

Aging mechanism for improving the tenderness and taste characteristics of meat

Seon-Tea Joo^{1,2}, Eun-Yeong Lee¹, Yu-Min Son¹, Md. Jakir Hossain¹,
Chan-Jin Kim¹, So-Hee Kim¹ and Young-Hwa Hwang^{2*}

¹Division of Applied Life Science (BK21 Four), Gyeongsang National University, Jinju 52828, Korea

²Institute of Agriculture & Life Science, Gyeongsang National University, Jinju 52828, Korea



Received: Sep 22, 2023

Revised: Oct 7, 2023

Accepted: Oct 10, 2023

*Corresponding author

Young-Hwa Hwang

Institute of Agriculture & Life Science,
Gyeongsang National University, Jinju
52828, Korea.

Tel: +82-55-772-1943

E-mail: philoria@gnu.ac.kr

Copyright © 2023 Korean Society of
Animal Sciences and Technology.
This is an Open Access article
distributed under the terms of the
Creative Commons Attribution
Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0/>) which permits unrestricted
non-commercial use, distribution, and
reproduction in any medium, provided
the original work is properly cited.

ORCID

Seon-Tea Joo

<https://orcid.org/0000-0002-5483-2828>

Eun-Yeong Lee

<https://orcid.org/0000-0002-3467-7349>

Yu-Min Son

<https://orcid.org/0000-0002-0793-4055>

Md. Jakir Hossain

<https://orcid.org/0009-0008-7663-9202>

Chan-Jin Kim

<https://orcid.org/0000-0001-5020-6873>

So-Hee Kim

<https://orcid.org/0000-0003-3966-6160>

Yong-Hwa Hwang

<https://orcid.org/0000-0003-3687-3535>

Competing interests

No potential conflict of interest relevant
to this article was reported.

Funding sources

This work was supported by the
National Research Foundation of Korea

Abstract

Tenderness and taste characteristics of meat are the key determinants of the meat choices of consumers. This review summarizes the contemporary research on the molecular mechanisms by which postmortem aging of meat improves the tenderness and taste characteristics. The fundamental mechanism by which postmortem aging improves the tenderness of meat involves the operation of the calpain system due to apoptosis, resulting in proteolytic enzyme-induced degradation of cytoskeletal myofibrillar proteins. The improvement of taste characteristics by postmortem aging is mainly explained by the increase in the content of taste-related peptides, free amino acids, and nucleotides produced by increased hydrolysis activity. This review improves our understanding of the published research on tenderness and taste characteristics of meat and provides insights to improve these attributes of meat through postmortem aging.

Keywords: Aging, Tenderness, Taste characteristics, Proteolysis, Taste-related compounds

INTRODUCTION

The sensory properties such as taste, flavor, and tenderness are among the most important determinants of meat purchase by consumers [1–3]. Several studies have shown that consumers are willing to pay more for better-quality meat [4–6]. Post-slaughter aging is an essential process to enhance the sensory properties of meat through the action of proteolytic systems inherent in meat. Industrially, several methods are used for the aging of meat to enhance its value. These methods range from traditional carcass hanging to storing vacuum-packed meat at refrigerated temperatures for a certain period. In general, two techniques are used for meat aging, i.e., dry-aging and wet-aging. Wet-aging has the advantage of convenience while dry-aging has the advantage of conferring excellent sensory properties [7–9].

Although aging generally improves the sensory properties of meat, the specific conditions for maximizing the sensory properties according to the aging method have not been fully established. Therefore, it is important to investigate the optimal aging conditions by exploring the rate and extent of the aging effect according to the aging method to improve meat quality and value. From that perspective, this review summarizes the underlying molecular mechanisms by which aging induces

(NRF) grant funded by the Korea government (MSIT). (No. 2023R1A2C1004867).

Acknowledgements

Not applicable.

Availability of data and material

Upon reasonable request, the datasets of this study can be available from the corresponding author.

Authors' contributions

Conceptualization: Joo ST, Hwang YH.
Data curation: Joo ST, Lee EY, Hwang YH.
Formal analysis: Hwang YH.
Methodology: Hossain MJ, Kim SH.
Software: Kim CJ.
Validation: Kim SH.
Investigation: Joo ST, Lee EY, Son YM, Hossain MJ, Kim CJ, Kim SH, Hwang YH.
Writing - original draft: Joo ST, Hwang YH.
Writing - review & editing: Joo ST, Lee EY, Son YM, Hossain MJ, Kim CJ, Kim SH, Hwang YH.

Ethics approval and consent to participate

This manuscript does not require IRB/IACUC approval because there are no human and animal participants.

changes in meat quality and discusses the mechanisms and factors for improving the sensory properties of aged meat. During aging, the natural enzymes in the meat break down the proteins and connective tissue, increasing the tenderness of meat [10,11]. Moreover, during the dry-aging process, meat juice is further concentrated in meat and the chemical breakdown of protein and fat constituents creates a more intense nutty and meaty flavor [12]. However, the dry-aging process is more expensive and time-consuming than the wet-aging process due to high aging shrinkage, trim loss, contamination risk, and requirements for aging conditions and space [13,14].

The aging process improves both the tenderness the taste characteristics of meat. The improvement of the savory taste of meat is largely attributable to the increased content of amino acids related to the umami, such as glutamic acid and aspartic acid, caused by proteolysis [15]. With the recent advances in omics analysis techniques, several studies have investigated the mechanism of the breakdown of meat proteins and the increase of taste-related substances due to aging [16–19]; however, the underlying mechanisms are not well characterized. In addition, novel technologies or new aging techniques are being developed and applied to enhance the effect of meat aging [10,11,20,21]. However, there is a lack of review related to the increase in sensory properties. Therefore, this review summarizes the available evidence regarding the molecular mechanism of the degradation of proteins and the changes in meat quality and taste characteristics during postmortem aging.

MECHANISM OF POSTMORTEM AGING ON CHANGES IN MEAT QUALITY

Several reports have described significant biochemical and biophysical changes during muscle conversion to meat, and these changes have a direct effect on meat quality [22–25]. During the postmortem aging process, cytoskeletal myofibrillar protein degradation by endogenous proteases results in significant improvements in the sensory properties of meat [25]. Meat color, water-holding capacity (WHC), tenderness, and texture are the major quality attributes of meat [1]. Tenderness is the most important attribute influencing beef palatability [25,26] while WHC is the most important attribute for the sensory properties of pork [1,27]. Therefore, in this respect, improvements in tenderness and WHC have been extensively studied in beef and pork, respectively, in relation to the development of aging techniques [11,21].

