012).

Although work continues on mature cross-links in relation to animal age, breed, and growth promoters (Roy et al., 2015), interest in collagen cross-linking has declined in the meat science field. The fact that connective tissue contributions to cooked meat texture do not diminish meaningfully with postmortem aging has led to the view that it is rather immutable and forms a "background toughness" that we can do little about in practical terms (Ouali, 1992; Sentandreu et al., 2002).

Myofibrillar disruption and degradation

Early work on meat toughness considered both myofibrillar and connective tissue mechanisms controlling tenderness, but in the last 30 y, the principal focus has been on proteolysis of myofibrillar proteins as the most practical mechanism to manipulate and control tenderness. The earliest study showing that postmortem aging of meat is due to proteolysis was Hoagland et al. (1917), as cited by Davey and Gilbert (1966). Despite problems in their 1966 paper relating rates of tenderness development with proteolysis rates, Davey and Gilbert (1969) later showed that proteolysis gave rise to Z-disc weakening and myofibrillar fragmentation. This proteolysis could be negated by chelation of calcium ions by the chemical EDTA (ethylenediaminetetraacetic acid). Møller et al. (1973) then related the increasing fragmentation of myofibrils to reductions in WBSF.

By the late 1930s, cathepsins were known to be a family of intracellular enzymes (Bergmann et al., 1937). Goll et al. (1983) reviewed the history and properties of the 7 cathepsins found within muscle cells, the majority of which are capable of degrading actin and myosin. They crucially pointed out that, because there is relatively little cleavage of actin and myosin in normal postmortem aging, the development of tenderness during aging was more likely to be due to a "calcium-activated factor" (Dayton et al., 1976). Recent research has shown that cathepsins remain active during heating and contribute to muscle fibers' shrinkage during cooking (Vaskoska et al., 2020b) and hence tenderness. Thus, these enzymes' role in tenderness development during cooking needs to be revisited and is discussed further in this text. The history of research showing that the calcium-activated proteases (now known as the calpain family of enzymes) are critically involved in the development of tenderness postmortem is reviewed by Koohmaraie (1988). Koohmaraie and his colleagues were prominent in focusing attention on the role of calpains (and especially μ-calpain, or calpain-1, the product of the *CAPN1* gene) in tenderness development and focusing attention on the use of postmortem aging as a principal tool for the practical manipulation of tenderness (Koohmaraie et al., 1988; Koohmaraie, 1994; Koohmaraie, 1996; Veiseth et al., 2001; Geesink et al., 2006). Other protease systems such as the proteasome and caspase systems are active in muscle. Kemp et al. (2010) reviewed the evidence and suggested that the proteasome, while an important degradative pathway in living muscle, is not currently thought to play a major role in postmortem degradation associated with tenderness development. At the same time, the possibility of caspase involvement appears much more open.

Sarcomere length and effects of chilling rate and metabolism

A shortening of sarcomere length can occur as muscle enters rigor mortis, depending on the degree of restraint on the muscle, the temperature, and the glycolytic metabolism within the muscle fibers. As well as affecting sarcomere shortening, there are also effects of chilling rate on (via effects on temperature) postmortem energy metabolism, pH, and proteolytic activity.

Shortening. Although the shear strength of raw muscle decreases with decreasing sarcomere length in raw muscle (Rhodes and Dransfield, 1974), shorter sarcomere lengths are associated with higher shear values in the cooked state. Bendall (1951) and Marsh (1954) related shortening at higher temperatures to the rate of consumption of adenosine triphosphate (ATP). Heating prerigor muscles was also shown to provoke an active shortening, leading to increased toughness (Abugroun et al., 1985). Locker and Hagyard (1963) demonstrated that—in addition to the delayed, moderate "heat shortening" of unrestrained muscles in the range of 25°C to 40°C, which is linked to glycolytic metabolism—a rapid and severe shortening of muscles could occur at temperatures in the 0°C to 5°C range, an effect that they described as cold shortening. These effects are shown in Figure 3. Cold shortening occurred too rapidly to be related to glycolytic metabolism and falling levels of ATP. In further studies, Marsh and Leet (1966) showed that bite-type tenderometer values in cooked meat were higher with moderate levels (40%) of cold shortening than extreme levels (55%–60%). Subsequent ultrastructural studies on cold-shortened raw muscle (Marsh et al., 1974; Voyle, 1969) showed zones of widely variable sarcomere length on extremely cold-shortened muscle with zones of "super-contraction" interspersed with longer, damaged sarcomeres. The supposition was that, after cooking, these longer, weaker sarcomeres would determine toughness. Cold shortening was considered to arise from the inefficiency of calcium pumps in the sarcoplasmic reticulum at low temperatures. The variable extent of cold shortening seen between red and white muscles and between species such as beef and rabbit led to the theory that calcium release from mitochondria also played a role (Buege and Marsh, 1975; Cornforth et al., 1980). Mechanisms underlying the contributions of muscle shortening and sarcomere length to cooked meat toughness have been reviewed in more detail by Asghar and Pearson (1980) and, more recently, by Ertbjerg and Puolanne (2017).