Tenderizing mechanism of postmortem aging

Proteolysis is a major factor in improving meat quality traits such as tenderness and WHC [26,27]. Several factors influence the rate and extent of proteolysis such as species, breed, animal age, diet, individual muscle, marbling content, and aging method [17,28–31]. The effect of aging on the tenderness of beef has long been studied, and many theories have emerged, such as those related to calpain, calcium ion, and cathepsin [32]. Among these theories, the calpain system has received much attention and is considered a major cause of proteolysis during postmortem storage. Proteolysis of myofibrillar proteins has been reported to be the main cause of improvement in meat tenderness during postmortem storage [33]. Specifically, the weakening of Z-disks and degradation of desmin, titin, troponin-T, and nebulin increase the fragility of myofibrils [34–36]. As shown in Fig. 1, the mechanism by which the calpain system affects meat tenderness is summarized into four points. First, calpain weakens the interactions between myofilaments and the Z-disk with the breakdown of titin and nebulin and fractures the I-band and Z-disk in myofibrils, loosening the microstructure of myofibers [35]. Second, the calpain breaks down costamere and desmin, deranging the orderly structure of myofibrils or the integrity between myofibrils and peripheral

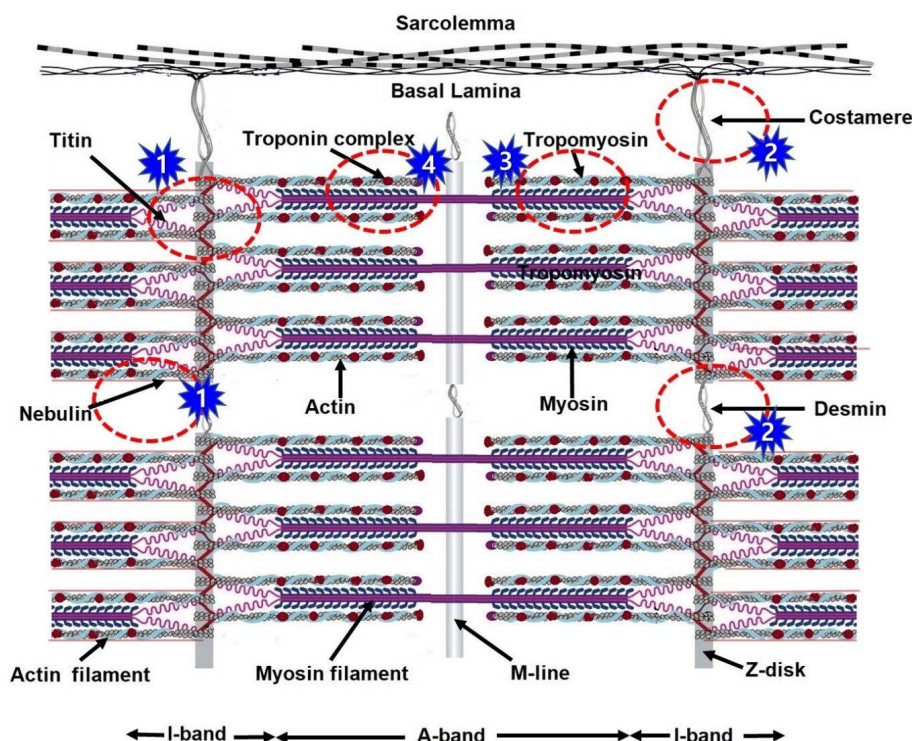


Fig. 1. Schematic illustration of the sites of muscle microstructure collapse due to the activity of muscle proteolytic enzyme calpain during aging. (1) Calpain breaks down the titin connecting myosin filament and Z-disk to loosen the I-band and Z-disk structures of myofibril. (2) Degradation of costamere and desmin by calpain destroys the orderly structure of myofibers and/or the integrity between myofibrils and peripheral muscles. (3) Calpain plays a crucial role in the degradation of tropomyosin, thus weakening the interaction between myosin filaments and actin filaments. (4) Calpain breaks down troponin-T, a troponin subunit that binds to tropomyosin, weakening the structure of actin filaments.

muscles [37]. Third, calpain plays a decisive role in the degradation of tropomyosin, weakening the bond between thick and thin filaments [38]. Fourth, calpain degrades troponin-T, a tropomyosin-binding subunit, weakening the structure of thin actin filaments [39].

In general, there is a rapid change in tenderness between 3 and 7 days postmortem, after which the rate of change in tenderness slows significantly [36,40]. However, in the case of beef produced from innate tough muscles or old cattle muscles, some reports suggest that tenderness may gradually improve up to 28 days postmortem [8,41–43]. The aging-induced improvement in tenderness is attributable to the decrease in mechanical strength of the intramuscular connective tissue due to proteolysis caused by endogenous enzymes [10,44–46]. This decrease in mechanical strength is mainly caused by an increase in collagen solubility and dissociation of the structural integrity of muscle connective tissue [15,47,48]. The strength and structural integrity of collagen fibrils, usually stabilized by proteoglycan, degrade with the progression of postmortem aging. This leads to further exposure of the active sites of potential degradative enzymes, such as lysosomal glycosidase or β -glucuronidase, further weakening the structural integrity and making the meat tender [15].

Recent studies have further clarified the tenderizing mechanism of postmortem aging. A schematic illustration of the newly proposed muscle aging mechanisms is presented in Fig. 2. Tenderizing of postmortem muscle is driven by the calpain system, which depends on the concentration of Ca^{2+} in the sarcoplasm [49], and the increase in Ca^{2+} concentration in postmortem muscle is due to apoptosis [50]. Postmortem aging generates reactive oxygen species (ROS)

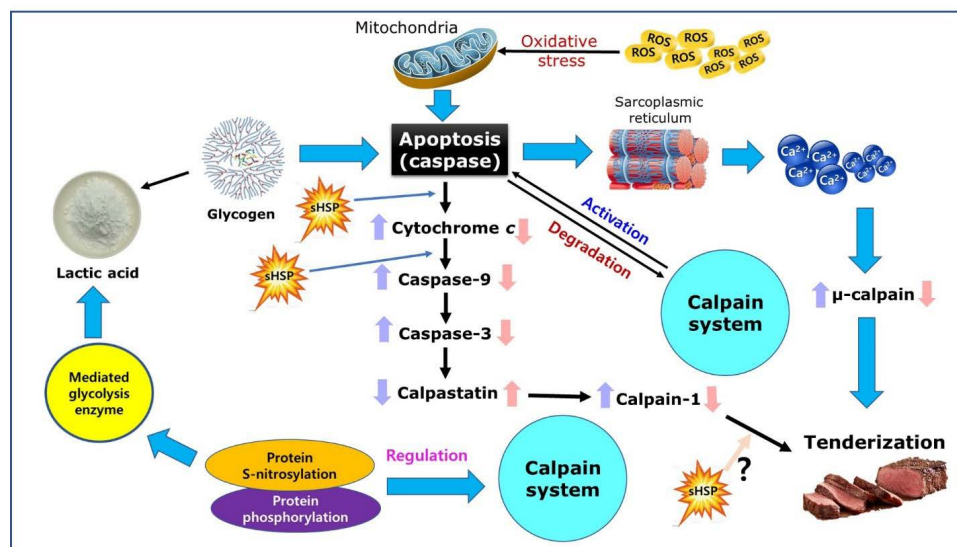


Fig. 2. Schematic illustration of tenderizing mechanism by postmortem aging. (1) The calpain system activated by Ca^{2+} plays a leading role in the process of muscle ageing or tenderization. (2) The apoptotic enzymes participate in the early stages of muscle aging to degrade cytoskeletal myofibrillar proteins such as titin and nebulin and regulate the Ca^{2+} activating enzyme system. (3) Cysteine residues at the calpain active site are modified by protein S-nitrosylation, affecting autolysis and proteolytic activity. (4) The activity of enzymes involved in postmortem glycolysis such as phosphofructokinase, can be inhibited by S-nitrosylation and affects the quality of aged meat.