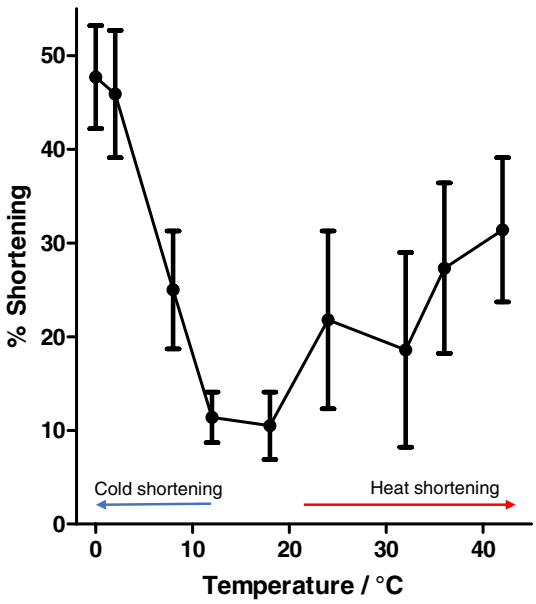

Figure 3. Mean values of ultimate muscle shortening at various temperatures. Bars represent ± 1 standard deviation. From Locker and Hagyard (1963), with permission and with annotation to show cold-shortening and heat-shortening temperature zones.

Electrical stimulation. Given that shortening of muscle postmortem is a highly variable process dependent on the degree of restraint and essentially driven by the availability of ATP, researchers then began to explore electrical stimulation application to hot carcasses, to speed up glycolysis. High-voltage electrical stimulation (250 V; Carse, 1973) (3,600 V; Chrystall and Hagyard, 1976) was initially explored, followed by low-voltage variants (45–80 V; Fabiansson and Buchter, 1984) (32 V; Taylor and Marshall, 1980). Variability in the effects of various electrical stimulation treatments and the effects on glycolysis and consequent shortening of muscle fibers was demonstrated by Smulders et al. (1990).

Stretching methods. In addition to electrical treatments to prevent shortening, the extension of sarcomere length in some of the more valuable muscles in a carcass was developed by the application of pelvic suspension and was shown to lower WBSF values after cooking (Hostetler et al., 1972). In addition to pelvic suspension ("Tenderstretch"), other treatments applied either to the suspended half-carcass (such as "Tendercut," i.e., sawing the vertebral column at the 12th/13th rib junction and the ischium at the rump/butt junction to stretch the loin and hindlimb muscles) or to individual hot-boned muscles (such as the "Pi-Vac" system that uses elastic packaging or the "Smartstretch" procedure that uses a combination of vacuum/air pressure to stretch muscles along their axis and then hold them extended with packaging) have been developed to produce greater tenderness in some, but not all, muscles by lengthening of the sarcomere (Ludwig et al., 1997; Sorheim and Hildrum, 2002; Ahnström et al., 2006; Toohey et al., 2012).

The interactive effects of normal versus pelvic suspension with chilling rate on tenderness were demonstrated, by Joseph and Connolly (1977), to vary from muscle to muscle in beef carcasses. They reported

increasing tenderness of the *longissimus* with both tenderstretching and slow chilling but no effect of slow chilling on *psoas major*, *biceps femoris*, *semitendinosus*, or *semimembranosus*. Møller et al. (1987) also found a variable interaction of tenderstretching with chilling rate in tenderness development of pork muscles. Smith et al. (1976) found that carcasses with more fat cover chilled more slowly and had less sarcomere shortening and better tenderness in the *longissimus*, *biceps femoris*, and *semimembranosus*, which they ascribed to both decreased sarcomere shortening and increased proteolysis in the carcasses with slower cooling. On the other hand, rapid chilling is known to ameliorate the PSE (pale soft exudative) condition in pig carcasses with rapid postmortem glycolysis (Honikel, 1987; Feldhusen and Kuhne, 1992). A detailed discussion of the interactions of postmortem metabolism, muscle restraint, and sarcomere length and chilling rate is given by Savell et al. (2005).

Metabolism and pH–temperature decline. Following on from earlier, it is evident that both muscle pH and temperature decline influence meat tenderization postmortem (Savell et al., 2005; Warner et al., 2010; Hopkins et al., 2011). Thompson et al. (2005) found that temperature at pH 6 was a critical control point for improving sensory tenderness in sheep carcasses suspended by the Achilles tendon hanging method. Temperatures lower than 10°C or higher than 30°C at pH 6 were associated with lower sensory tenderness. The influence of temperature at pH 6 is not significant for tenderstretched lamb (Thompson et al., 2005) and beef (Warner et al., 2014b) carcasses. Hopkins et al. (2015) referred to pH 6 between temperature 18°C and 25°C as "ideal pH decline" or "ideal shortening." They identified that pH at 24 h postmortem of *longissimus* was significantly related to tenderness and could be used in abattoirs for quality control. Besides pH and temperature decline, meat tenderness is also determined by ultimate pH. Lomiwes et al. (2014) categorized beef *longissimus* tenderness according to ultimate pH and found that the toughest beef was obtained in intermediate ultimate pH samples. This has been attributed to the faster degradation of myofibrillar proteins in muscle with ultimate pH higher than 6.2 or lower than 5.79 (Wu et al., 2014) and also potentially attributed to lack of access of calpains to substrate in the shortened sarcomeres (Weaver et al., 2008) although Wheeler and Koohmariae (1999) reported that sarcomere length did not affect the degree of calpain proteolysis. The decline of pH is coupled with a decline in temperature during the rigor phase. Liu et al. (2015) reported decreased WBSF of beef by controlling prerigor temperature within the range of 12°C to 18°C. Postrigor temperatures have significant effects on rigor development and thus the rate of tenderization. Tenderization increases with higher temperature and faster rigor development, and holding postrigor beef carcasses at 30°C for 24 h after slaughter has been shown to produce as much as 86% of aging (Dransfield, 1994a, 1994b; Devine et al., 2014), although this is, of course, not practical for reasons of microbiological growth and food safety.