which induce oxidative stress and apoptosis [51]. Some of the apoptotic proteins released from mitochondria in response to ROS participate in regulating apoptosis [52]. These apoptotic enzymes participate in the early stages of muscle aging, leading to the degradation of titin and nebulin, as well as regulation of the Ca^{2+} -activated enzyme system [53–55]. Activation of apoptotic enzymes such as caspase-3 by denitrification induces apoptosis for myofibril fragmentation, as well as direct proteolytic activity against calpastatin [56–58]. Moreover, chaperone proteins such as small heat shock proteins (sHSPs) have an anti-apoptotic effect [59]. sHSPs delay the postmortem tenderizing process by inhibiting the onset of apoptosis by directly binding to key proteins in the apoptotic cascade such as cytochrome c and caspase-3 [60]. On the other hand, calpain is a cysteine protease, and the cysteine residue at the active site can be modified by protein S-nitrosylation, which consequently affects its autolysis and proteolytic activity [61,62]. Protein S-nitrosylation modifies the release channels of Ca^{2+} , affecting the rate of Ca^{2+} release and resulting in muscle contraction and altered moisture distribution in myofibrils [63]. In addition, S-nitrosylation inhibits the activity of enzymes such as phosphofructokinase involved in postmortem glycolysis, affecting the rate of decline in pH, ultimate pH, and meat quality traits including tenderness [64].

Change in water-holding capacity and meat color during postmortem aging

WHC is one of the most important quality traits of fresh meat because it is closely related to meat color, texture, and tenderness [1,11]. An increase in water loss is unavoidable due to the occurrence of rigor mortis in the process of conversion from muscle to meat. The formation of crosslinks between thick and thin filaments within the myofibrils stiffens the muscle fibers and leads to the extrusion of intracellular water from the myofibrils [65]. Subsequently, with the resolution of rigor and initiation of postmortem aging, intracellular water continues to move to the surface of the meat and is observed in the form of a purge or drip. However, long-term aged

meat often shows improved WHC due to the degradation of proteins. Postmortem proteolysis of structural/cytoskeleton proteins, including desmin, titin, nebulin, and integrin, is associated with the improvement of WHC [66–68]. Changes in the microstructure of muscle fibers during postmortem aging are believed to improve WHC. First, during postmortem aging, degradation of costamere linkages reduces myofibril shrinkage, resulting in more space within muscle fibers to retain water [65,68,69]. In addition, the so-called ‘sponge effect’ occurs wherein the myofibrillar proteins break down and disturb the drip channels, resulting in water trapping within the myofiber [70]. This is the likely underlying mechanism by which aging beef improves the juiciness of steak [8,71,72].

However, the relationship of juiciness of aged meat with tenderness and WHC has not yet been clearly identified. Several studies have shown a positive correlation between sensory tenderness and juiciness [73,74]. Therefore, the improved juiciness of aged meat is likely attributable to the synergistic effect due to the increase in sensory tenderness [10]. Many sensory studies and consumer surveys have reported a positive correlation between tenderness and juiciness of meat; however, the coefficient of determination (R^2) was not high enough and varied depending on the species or muscles [75]. Thus, although there is less correlation between objective shear force measurements and sensory tenderness of cooked meat, a positive correlation between sensory tenderness and juiciness can be inferred. In this respect, some studies have proposed the so-called ‘halo effect’ whereby improved tenderness increases the perception of juiciness, and vice versa [76,77]. Indeed, there is an increase in WHC associated with the swelling of myofibers during postmortem aging, but this does not lead to lower cooking loss [78]. This is because aged meat not only causes pronounced shrinkage of myofibers during cooking but also exhibits a significant decrease in myofibrillar water after cooking. The water lost during cooking is higher in meat aged for at least 3–6 days than unaged meat, but this depends on the aging period [79–81]. Compared to un-aged meat, the increase in cooking loss in aged meat varies depending on the pre-rigor temperature conditions of muscles and sarcomere length [82]. In aged meat, weakened protein structure appears to be unable to retain or trap water during cooking because the swelling of muscle fibers is limited due to the degradation of myofibrillar and cytoskeletal proteins [83]. However, even if the cooking loss of aged meat is high, a recent study showed that juiciness is improved at the same time as the early activation of calpain-2, suggesting that postmortem proteolysis may play a role in improving the juiciness of aged meat [84].

The meat color, color stability, and WHC of meat undergo significant changes during postmortem aging. The surface redness of aged meat is initially improved compared to non-aged meat or relatively short-term aged meat [27,85]. The temporary improvement in the redness of the aged meat surface is due to a decrease in oxygen consumption of respiratory enzymes within mitochondria. However, with the prolongation of the aging period, the oxidative stability of the myoglobin or lipid eventually deteriorates. Extended aging period under lighting conditions of meat retailers accelerates surface discoloration and promotes off-flavor generation [86,87,88]. Even if aging improves the eating quality of meat, discoloration due to metmyoglobin and darkening due to surface dehydration as a result of extended aging will inevitably cause economic losses [89,90]. The negative effect of extended aging on meat color and oxidative stability is due to the accumulation of pro-oxidants (heme and non-heme iron) and the depletion of endogenous reducing compounds (NAD⁺, α -Tocopherol, and β -Carotene) or antioxidants (acylcarnitines, nucleotides, nucleosides, and glucuronides) [91,92,93].

CHANGES IN TASTE CHARACTERISTICS OF MEAT DUE TO AGING

Postmortem aging causes a significant increase in meat flavor. This phenomenon is related to the reducing sugars, the release of free amino acids and peptides, and the increase in the content of inosine monophosphate (IMP), guanosine monophosphate (GMP), inosine, and hypoxanthine due to the breakdown of ribonucleotides [94–96]. In addition, flavor enhancement in aged beef is associated with the production of other flavor-related volatile compounds such as n-aldehydes (e.g., pentanal and hexanal) and ketones, which also contain lipid oxidation-related products [10,12,97]. These flavor precursors interact with each other throughout the cooking process, generating new flavor components [12]. Therefore, the development of meat flavor can be considered as a dynamically evolving process, as illustrated in Fig. 3.

Mechanism of improvement in meat flavor during postmortem aging

The improvement of meat taste characteristics during aging is mainly due to hydrolysis activity. In addition, the activity of various hydrolases such as calpain, which fragments the muscle structure, and cathepsin, which is involved in the production of taste peptides, also plays an important role in improving taste characteristics [95]. During the longer aging period, more taste-related peptides and free amino acids are broken down due to the enzymatic activity in meat. Among them, aliphatic amino acids are related to the sweetness of meat while Cys and Met, containing a sulfur atom, and Glu and Asp are associated with the umami taste [98]. Furthermore, during aging, carbohydrates are broken down into sugars, enhancing the sweetness of meat, and fats and fat-like membrane molecules are broken down into aromatic fatty acids. All these end-products produced during postmortem aging contribute to the intensity of meat aroma, nut-like flavor, and umami taste of cooked aged meat [98,99].

The taste characteristics of aged meat, such as umami intensity or flavor, are not determined by any single factor, but rather by the complex interaction between sulfur-containing amino acids, aspartic acid, glutamic acid, nucleotide compounds, and β -histidyl dipeptides [98,100]. Moreover,

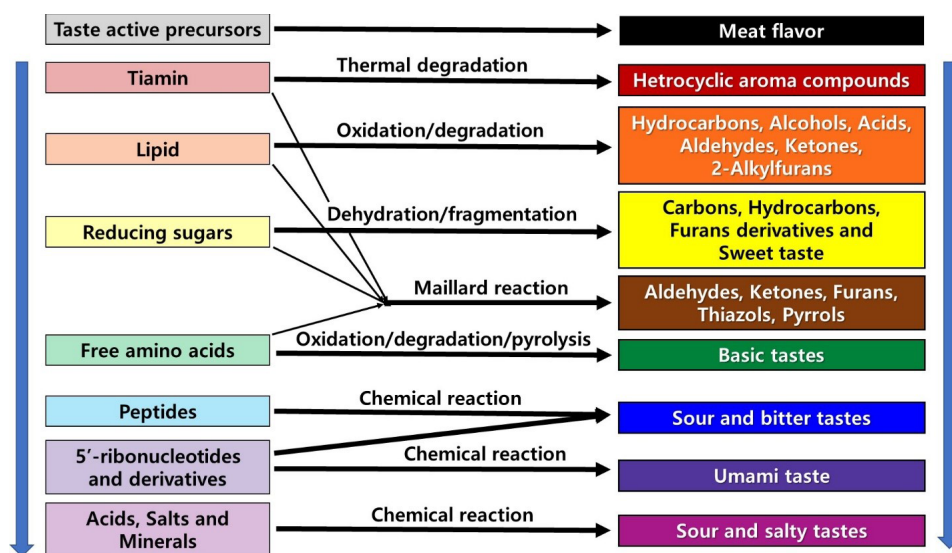


Fig. 3. Schematic representation of meat flavor developing reactions from taste-active water-soluble precursors. Adapted from Dashdorj et al. [98] with permission of Springer Nature.

postmortem energy metabolism also affects the taste of meat by causing an increase in sugar fragments through the degradation of glycogen content, resulting in an increase in the substrate for the Maillard reaction [101]. In addition, prolonging the aging period to > 28 days was found to considerably increase the aromatic volatile compounds [59,102]. While it is generally agreed that aging improves meat flavor, prolonged aging may adversely affect the flavor. Aging of beef for 4 days at 4°C desirably improves the sweetness and beefy flavor; however, further prolongation of the aging time may increase undesirable taste characteristics such as bitterness and sourness [95]. In addition, on prolonged aging, free fatty acids (FFAs) that are easy to oxidize are released, which react with proteins and other flavor precursors to negatively affect the aroma and/or flavor of aged meat [103]. Therefore, controlling the appropriate aging method is necessary to maximize the desirable taste and flavor of aged meat and minimize the off-flavor and off-odor.

Formation of taste-enhancing peptides by aging

Several peptides that are released during proteolysis in aging meat affect the taste characteristics. These peptides show different taste characteristics depending on the specific size (i.e., fraction). The small peptides (< 5 kDa) that are most noticeable and reproducible during postmortem aging are fragments of troponin T, nebulin, pro-collagen, and cipher proteins [104–106]. In particular, 1- to 5-kDa peptides, so-called Maillard peptides, and 3- to 10-kDa peptides were found to improve the flavor and taste intensity of grilled beef [107,108]. In addition, 1- to 10-kDa and 0.5- to 1-kDa fractions significantly inhibit the sourness of beef and pork [109,110].

In the past few decades, many peptides related to the taste characteristics of meat have been reported. The content of oligopeptides increases during the refrigerated aging of meat. Among the oligopeptides, glutamic acid especially improves the savory taste of beef [111]. Octapeptide (Lys-Gly-Asp-Glu-Glu-Ser-Leu-Ala), called “beefy meaty peptide”, also occurs naturally during postmortem aging and is responsible for the delicious taste of beef [112]. In addition, the peptides (Glu-Glu, Glu-Val, Ala-Asp-Glu, Ala-Glu-Asp, Asp-Glu-Glu, and Ser-Pro-Glu) found in chicken are related to umami intensity, and the peptides (Glu-Asp-Glu, Asp-Glu-Ser, and Ser-Glu-Glu) found in fish hydrolysates are related to savory taste [113]. The peptide (Ala-Pro-Pro-Pro-Ala-Glu-Val-His-Glu-Val) found in pork suppresses sourness [110].

On the other hand, there is no clear consensus on the effect of naturally occurring dipeptides produced during aging on the taste characteristics. These dipeptides include carnosine, β -alanyl-L-histidine; anserine, β -alanyl-L-1-methylhistidine; balenine, β -alanyl-L-3-methylhistidine. Some studies have found a positive effect of these dipeptides on the taste characteristics of meat [114]. However, other reports suggest that anserine and carnosine produce bitterness if the presence of glutamic acid oligomers such as Glu-Leu, Pro-Glu, and Val-Glu is not effective in masking the bitter taste [115]. In addition, some dipeptides may indirectly affect the taste characteristics of meat. For example, carnosine and histidine, including dipeptide anserine, destroy unsaturated aldehydic products, reducing the lipid oxidation products and minimizing the rancidity in meat [116].

Studies have investigated the interrelationship between peptides and taste characteristics using various model systems. One such study evaluated the taste of synthesized oligopeptides containing Phe, Tyr, and Leu and found that hydrophobic residues in the peptides function as a bitter taste determinant site. Moreover, the intensity of its bitterness increased when the hydrophobic amino acid with the L-configuration was located at the C terminus and the number of hydrophobic amino acids at the C-terminal increased [117]. In addition, as a result of identifying amino acid compositions and amino acid sequences by separating two peptide fractions from a commercial beef extract as a macromolecular meaty flavor enhancer, it was confirmed that two peptides were composed of collagen and tropomyosin [118]. These results suggested that collagen and

tropomyosin are precursors of the macromolecular meaty flavor enhancer. Studies involving other types of meat have identified different strips of amino acids responsible for the unique taste of individual meats. This means that the function of small peptides that affect the taste characteristics of meat depends on the type of meat (i.e., species or muscles).

Production of free amino acids during postmortem aging

Free amino acids (FAAs), which are related to improving the taste of meat, show dramatic changes during postmortem aging. Many studies have reported concentrated taste-activated compounds produced during the aging of meat; of these, FAAs in particular, are cited as a major contributor to the taste of aged meat [98]. Dry aging offers a great advantage in this regard as it can promote an increase in the FAA content. This increased FAA content directly increases the flavor of the meat. In addition, as a Maillard reaction and a Strecker degradation substrate, FAAs react to form aroma-active components and affect various taste characteristics [119]. For example, glutamine, alanine, glycine, methionine, and serine are related to sweetness, while leucine, isoleucine, phenylalanine, tyrosine, and valine are related to bitterness. Furthermore, cysteine, methionine, and glutamic acid are associated with umami, while aspartic acid and histidine are associated with sourness [120]. Some amino acids have more than one taste characteristic. Valine has a combination of bitterness and slight sweetness, threonine and lysine have sweetness, slight bitterness, and sourness, and aspartic acid has both sourness and sweetness [94, 120]. As shown in Fig. 3, all these water-soluble metabolites affect the flavor of cooked meat to some extent as precursors to the Maillard reaction or by themselves.