Very fast chilling. The prerigor temperature also has an impact on lamb tenderization in terms of both cold shortening and heat shortening as described earlier and in other references (Devine et al., 2014; Kim et al., 2014a, 2014b; Warner et al., 2014a). It has been shown that very fast chilling—defined as chilling to below 0°C within 1 to 3 h post mortem—does not induce either cold toughening or cold shortening but greater tenderization in beef (Sikes et al., 2017) and lamb muscle (Jacob et al., 2012), compared to conventional chilling. It should be noted that, unless the temperature and pH decline is carefully managed, cold toughening can result, as shown in a study on the very fast chilling of lamb *longissimus* (Jacob et al., 2012). The detailed effects and mechanisms of the influence of sarcomere length variation on meat quality were recently reviewed by Ertbjerg and Puolanne (2017).

Intramuscular fat

It is generally accepted that certain levels of IMF content increase the acceptability of cooked meat (Savell and Cross, 1988), especially based on flavor and juiciness. Still, there has long been debate as to whether the IMF has a direct and causal relationship to meat tenderness. Szczesniak and Torgeson (1965) and Smith and Carpenter (1976) reviewed work from the 1930s onward that confirm and deny this relationship. The very comprehensive Table 5 in Smith and Carpenter (1976) listed approximately 200 references on the relationship between IMF and tenderness in beef, pork, and lamb, ranging from high to very low correlations in meat from all 3 species. Taking just beef *longissimus* as an example, Suess et al. (1966) gave a correlation of −0.06 between sensory tenderness and percentage fat, whereas Dryden and Maechello (1970) report a correlation coefficient of 0.68 between sensory tenderness and the percentage of lipid in the muscle on a dry weight basis, or a correlation of 0.64 with percentage lipid on a wet weight basis.

It is interesting to note that Dryden and Maechello (1970) also reported differences in the relationship between IMF and tenderness between muscles, with a correlation between percentage lipid (dry weight basis) and sensory tenderness of 0.09 for the *semimembranosus* muscles of the same animals. More recent reviews—e.g., that of Aaslyng (2002)—continued to produce evidence on both sides of the argument. Smith and Carpenter (1976) summarized 4 possible mechanisms whereby higher IMF content could directly lead to a reduced perception of toughness or lower resistance to rupture in a mechanical test.

i. Cooked fat is easier to shear than heat-set protein. A high IMF reduces protein density in a specimen presented to a shear test or mouth-sized sample of cooked meat.
ii. Fat deposits within the endomysium and perimysium weaken and loosen the connective tissue after cooking.
iii. The lubricating effect of melted fat during mastication contributes directly to sensory juiciness and indirectly to the sensation of tenderness.
iv. IMF ameliorates the toughing of overcooked meat.

Only the first 2 of these theories provide a physical/structural basis for reduced toughness with high IMF content; the last 2 are related to the strong interdependence of the perceptions of juiciness and tenderness. More recent work has suggested a threshold of 4% to 5% of IMF to obtain satisfactory overall liking (palatability) from consumers (Pannier et al., 2014). Although their work was on lamb, Pannier et al. (2014) cited previous work on lamb, pork, and beef, suggesting a minimum IMF level to achieve acceptable palatability. However, this is not to suggest that a threshold level of IMF is required before it affects tenderness. Pannier et al. (2014) cited Hopkins et al. (2006) as the source of the concept of threshold of 4% to 5% of IMF to obtain satisfactory overall liking; Hopkins et al. (2006) only used the word "threshold" to describe a maximum WBSF value to achieve a given palatability score. There was no mention of thresholds in relation to IMF by Hopkins et al. (2006). Fortin et al. (2005) showed a linear relation between percentage IMF and tenderness in the *longissimus* of pork over the range of 0.7%–2.93% IMF. They stated that their finding of a significant ($P < 0.01$) but weak relationship between percentage IMF and tenderness was in line with a number of previous studies. It is interesting that, although Fortin et al. (2005) graphically showed that the relationship between percentage IMF and all 4 sensory aspects related to tenderness were continuous distributions, they then divided their 85 loins into 5 categories based on cutoff levels of percentage IMF and proceeded to discuss a "threshold level of IMF" for ensuring a positive consumer response based on tenderness. In this context, the idea of threshold values for IMF are simply minimum values for a predicted level of consumer acceptability; they do not imply a level of IMF below which there is no effect on tenderness.

Support for the weakening of intramuscular connective tissue at very high IMF content comes from studies of Japanese Black Wagyu cattle, in which IMF content of greater than 30% in the *longissimus* has been reported (Gotoh et al., 2014). Nishimura et al. (1999) reported that deposition of adipose tissue within *longissimus* with up to 18% IMF disrupts endomysial and perimysial structures and is associated with a decreased shear strength, but that this disruption was not evident in the *semitendinosus* of the same animals. Ueda et al. (2007) showed a correlation between IMF and WBSF on cooked *longissimus* from Japanese Black cattle that suggested that an increase from 5% IMF to 35% IMF is associated with a 1.5 kg/cm^2 reduction in WBSF.

Denaturation of proteins during cooking

Cooking is the final step before consumption and has a significant effect on sensory qualities. The complex changes in the structure of proteins in meat brought about by cooking are reviewed by Tornberg (2005). Heat denaturation causes changes in the structure and properties of the protein components, which drive a series of changes in the water content of muscle tissue, contributing to differences in texture (Hughes et al., 2014).