In general, dry-aging of beef increases the content of FAAs such as leucine, phenylalanine, valine, tyrosine, glutamate, and tryptophan compared to wet-aging [119]. In addition, the FAA content increases with the decrease in the moisture content of dry-aged beef; however, FAAs such as glycine, arginine, and alanine decrease with the decrease in moisture content. Therefore, the increase in FAA content in dry-aged beef cannot be entirely explained by the changes in moisture content. Rather, the greater content of taste-active compounds in dry-aged beef compared to wet-aged beef is likely attributable to the concentration effect of moisture evaporation. Studies have shown that the difference in the concentration of metabolites and the rate of protein degradation due to the evaporation of moisture can increase the FAA content [120,121].

Two main mechanisms promote the production of FAAs during postmortem aging: proteolytic enzyme activity and microbial activity. The proteolytic enzymes that cause hydrolysis of proteins include endonucleases (such as calpain and cathepsin) and exonucleases (such as peptidase and aminopeptidase) that release amino peptidase C and H from muscles [122–124]. However, the endogenous enzymes in dry-aged beef can be inactivated with an extension of the aging time. Therefore, further hydrolysis of protein in dry-aged beef may be related to the action of microorganisms in the dry-aging process [119]. In a study, dry-aging of beef for 28 days led to a significant increase in mold distribution from 1.22% to 11.67%, which improved the flavor and tenderness [125]. This is because the growth of mold and yeast during the dry-aging process can induce additional proteolysis of dry-aged beef by activating muscle aminopeptidase and/or proteolytic enzymes [126,127]. The growth of beneficial molds or fungi during dry-aging of beef releases protease and collagenase, and breaks down myofibrillar proteins and connective tissue to improve the taste and flavor of meat.

Changes in taste-related chemicals during postmortem aging

One of the most notable chemicals in relation to changes in taste of aged meat is nucleotides. In particular, disodium 5-inosinate (5'-IMP) and disodium 5-guanosinate (5'-GMP), the so-

called taste nucleotides, have a positive effect on meat taste and umami intensity [128,129]. IMP is widely known to improve the flavor and palatability of meat. The IMP content changes during postmortem aging. Therefore, changes in meat taste during aging are related to changes in IMP content, especially glutamic acid and aspartic acid, which have a synergistic effect on amplifying the umami intensity [15,99,130, 131]. In a study, the change in flavor intensity of high-marbling beef was consistent with the change in umami intensity [122].

The aging method also affects the extent of change in the IMP content. Therefore, the taste of meat varies considerably depending on the aging method. The IMP content in beef decreases rapidly during dry-aging compared to wet-aging [119,120,128]. Dry-aging increases the activity of enzymes related to IMP degradation, reducing IMP content which can negatively affect the taste of meat. Furthermore, in dry-aged beef, hypoxanthine produced by further degradation of IMP increases the bitterness of meat [119]. On the other hand, low-temperature aging not only greatly increases the IMP content but also induces the formation of GMP, resulting in a significant increase in the saltiness and umami intensity of chicken and pork. However, the changes in IMP and GMP in cooked beef were found to be minimal or even undetectable [98].

The content of reducing sugars, which provides a desirable sweetness for meat, is lower in wet-aged beef than in dry-aged beef [124]. Beef contains reducing sugars, such as glucose, fructose, and ribose, which are formed by glycolysis and adenosine triphosphate (ATP) degradation [98]. These reducing sugars not only confer sweetness but also react with amino acids to produce volatile flavor components. For example, ribose and cysteine form many sulfur compounds by the Maillard reaction [98]. Maillard reaction refers to the reaction between a carbonyl compound (such as reducing sugars) and an amino compound (such as amino acids or proteins). This reaction produces sulfur and nitrogen compounds, such as pyrazine, resulting in the formation of brown or even black macromolecular substance melanoid or pseudomelanins [110]. The final product of the Maillard reaction varies depending on the substrate and affects the taste of meat. For example, cysteine and glucose mainly produce sulfide, while cysteine and glucose produce more pyrazines and furans under oxidative conditions [132]. Glutathione and glucose have a meat-like taste if they cause a thermal reaction, with or without chicken fat/oxidized chicken fat [133]. With the prolongation of the aging period of beef, the content of two sulfur compounds (methyl mercaptan and dimethyl disulfide) and one pyrazine (2-methyl pyrazine) showed a significant increase [134]. These sulfur compounds and pyrazine have a low odor detection threshold and play an important role in the flavor and taste of cooked beef.

CONCLUSION

Many studies have shown that the aging of meat improves both the tenderness of meat and the taste characteristics by producing taste-related substances. The fundamental mechanism by which aging improves the tenderness of meat involves the operation of the calpain system due to apoptosis, resulting in proteolytic enzyme-induced degradation of cytoskeletal myofibrillar proteins. The improvement of taste characteristics by aging is mainly explained by an increase in the content of taste-related peptides, free amino acids, and nucleotides produced by increased hydrolysis activity. However, the method or conditions of aging greatly influence the improvement of the tenderness and/or taste characteristics of meat. More robust studies on meat aging are required to obtain optimal tenderness and taste of different types of meat.

REFERENCES

1. Joo ST, Kim GD, Hwang YH, Ryu YC. Control of fresh meat quality through manipulation of muscle fiber characteristics. *Meat Sci.* 2013;95:828-36. <https://doi.org/10.1016/j.meatsci.2013.04.044>
2. Savell JW, Branson RE, Cross HR, Stiffler DM, Wise JW, Griffin DB, et al. National consumer retail beef study: palatability evaluations of beef loin steaks that differed in marbling. *J Food Sci.* 1987;52:517-9. <https://doi.org/10.1111/j.1365-2621.1987.tb06664.x>
3. Park S, Kim N, Kim W, Moon J. The effect of Korean native chicken breed information on consumer sensory evaluation and purchase behavior. *Food Sci Anim Resour.* 2022;42:111-27. <https://doi.org/10.5851/kosfa.2021.e67>
4. Polkinghorne RJ, Thompson JM. Meat standards and grading: a world view. *Meat Sci.* 2010;86:227-35. <https://doi.org/10.1016/j.meatsci.2010.05.010>
5. Bonny SPF, Hocquette JF, Pethick DW, Legrand I, Wierzbicki J, Allen P, et al. Review: the variability of the eating quality of beef can be reduced by predicting consumer satisfaction. *Animal.* 2018;12:2434-42. <https://doi.org/10.1017/S1751731118000605>
6. Makweya FL, Oluwatayo IB. Consumers' preference and willingness to pay for graded beef in Polokwane municipality, South Africa. *Ital J Food Saf.* 2019;8:7654. <https://doi.org/10.4081/ijfs.2019.7654>
7. Kim SJ, Kim GH, Moon C, Ko KB, Choi YM, Choe JH, et al. Effects of aging methods and periods on quality characteristics of beef. *Food Sci Anim Resour.* 2022;42:953-67. <https://doi.org/10.5851/kosfa.2022.e63>
8. Tuell JR, Nondorf MJ, Kim YHB. Post-harvest strategies to improve tenderness of underutilized mature beef: a review. *Food Sci Anim Resour.* 2022;42:723-43. <https://doi.org/10.5851/kosfa.2022.e33>
9. Terjung N, Witte F, Heinz V. The dry aged beef paradox: why dry aging is sometimes not better than wet aging. *Meat Sci.* 2021;172:108355. <https://doi.org/10.1016/j.meatsci.2020.108355>
10. Kim YHB, Ma D, Setyabrata D, Farouk MM, Lonergan SM, Huff-Lonergan E, et al. Understanding postmortem biochemical processes and post-harvest aging factors to develop novel smart-aging strategies. *Meat Sci.* 2018;144:74-90. <https://doi.org/10.1016/j.meatsci.2018.04.031>
11. Lee EY, Rathnayake D, Son YM, Bakhsh A, Hwang YH, Seo JK, et al. Effect of novel high-intensity ultrasound technique on physio-chemical, sensory attributes, and microstructure of bovine semitendinosus muscle. *Food Sci Anim Resour.* 2023;43:85-100. <https://doi.org/10.5851/kosfa.2022.e60>
12. Dashdorj D, Tripathi VK, Cho S, Kim Y, Hwang IH. Dry aging of beef; review. *J Anim Sci Technol.* 2016;58:20. <https://doi.org/10.1186/s40781-016-0101-9>
13. Kim JH, Kim TK, Shin DM, Kim HW, Kim YB, Choi YS. Comparative effects of dry-aging and wet-aging on physicochemical properties and digestibility of Hanwoo beef. *Asian-Australas J Anim Sci.* 2020;33:501-5. <https://doi.org/10.5713/ajas.19.0031>
14. Kim JH, Kim JH, Yoon DK, Ji DS, Jang HJ, Lee CH. A comparison of dry and wet aging on physicochemical and sensory characteristics of pork loin with two aging times. *Food Sci Biotechnol.* 2018;27:1551-9. <https://doi.org/10.1007/s10068-018-0418-x>
15. Nishimura T. Mechanism involved in the improvement of meat taste during postmortem aging. *Food Sci Technol Int.* 1998;4:241-9. <https://doi.org/10.3136/fsti9596t9798.4.241>
16. Wang Y, Liu X, Wang Y, Zhao G, Wen J, Cui H. Metabolomics-based analysis of the major

- taste contributors of meat by comparing differences in muscle tissue between chickens and common livestock species. *Foods*. 2022;11:3586. <https://doi.org/10.3390/foods11223586>
17. Jin SK, Yim DG. Influences of aging methods and temperature on meat quality of pork belly from purebred Berkshire and crossbred Landrace × Yorkshire × Duroc (LYD) pigs. *Food Sci Anim Resour*. 2022;43:398–410. <https://doi.org/10.5851/kosfa.2022.e7>
 18. Lana A, Longo V, Dalmasso A, D'Alessandro A, Bottero MT, Zolla L. Omics integrating physical techniques: aged Piedmontese meat analysis. *Food Chem*. 2015;172:731–41. <https://doi.org/10.1016/j.foodchem.2014.09.146>
 19. Ji C, You L, Luo R. Proteomics and metabolomics combined study on endopathic changes of water-soluble precursors in Tan lamb during postmortem aging. *Food Sci Nutr*. 2022;10:1564–78. <https://doi.org/10.1002/fsn3.2780>
 20. Zhang R, Yoo MJY, Ross AB, Farouk MM. Mechanisms and strategies to tailor dry-aged meat flavour. *Trends Food Sci Technol*. 2022;119:400–11. <https://doi.org/10.1016/j.tifs.2021.12.023>
 21. Eastwood LC, Arnold AN, Miller RK, Gehring KB, Savell JW. Novel approach to aging beef: vacuum-packaged foodservice steaks versus vacuum-packaged subprimals. *Meat Sci*. 2016;116:230–5. <https://doi.org/10.1016/j.meatsci.2016.02.012>
 22. Huff Lonergan E, Zhang W, Lonergan SM. Biochemistry of postmortem muscle - lessons on mechanisms of meat tenderization. *Meat Sci*. 2010;86:184–95. <https://doi.org/10.1016/j.meatsci.2010.05.004>
 23. Kim YHB, Warner RD, Rosenvold K. Influence of high pre-rigor temperature and fast pH fall on muscle proteins and meat quality: a review. *Anim Prod Sci*. 2014;54:375–95. <https://doi.org/10.1071/AN13329>
 24. Cheng H, Song S, Park TS, Kim GD. Comparison of meat quality characteristics and proteolysis trends associated with muscle fiber type distribution between duck Pectoralis major and Iliotibialis muscle. *Food Sci Anim Resour*. 2022;42:266–79. <https://doi.org/10.5851/kosfa.2022.e2>
 25. Kemp CM, Sensky PL, Bardsley RG, Buttery PJ, Parr T. Tenderness - an enzymatic view. *Meat Sci*. 2010;84:248–56. <https://doi.org/10.1016/j.meatsci.2009.06.008>
 26. Robbins K, Jensen J, Ryan KJ, Homco-Ryan C, McKeith FK, Brewer MS. Consumer attitudes towards beef and acceptability of enhanced beef. *Meat Sci*. 2003;65:721–9. [https://doi.org/10.1016/S0309-1740\(02\)00274-7](https://doi.org/10.1016/S0309-1740(02)00274-7)
 27. Hwang YH, Sabikun N, Ismail I, Joo ST. Changes in sensory compounds during dry aging of pork cuts. *Food Sci Anim Resour*. 2019;39:379–87. <https://doi.org/10.5851/kosfa.2019.e29>
 28. Park J Song S, Cheng H, Im C, Jung EY, Moon SS, et al. Comparison of meat quality and muscle fiber characteristics between porcine skeletal muscles with different architectures. *Food Sci Anim Resour*. 2022;42:874–88. <https://doi.org/10.5851/kosfa.2022.e40>
 29. Bratcher CL, Johnson DD, Littell RC, Gwartney BL. The effects of quality grade, aging, and location within muscle on Warner-Bratzler shear force in beef muscles of locomotion. *Meat Sci*. 2005;70:279–84. <https://doi.org/10.1016/j.meatsci.2005.01.013>
 30. Smith RD, Nicholson KL, Nicholson JDW, Harris KB, Miller RK, Griffin DB, et al. Dry versus wet aging of beef: retail cutting yields and consumer palatability evaluations of steaks from US Choice and US Select short loins. *Meat Sci*. 2008;79:631–9. <https://doi.org/10.1016/j.meatsci.2007.10.028>
 31. Zhao Y, Chen L, Bruce HL, Wang Z, Roy BC, Li X, et al. The influence of vacuum packaging of hot-boned lamb at early postmortem time on meat quality during postmortem chilled storage. *Food Sci Anim Resour*. 2022;42:816–32. <https://doi.org/10.5851/kosfa.2022.e34>