General denaturation. One approach to understanding changes during cooking is neatly exemplified by Davey and Gilbert (1974). They used the Macfarlane and Marer (1966) bite tenderometer to assess the toughness of beef *sternomandibularis* muscles cooked to 20 different temperatures between 25°C and 100°C. As shown in Figure 1a, they showed a 3- to 4-fold increase in bite force between 40°C and 50°C, followed by a further 2-fold increase in a second phase occurring between 65°C and 75°C. They then associated these 2 toughening phases to known changes in myofibrillar proteins (principally myosin) and collagen with temperature, ascribing the rise in toughness between

40°C and 50°C to denaturation of "the contractile system" (principally myosin) and the second rise between 65°C and 75°C to denaturation and shrinkage of collagen, which they supposed drove water out from the meat. Martens et al. (1982) reinforced essentially the same view when they found a good correspondence between the denaturation temperatures of myosin (40°C–60°C), collagen (56°C–62°C), and actin (66°C–73°C) measured by differential scanning calorimetry and detailed sensory evaluations of tenderness and color. However, this interpretation was at odds with the interpretation of other studies by groups using various configurations of the Warner-Bratzler device. Møller (1981) elegantly demonstrated that the intramuscular connective tissue component dominates WBSF at temperatures up to 60°C, but at higher temperatures, this collagenous contribution drops and WBSF is then dominated by the high resistance of the myofibrillar components. This was the opposite interpretation of the 2 "phases" of toughening on cooking given by Davey and Gilbert (1974) and Martens et al. (1982). Bouton and Harris (1972c) and Harris and Shorthose (1988) confirmed and extended Møller's interpretation. As shown in Figure 2, a comparison of tensile tests on both muscle fibers and perimysial connective tissue isolated from cooked meat to WBSF measures on the same meat demonstrated that the strength of intramuscular connective tissue does indeed increase at low temperatures but falls away after 60°C, whereas the strength of muscle fibers continues to rise above 60°C (Christensen et al., 2000). Later detailed studies of the precise mechanisms of cooking losses have also argued against the interpretation that collagen shrinkage above 60°C is the driving force for shrinkage of muscle fibers (Purslow et al., 2016). Furthermore, recent data show that shrinkage and denaturation occur at different temperatures in red and white muscles as shown in Figure 4 (Vaskoska, 2020).

Collagen. Hamm (1966) hypothesized that the softening and disintegration of meat during cooking is solely due to the formation of gelatin from collagen at a temperature of around 63°C. In agreement with Hamm (1966), many studies have attributed the decrease in shear force around 55°C or 60°C to the solubilization of connective tissue (Machlik and Draudt, 1963; Bouton et al., 1981; Bertola et al., 1994). As collagen denaturation is heating rate dependent, significant collagen denaturation can occur at 58°C to 60°C in long-time, low-temperature (LTLT) cooking (Purslow, 2018; Latorre et al., 2019). Li et al. (2019) showed that the greatest tenderization of pork with LTLT cooking

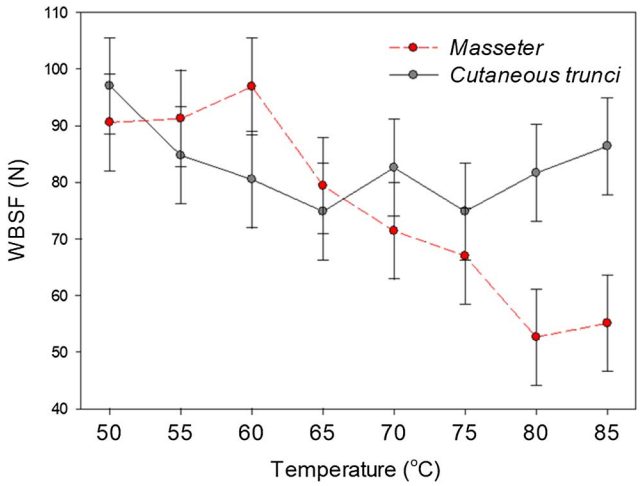

Figure 4. Effect of muscle (*masseter*, 100% type I red oxidative fibers; *cutaneous trunci*, 93% type II oxidative and oxidative glycolytic fibers) and cooking temperature on Warner-Bratzler peak shear force (WBSF). From Vaskoska (2020) with permisssion.

(in this case, 58°C for 30 min) was correlated to the greatest amount of solubilized collagen and reduced perimysium in histological sections of the cooked meat.

Myosin. As discussed earlier, denaturation of proteins occurs at different temperatures during cooking, and these denaturation events can be linked to changes in WBSF with temperature. The denaturation temperature of collagen and actin is fairly consistent and uniform. But in the case of myosin, the thermal sensitivity changes with fiber type and occurs at a lower temperature in muscles with predominantly white type II fibers, such as the *cutaneous trunci*, relative to a muscle that has predominantly red type I fibers, such as the *masseter* (Vaskoska et al., 2020c). Differential scanning calorimetry showed that the myosin peak for the masseter was about 63°C to 64°C and not differentiated from connective tissue, whereas the myosin peak in *cutaneous trunci* was 55°C to 56°C. This difference in the myosin denaturation peak between the muscles was reflected in water-holding capacity and meat tenderness, as shown in Figure 4 for WBSF (Vaskoska, 2020). Although the protein peaks are generally used to identify protein denaturation events, Vaskoska (2020) calculated the total denaturation enthalpy and showed that it was directly related to the WBSF in the *masseter* but not in the *cutaneous trunci*.

Proteolysis. Another possible factor contributing to tenderness of meat is proteolysis during cooking. The role of calpains in development of tenderness during cooking of meat remains largely unreported, most

likely due to calpain inactivation at high temperatures. However, desmin (degradation of which by μ-calpain is a well-established marker of meat tenderization during aging) is degraded further during cooking of porcine *longissimus thoracis et lumborum* (Ertbjerg et al., 2012), suggesting involvement of cathepsins in proteolysis occurring during cooking of meat. Cathepsins are endogenous carboxyl proteases in muscle that have generally been considered to have no contribution, or a minor contribution, to tenderization during aging (see earlier). However, recent studies have suggested that cathepsins remain active during cooking, possibly with increased activity between 53°C and 63°C (Christensen et al., 2011). Injecting prerigor lamb with carboxyl protease inhibitors (pepstatin and 1,2-epoxy-3-(p-nitrophenoxy) propane) resulted in increases in WBSF (from 5.8 to 6.5 kg and from 6.1 to 8.2 kg, respectively) of lamb *longissimus* cooked at 60°C (King and Harris, 1982). Similarly, the activity of cathepsins B + L was negatively correlated ($r = -0.50$) with the WBSF of cooked porcine *longissimus* (Christensen et al., 2011). In addition, inhibition of cathepsins during heating of muscle fiber fragments causes changes in longitudinal and transverse shrinkage, both of which were related to meat tenderness (Vaskoska et al., 2020b). These studies together indicate that cathepsins may contribute to meat tenderness, particularly when cooked under conditions conducive to their proteolytic activity, e.g., LTLT cooking.