32. Shi H, Shahidi F, Wang J, Huang Y, Zou Y, Xu W, et al. Techniques for postmortem tenderisation in meat processing: effectiveness, application and possible mechanisms. *Food Prod Process Nutr.* 2021;3:21. <https://doi.org/10.1186/s43014-021-00062-0>
33. Koohmaraie M. Muscle proteinases and meat aging. *Meat Sci.* 1994;36:93-104. [https://doi.org/10.1016/0309-1740\(94\)90036-1](https://doi.org/10.1016/0309-1740(94)90036-1)
34. Shackelford SD, Wheeler TL, Meade MK, Reagan JO, Byrnes BL, Koohmaraie M. Consumer impressions of Tender Select beef. *J Anim Sci.* 2001;79:2605-14. <https://doi.org/10.2527/2001.79102605x>
35. Tanabe R, Tatsumi R, Takahashi K. Purification and characterization of the 1, 200-kDa subfragment of connectin filaments produced by 0.1 mM calcium ions. *J Biochem.* 1994;115:351-5. <https://doi.org/10.1093/oxfordjournals.jbchem.a124341>
36. Koohmaraie M, Geesink GH. Contribution of postmortem muscle biochemistry to the delivery of consistent meat quality with particular focus on the calpain system. *Meat Sci.* 2006;74:34-43. <https://doi.org/10.1016/j.meatsci.2006.04.025>
37. Uytterhaegen L, Claeys E, Demeyer D. Effects of exogenous protease effectors on beef tenderness development and myofibrillar degradation and solubility. *J Anim Sci.* 1994;72:1209-23. <https://doi.org/10.2527/1994.7251209x>
38. Takahashi K, Nakamura F, Hattori A, Yamanoue M. Paratropomyosin: a new myofibrillar protein that modifies the actin-myosin interaction in postrigor skeletal muscle. I. Preparation and characterization. *J Biochem.* 1985;97:1043-51. <https://doi.org/10.1093/oxfordjournals.jbchem.a135146>
39. Whipple G, Koohmaraie M. Effects of lamb age, muscle type, and 24-hour activity of endogenous proteinases on postmortem proteolysis. *J Anim Sci.* 1992;70:798-804. <https://doi.org/10.2527/1992.703798x>
40. Colle MJ, Richard RP, Killinger KM, Bohlscheid JC, Gray AR, Loucks WI, et al. Influence of extended aging on beef quality characteristics and sensory perception of steaks from the biceps femoris and semimembranosus. *Meat Sci.* 2016;119:110-7. <https://doi.org/10.1016/j.meatsci.2016.04.028>
41. Campbell RE, Hunt MC, Levis P, Chambers E4th. Dry-aging effects on palatability of beef longissimus muscle. *J Food Sci.* 2001;66:196-9. <https://doi.org/10.1111/j.1365-2621.2001.tb11315.x>
42. Phelps KJ, Drouillard JS, Silva MB, Miranda LDF, Ebarb SM, Van Bibber-Krueger CL, et al. Effect of extended postmortem aging and steak location on myofibrillar protein degradation and Warner-Bratzler shear force of beef M. semitendinosus steaks. *J Anim Sci.* 2016;94:412-23. <https://doi.org/10.2527/jas.2015-9862>
43. Santos C, Moniz C, Roseiro C, Tavares M, Medeiros V, Afonso I, et al. Effects of early post-mortem rate of pH fall and aging on tenderness and water holding capacity of meat from cull dairy Holstein-Friesian cows. *J Food Res.* 2016;5:1-12. <https://doi.org/10.5539/jfr.v5n2p1>
44. Lewis GJ, Purslow PP, Rice AE. The effect of conditioning on the strength of perimysial connective tissue dissected from cooked meat. *Meat Sci.* 1991;30:1-12. [https://doi.org/10.1016/0309-1740\(91\)90029-P](https://doi.org/10.1016/0309-1740(91)90029-P)
45. Wu JJ, Dutson TR, Carpenter ZL. Effect of postmortem time and temperature on the release of lysosomal enzymes and their possible effect on bovine connective tissue components of muscle. *J Food Sci.* 1981;46:1132-5. <https://doi.org/10.1111/j.1365-2621.1981.tb03008.x>
46. Purslow PP. New developments on the role of intramuscular connective tissue in meat toughness. *Annu Rev Food Sci Technol.* 2014;5:133-53. <https://doi.org/10.1146/annurev-food-030212-182628>

47. Nishimura T, Fang S, Ito T, Wakamatsu J, Takahashi K. Structural weakening of intramuscular connective tissue during postmortem aging of pork. *Anim Sci J*. 2008;79:716-21. <https://doi.org/10.1111/j.1740-0929.2008.00585.x>
48. Bakhsh A, Hwang YH, Joo ST. Effect of slaughter age on muscle fiber composition, intramuscular connective tissue, and tenderness of goat meat during post-mortem time. *Foods*. 2019;8:571. <https://doi.org/10.3390/foods8110571>
49. Stamler JS, Lamas S, Fang FC. Nitrosylation: the prototypic redox-based signaling mechanism. *Cell*. 2001;106:675-83. [https://doi.org/10.1016/s0092-8674\(01\)00495-0](https://doi.org/10.1016/s0092-8674(01)00495-0)
50. Huang M, Huang F, Xue M, Xu X, Zhou G. The effect of active caspase-3 on degradation of chicken myofibrillar proteins and structure of myofibrils. *Food Chem*. 2011;128:22-7. <https://doi.org/10.1016/j.foodchem.2011.02.062>
51. Zhang J, Ma G, Guo Z, Yu Q, Han L, Han M, et al. Study on the apoptosis mediated by apoptosis-inducing-factor and influencing factors of bovine muscle during postmortem aging. *Food Chem*. 2018;266:359-67. <https://doi.org/10.1016/j.foodchem.2018.06.032>
52. Desagher S, Martinou JC. Mitochondria as the central control point of apoptosis. *Trends Cell Biol*. 2000;10:369-77. [https://doi.org/10.1016/s0962-8924\(00\)01803-1](https://doi.org/10.1016/s0962-8924(00)01803-1)
53. Huang F, Ding Z, Zhang C, Hu H, Zhang L, Zhang H. Effects of calcium and zinc ions injection on caspase-3 activation and tenderness in post-mortem beef skeletal muscles. *Int J Food Sci Technol*. 2018;53:582-9. <https://doi.org/10.1111/ijfs.13631>
54. Kaur L, Hui SX, Morton JD, Kaur R, Chian FM, Boland M. Endogenous proteolytic systems and meat tenderness: influence of post-mortem storage and processing. *Food Sci Anim Resour*. 2021;41:589-607. <https://doi.org/10.5851/kosfa.2021.e27>
55. Wang LL, Yu QL, Han L, Ma XL, Song RD, Zhao SN, et al. Study on the effect of reactive oxygen species-mediated oxidative stress on the activation of mitochondrial apoptosis and the tenderness of yak meat. *Food Chem*. 2018;244:394-402. <https://doi.org/10.1016/j.foodchem.2017.10.034>
56. Wu W, Wan OW, Chung KKK. S-nitrosylation of XIAP at Cys 213 of BIR2 domain impairs XIAP's anti-caspase 3 activity and anti-apoptotic function. *Apoptosis*. 2015;20:491-9. <https://doi.org/10.1007/s10495-015-1087-3>
57. Mandic A, Viktorsson K, Strandberg L, Heiden T, Hansson J, Linder S, et al. Calpain-mediated Bid cleavage and calpain-independent Bak modulation: two separate pathways in cisplatin-induced apoptosis. *Mol Cell Biol*. 2002;22:3003-13. <https://doi.org/10.1128/MCB.22.9.3003-3013.2002>
58. Pörn-Ares MI, Samali A, Orrenius S. Cleavage of the calpain inhibitor, calpastatin, during apoptosis. *Cell Death Differ*. 1998;5:1028-33. <https://doi.org/10.1038/sj.cdd.4400424>
59. Ba HV, Reddy BV, Hwang I. Role of calpastatin in the regulation of mRNA expression of calpain, caspase, and heat shock protein systems in bovine muscle satellite cells. *In Vitro Cell Dev Biol Anim*. 2015;51:447-54. <https://doi.org/10.1007/s11626-014-9849-8>
60. Cramer T, Penick ML, Waddell JN, Bidwell CA, Kim YHB. A new insight into meat toughness of callipyge lamb loins - the relevance of anti-apoptotic systems to decreased proteolysis. *Meat Sci*. 2018;140:66-71. <https://doi.org/10.1016/j.meatsci.2018.03.002>
61. Hou Q, Liu R, Tian X, Zhang W. Involvement of protein S-nitrosylation in regulating beef apoptosis during postmortem aging. *Food Chem*. 2020;326:126975. <https://doi.org/10.1016/j.foodchem.2020.126975>
62. Li Y, Liu R, Zhang W, Fu Q, Liu N, Zhou G. Effect of nitric oxide on μ -calpain activation, protein proteolysis, and protein oxidation of pork during post-mortem aging. *J Agric Food Chem*. 2014;62:5972-7. <https://doi.org/10.1021/jf501332d>