It is clear that the mechanisms discussed in this section all interact to determine the tenderness of any specific meat sample and thus should all be evaluated to most accurately interpret their individual impacts on tenderness in an experiment.

Sensory and Consumer Testing

History and developments in sensory research

Since the early 1900s, meat scientists have strived to understand the relationships between meat tenderness and consumer liking. The USDA Beef Quality Grading System, implemented in 1916 (USDA, 2016), was developed to segment beef carcasses into homogeneous groups based on expected palatability. Watkins (1936) presented the concept that animal fatness was related to meat palatability, and he related carcass fatness, meat palatability, and consumer preference. Scott (1939) concluded that tenderness and flavor were important factors related to consumer acceptability and stated that tenderness was the most important consumer sensory attribute and that flavor, while important, was secondary. Around the same time, Macintosh et al. (1936) reported a −0.99 correlation between the newly developed WBSF and tenderness determined by trained evaluators for beef, indicating that lower WBSF values or improved beef tenderness would increase consumer acceptance of beef. Through this early work, the predominant thought that beef tenderness was related to overall consumer acceptance was established. More recent research has shown that, as overall tenderness improved and tenderness variation decreased, flavor has become a more important driver of beef consumer liking.

In contrast to beef, it has been shown in both pork and sheep meat that flavor is the main driver of consumer liking, although, of course, tenderness is also important. One reason for this difference between species is likely because, in general, beef is more variable in tenderness and requires longer aging relative to sheep meat and pork. But also, pork and sheep meat have more variation in flavor, including unacceptable flavors such as boar taint or "piggy" odor in pork (Warner et al., 2018) and "pastoral" or "mutton" odor in sheep meat (Watkins et al., 2013).

Consumer sensory science evolved from Peryam and Swartz (1950), who discussed the use and definition of hedonic scales. While meat scientists did not start using consumer sensory work in the 1950s, Brady (1957) stated that consumer preference had been inferred from laboratory panels or trained sensory panels and advocated research to understand the linkage between consumer research and trained sensory evaluation. One of the first documented extensive consumer sensory studies was conducted by Francis et al. (1977), who used consumers from the Farm Progress Show ($n = 806$) to understand relationships between tenderness and consumer liking in ribeye steaks and found that consumers preferred steaks with higher marbling levels and rated these steaks as juicier, more tender, and more flavorful. However, the relationships between consumer acceptance and beef tenderness were not addressed nationally in the USA until the 1980s. In 1987, Savell et al. (1987) conducted the National Consumer Retail Beef Study. They evaluated consumer preferences in 540 households in 3 cities and showed regional preferences based on marbling level. They also documented that trained and consumer sensory results were similar. In the second phase of the study, Savell et al. (1989) reported that consumers rated steaks across marbling scores for different

reasons, with some preferring the taste of USDA Choice beef and others preferring the leanness of USDA Select beef.

Consumer sensory research in the USA and overseas

From the 1990s, Central Location Tests (CLT) or Home Use Tests (HUT) were used to assess pre- and postharvest factors that affect beef eating quality. Recent examples of using this method worldwide are in Boleman et al. (1997), Robinson et al. (2012), and Garmyn et al. (2014). CLT allow control of the environment, product preparation and presentation, and panelist orientation, but they are conducted in an artificial environment, and therefore some investigators have conducted research in restaurant environments. The HUT approach allows consumers to prepare and evaluate meat in their homes, thus using the same environment where the product is consumed, and this enables information on cooking preparation to be collected. However, the researcher is dependent on consumers to follow directions.

Meat Standards Australia (MSA) went a step further and conducted extensive consumer evaluation to establish an integrated grading system that incorporates pre- and post-harvest factors to predict beef eating quality (Egan et al., 2001; Polkinghorne et al., 2008a, 2008b; Watson et al., 2008; Channon and Warner, 2011). This was the first extensive national grading system to utilize consumer perception as a basis for the segmentation of carcasses and cuts into palatability categories. The MSA consumer evaluation methodology has been used to assess consumer liking across Europe (e.g., Verbeke et al., 2010; Legrand et al., 2013; Morales et al., 2013; Hocquette et al., 2014; Van Wezemael et al., 2014; Guzek et al., 2015; Chong et al., 2019), Asia (e.g., Cho et al., 2007; Hwang et al., 2008; Park et al., 2008; Thompson et al., 2008; Polkinghorne et al., 2011, 2014), and the USA (e.g., O'Quinn et al., 2012; Corbin et al., 2015; Legako et al., 2016). MSA was extended to assuring sheep meat quality in Australia in 2005. However, the pathways for quality assurance for sheep meat are based on a group of animals rather than an individual animal, and the requirements are a lot simpler (Pannier et al., 2018). In a recent comprehensive review, a global perspective was given that while consumers generally respond similarly to differences in tenderness for beef, sheep meat and pork, the flavor is more affected by cultural and environmental factors (Miller, 2020).

Cutoffs for sensory tenderness using Warner-Bratzler shear force

Conducting consumer research allows meat scientists to understand factors that drive consumer preferences and liking, but there are challenges in analyzing and interpreting these data. Consumer research is more variable than trained descriptive sensory data and objective data such as WBSF. As consumers have individual perceptions, they also have different drivers of overall liking and tenderness, allowing segmentation of consumers into groups or categories. If consumer data are analyzed without segmentation, simple correlation relationships between consumer overall liking or tenderness liking and WBSF may be weak. Some research has shown a high correlation between consumer panel ratings for tenderness and instrumental measures of tenderness, particularly WBSF ($r = -0.72$) (Destefanis et al., 2008), while others report a low correlation ($r = -0.26$) (Lorenzen et al., 2003). The extent of the relationship between sensory tenderness/texture assessment and instrumental measures can be dependent on the level of aging, level of tenderness (Perry et al., 2001b), endpoint cooking temperature (Sasaki et al., 2014), and muscle (Shackelford et al., 1995). Consumers consistently scored 14-d-aged beef loins 6 units higher than 1-d-aged beef loins, even when standardized to a similar WBSF value, indicating that consumers detect an additional aspect not measured by WBSF (Perry et al., 2001b). Shackelford et al. (1995) found that the relationship between shear force and sensory tenderness scores ranged from very weak for M. *gluteus maximus* ($r^2 = 0.00$) to strong for M. *longissimus dorsi* ($r^2 = 0.73$). Perry et al. (2001b) showed a quadratic relationship between shear force and sensory tenderness scores and concluded that panelists better discriminate between levels of meat texture in more tender meat (lower values of shear force) than in tougher meat. In this context, Powell et al. (2011) used 7 muscles to examine WBSF thresholds for consumer overall liking and reported no clear thresholds and that consumer ratings were independent of WBSF. On the other hand, Shackelford et al. (1991) suggested WBSF thresholds of 4.6 and 3.9 kg for accurate (>74%) detection of tenderness by trained sensory and consumer panels, respectively. Destefanis et al. (2008) showed that for beef, WBSF values of >5.37 kg and <4.37 kg were perceived by most consumers as "tough" and "tender," respectively. Only consumer sensory panels can be used to report whether a treatment is "tender," and it is inappropriate to use either trained panels or WBSF

for a tenderness "rating" (Wheeler et al., 1997). Wheeler et al. (1997) state that the considerable variation in consumer response for a given shear force value makes a single threshold for acceptability not feasible. Hence, thresholds should not be used for tenderness acceptability. Using consumer testing of beef steaks in restaurants and homes, Huffman et al. (1996) derived a tenderness acceptability cutoff for the WBSF test of 4.1 kg. Wheeler et al. (1997) scrutinized the data and showed that, for the beef steaks rated as "acceptable" in tenderness, the WBSF range was 1.7–5.9, and for the steaks rated as unacceptable, the WBSF range was 3.0–7.9 kg. AMSA (2016) states that—due to the lack of tenderness ratings by consumers—scientists have overinterpreted instrumental measures of tenderness to apply "tough," "tender," or "acceptable" ratings; therefore, they recommend collection of more data. AMSA (2016) recommends that when WBSF data are used to establish premiums, instruments need to be calibrated daily, according to the USA standard American Standards for Testing and Materials (ASTM; www.ASTM.org) F2343. As a consequence of the earlier as well as subsequent discussion, the specifications in ASTM F2925-11 (ASTM, 2011) that a certified "tender" claim can be made for beef with WBSF < 4.4 kg and SSF < 20.0 kg should be reevaluated. Sasaki et al. (2014) recommend that instrumental measurements corresponding to international standards, such as ISO11036:1994 "chewiness" and "hardness" ratings, should be developed for the management and improvement of meat texture by meat producers and industries. Sasaki et al. (2014) also suggested that it is likely that several instrumental measures, rather than just one measure, will be more accurate in predicting the consumer sensory tenderness ratings. This was why the Australian beef and sheep CRC used compression data (derived from TPA, see "Alternatives to WBSF" earlier for description) and WBSF measurements (Perry et al., 2001a; Warner et al., 2010). The Australian MSA system for assurance of beef eating quality has established premiums for high quality and tenderness, using consumers rather than WBSF. Watson et al. (2008) discussed the modeling and statistical analysis techniques used to predict beef eating quality for the MSA system. In general, for global standardization, ISO standards are preferred over local standards such as ASTM.

Analytical tools for sensory

It is apparent that consumer data are much more variable than trained descriptive sensory data; understanding consumer perception is not simple. Data can be analyzed using traditional univariate or multivariate statistical tools. Univariate tools help establish differences in treatments based on consumer sensory attributes, although multivariate tools allow for understanding of relationships and are discussed below.

Multivariate statistical tools used in sensory data analysis include principal component analysis (PCA), partial least squares regression, partial least squares descriptive analysis, and partial least squares linear descriptive analysis. While these tools account for greater amounts of variation in consumer data, they do not always provide predictive equations that are repeatable. One of the underlying issues is that the drivers of liking are not the same for all consumers. Consumer clustering techniques have evolved and are commonly used in marketing or consumer insight research. Segmentation or clustering techniques such as k-means or agglomerative hierarchical clustering, Gaussian mixture models, and univariate clustering can provide a greater understanding of consumers, how to improve prediction of their overall liking, and how to segment consumers into groups based on similarities. These techniques have had minimal use in meat science literature. To demonstrate the strength of such an approach, Miller (2020) re-analyzed data from Luckemeyer (2015) and Laird (2015), using these new statistical tools. First, they showed that consumer sensory attributes and descriptive overall tenderness values were only moderately related to WBSF ($r = -0.42, -0.63$ respectively; $P < 0.05$ for both), whereas consumer attributes of overall liking and tenderness liking were highly correlated ($r = 0.81$; $P < 0.05$). Prediction equations for consumer sensory attributes can be calculated from these simple linear correlations, but the variation accounted for is low. Thus, a PCA multivariate approach was initially used to explain the relationships between consumer liking and WBSF more thoroughly, shown in Figure 5. Figure 5a shows that the 2 factors explain 48% of the model's variation (Factor 1, 34.95%; Factor 2, 12.91%). It is also apparent that the consumer sensory attributes are closely clustered or related to each other and inversely associated with WBSF, establishing a slightly more robust relationship between these variables than reported earlier. When the individual samples are plotted on a PCA biplot, the extensive variability in descriptive and consumer sensory attributes and WBSF between beef samples becomes apparent. Therefore, finally, agglomerative hierarchical clustering analysis was conducted, which identified 8 consumer clusters. Using these

8 consumer categories from the cluster analysis for each observation, data were again analyzed using PCA, and results are shown in Figure 5b.

Categories 1 and 4 closely clustered with consumer sensory attributes for overall tenderness and juiciness liking. For steaks and roasts in categories 2 and 5, tenderness was still important but not as strongly related to overall liking. For steaks and roasts in categories 3 and 6, tenderness was not as big a driver for overall liking, and these steaks and roasts had higher WBSF values, but these 2 categories were segmented based on flavor attributes as well, specifically with bloody/serumy, metallic, liver-like, sour, and cardboardy flavor attributes. These were most likely consumers who preferred

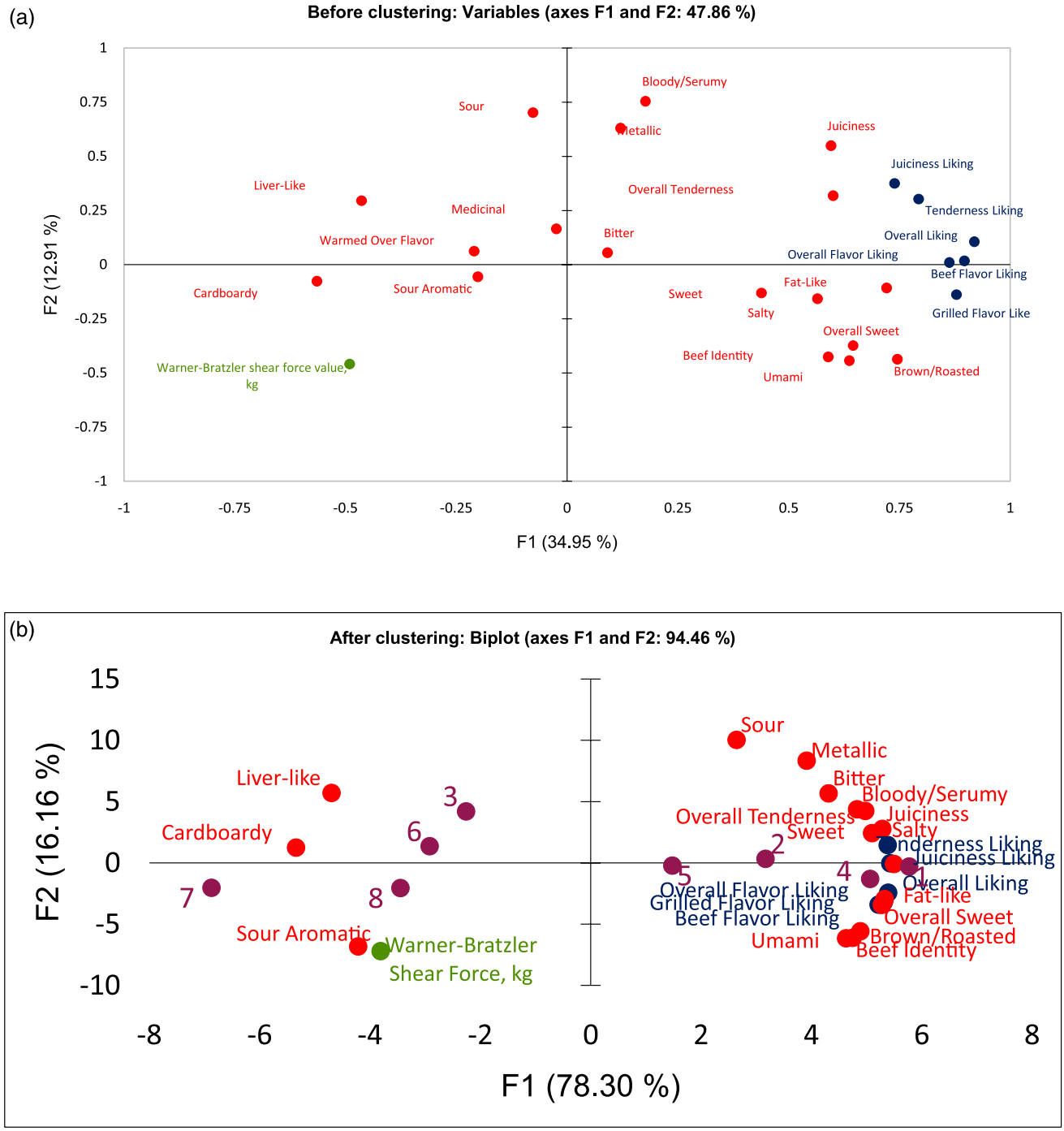

Figure 5. Principal component biplot of data in which descriptive flavor and texture attributes are in red text, Warner-Bratzler shear force values are in green text, and consumer sensory attributes are in blue text. (a) Before hierarchical clustering, (b) after hierarchical clustering, using the 8 agglomerative hierarchical clusters for Warner-Bratzler shear force, kg (ShearAVG), and Overall Consumer Like (OLike) (R. Miller, unpublished results).

beef cooked to lower degrees of doneness with moderate WBSF values. For steaks and roasts in categories 7 and 8, samples were rated lower for overall liking, with steaks and roasts in category 7 having the lowest consumer overall liking scores. However, steaks and roasts in categories 7 and 8 had consumer ratings affected by flavor attributes of fat-like, umami, beef identity, and brown/roasted descriptive flavor attributes. Ninety-five percent of the variation was accounted for in this final analysis with Factor 1, mainly associated with differences in tenderness and WBSF, accounting for 78.3% of the variation, and Factor 2, more closely associated with the effect of positive and negative flavor attributes, accounting for 16.16% of the variation. As shown by the example above, consumer sensory data may be more fully described and interpreted using multiple statistical approaches. The use of different univariate and multivariate tools helped aid understanding of the complexity of the relationships and improve the prediction of consumer liking. Also, consumer segmentation showed that consumers have different drivers for liking, and that consumers vary in their liking of tenderness. While some consumers prefer "tougher" meat, others are driven more by flavor, and these aspects would benefit from further research.

Novel methods to measure consumer response—A way forward

Meat scientists have embraced the use of consumer sensory research to answer questions of consumer liking and acceptance, although most of this research has used CLT and HUT designs and evaluated consumer sensory traits using category or line scales. However, a substantial proportion of consumer decisions are made subconsciously (see review by Torrico et al. [2018]). Therefore, the consumer sensory preferences and liking that are traditionally measured may only account for a small component of factors driving purchasing decisions. The environment also impacts consumer preferences, as discussed earlier and in Meilgaard et al. (2016). Consumer measurement tools have been used in other disciplines to understand consumer liking and drivers of liking more thoroughly. Research has compared consumer liking ratings when conducting sensory evaluation in a CLT conducted in a laboratory or sensory laboratory environment with one conducted in either a simulated or "real" environment (in which the consumer prepares and eats their meals). Results have shown that consumers respond differently in a real versus a simulated environment, as the environment provides sensory responses that may influence the sensory verdict. For example, consumers rated coffee samples that differed in flavor in a laboratory and a coffee shop environment, and responses differed based on the environment. Some sensory laboratories have been developed in which aromatics, sounds, and appearance of the normal consumption environment can be emulated to account for this. Augmented and virtual reality systems have also been used so that consumers see the environment they would be in when consuming the product (Crofton et al. 2019; Sinesio et al., 2019). Some consumer research has been conducted in restaurants to address this issue, but more research is needed to understand how much the environment affects consumer liking for meat products.

Other research tools are available to assess and further understand consumer perception and what drives consumer liking (Huseynov et al., 2018). Emotions have been shown to play a role in consumer perception, but as meat scientists, we have not consistently measured emotions as a component of consumer liking in meat. The reader is referred to the review by Torrico et al. (2018) for biometrics examples to assess some of the unconscious responses and potential application to meat science.

In summary, regardless of the tools used, tenderness is essential to consumers, and consumers can detect tenderness differences. However, consumers vary in their perception and response to tenderness. For most consumers, tenderness and juiciness are linked, as discussed in Perry et al. (2001b) and Miller (2020). Flavor is much more complex than tenderness and juiciness and may affect consumers differently. To more effectively understand consumer perception, meat scientists need to continue to expand the use of new statistical tools, including multivariate analysis, and to use new consumer evaluation tools that assist in estimating consumer emotions and subconscious responses.

Summary and Considerations for Future Research

It is evident that meat tenderness is an important quality for consumers. Tenderness in relation to food texture is generally only used to describe meat. Scientists often use the term meat "tenderness" interchangeably between sensory tenderness and instrumental measurements of tenderness, although some exclusively use the term "texture" for instrumental tenderness measurements. In addition, although the

WBSF test has been adopted globally as the standard instrumental measure of tenderness, the definition of the test varies, and therefore standardization is recommended. The terminology used in the standards developed by the ISO for trained panels and for sensory scales could prove useful in global standardization. The WBSF test applies a combination of tensile, compression, and shear stresses to a meat sample, and the test should be used cautiously when comparing different muscles or samples varying widely in structure. This is because the contribution of connective tissue and myofibrillar strength to the peak force measured in the WBSF varies with cooking temperature, aging, and other structural conditions. In the 1970s and 1980s, the complete force-deformation plot produced by the WBSF test was analyzed to inform about the different structural contributions of the muscle. With innovations in data analysis and biometrics, reconsideration of the whole force-deformation plot may yield new information.

The mechanisms underlying tenderization have been extensively studied, and this review has described them as sarcomere length, myofibril degradation through protease activity, collagen and the cross-links, IMF, and protein denaturation during cooking. These factors all interact to determine the relative tenderness of meat and should be evaluated collectively to accurately interpret their impact on tenderness in any given experiment. Of these, the role of collagen—including newly synthesized collagen—and the role of cathepsin activity during cooking have had less attention and warrant further research. Also, although collagen is challenging to isolate and purify, inclusion in future proteomic studies is warranted. Scientists have sometimes overinterpreted instrumental measures of tenderness and have developed WBSF test cutoffs for "tough" and "tender." A single cutoff value for tenderness no longer seems appropriate due to (1) variation between WBSF methods; (2) variation between samples from different muscles and conditions; (3) variation between consumers; (4) consumer segmentation in the liking for "tough," "chewy," and "tender"; and (5) some consumers being driven by factors other than tenderness, such as flavor. Initial data indicate the influence of the environment on consumer liking, and this requires further research. Finally, to more effectively understand consumer perception, meat scientists need to continue to expand the use of new statistical tools, including multivariate analysis, and to use new consumer evaluation tools that assist in estimating consumer emotions and subconscious responses.

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