63. Wang H, Viatchenko-Karpinski S, Sun J, Györke I, Benkusky NA, Kohr MJ, et al. Regulation of myocyte contraction via neuronal nitric oxide synthase: role of ryanodine receptor S-nitrosylation. *J Physiol*. 2010;588:2905-17. <https://doi.org/10.1113/jphysiol.2010.192617>
64. Liu R, Li Y, Wang M, Zhou G, Zhang W. Effect of protein S-nitrosylation on autolysis and catalytic ability of μ -calpain. *Food Chem*. 2016;213:470-7. <https://doi.org/10.1016/j.foodchem.2016.06.104>
65. Huff-Lonergan E, Lonergan SM. Mechanisms of water-holding capacity of meat: the role of postmortem biochemical and structural changes. *Meat Sci*. 2005;71:194-204. <https://doi.org/10.1016/j.meatsci.2005.04.022>
66. Kristensen L, Purslow PP. The effect of ageing on the water-holding capacity of pork: role of cytoskeletal proteins. *Meat Sci*. 2001;58:17-23. [https://doi.org/10.1016/S0309-1740\(00\)00125-X](https://doi.org/10.1016/S0309-1740(00)00125-X)
67. Lawson MA. The role of integrin degradation in post-mortem drip loss in pork. *Meat Sci*. 2004;68:559-66. <https://doi.org/10.1016/j.meatsci.2004.05.019>
68. Zhang WG, Lonergan SM, Gardner MA, Huff-Lonergan E. Contribution of postmortem changes of integrin, desmin and μ -calpain to variation in water holding capacity of pork. *Meat Sci*. 2006;74:578-85. <https://doi.org/10.1016/j.meatsci.2006.05.008>
69. Ge Y, Zhang D, Zhang H, Li X, Fang F, Liang C, et al. Effect of postmortem phases on lamb meat quality: a physicochemical, microstructural and water mobility approach. *Food Sci Anim Resour*. 2021;41:802-15. <https://doi.org/10.5851/kosfa.2021.e37>
70. Farouk MM, Mustafa NM, Wu G, Krsinic G. The “sponge effect” hypothesis: an alternative explanation of the improvement in the waterholding capacity of meat with ageing. *Meat Sci*. 2012;90:670-7. <https://doi.org/10.1016/j.meatsci.2011.10.012>
71. Go HY, Park SY, Kim HY. Analysis of quality after sous vide of pork loin wet-aged using pulsed electric field system. *Food Sci Anim Resour*. 2023;43:412-27. <https://doi.org/10.5851/kosfa.2023.e3>
72. Campo MM, Sañudo C, Panea B, Alberti P, Santolaria P. Breed type and ageing time effects on sensory characteristics of beef strip loin steaks. *Meat Sci*. 1999;51:383-90. [https://doi.org/10.1016/S0309-1740\(98\)00159-4](https://doi.org/10.1016/S0309-1740(98)00159-4)
73. Guzek D, Głabska D, Wierzbicka A, Wierzbicki J, Cierach M. Relationship between basic beef texture attributes and their perception by Polish consumers. *Ital J Food Sci*. 2012;24:231-9.
74. Song Z, Hwang I. Objective meat quality from quality grade and backfat thickness of Hanwoo steers. *Food Sci Anim Resour*. 2023;43:531-9. <https://doi.org/10.5851/kosfa.2023.e15>
75. Hughes JM, Oiseth SK, Purslow PP, Warner RD. A structural approach to understanding the interactions between colour, water-holding capacity and tenderness. *Meat Sci*. 2014;98:520-32. <https://doi.org/10.1016/j.meatsci.2014.05.022>
76. Jenkins KH, Vasconcelos JT, Hinkle JB, Furman SA, de Mello AS Jr, Senaratne LS, et al. Evaluation of performance, carcass characteristics, and sensory attributes of beef from finishing steers fed field peas. *J Anim Sci*. 2011;89:1167-72. <https://doi.org/10.2527/jas.2009-2552>
77. Roeber DL, Gill RK, DiCostanzo A. Meat quality responses to feeding distiller's grains to finishing Holstein steers. *J Anim Sci*. 2005;83:2455-60. <https://doi.org/10.2527/2005.83102455x>
78. Straadt IK, Rasmussen M, Andersen HJ, Bertram HC. Aging-induced changes in microstructure and water distribution in fresh and cooked pork in relation to water-holding capacity and cooking loss – a combined confocal laser scanning microscopy (CLSM) and low-field nuclear magnetic resonance relaxation study. *Meat Sci*. 2007;75:687-95. <https://doi.org/10.1016/j.meatsci.2007.05.008>

- org/10.1016/j.meatsci.2006.09.019
79. Shanks BC, Wulf DM, Maddock RJ. Technical note: the effect of freezing on Warner-Bratzler shear force values of beef longissimus steaks across several postmortem aging periods. *J Anim Sci*. 2002;80:2122-5. <https://doi.org/10.1093/ansci/80.8.2122>
 80. Warner RD, Ferguson DM, Cottrell JJ, Knee BW. Acute stress induced by the preslaughter use of electric prodders causes tougher beef meat. *Aust J Exp Agric*. 2007;47:782-8. <https://doi.org/10.1071/EA05155>
 81. Jo K, Lee S, Jeong HG, Lee DH, Yoon S, Chung Y, et al. Utilization of electrical conductivity to improve prediction accuracy of cooking loss of pork loin. *Food Sci Anim Resour*. 2023;43:113-23. <https://doi.org/10.5851/kosfa.2022.e64>
 82. Warner RD, Kerr M, Kim YHB, Geesink G. Pre-rigor carcass stretching counteracts the negative effects of high rigor temperature on tenderness and water-holding capacity – using lamb muscles as a model. *Anim Prod Sci*. 2014;54:494-503. <https://doi.org/10.1071/AN13062>
 83. Wu Z, Bertram HC, Kohler A, Böcker U, Ofstad R, Andersen HJ. Influence of aging and salting on protein secondary structures and water distribution in uncooked and cooked pork. A combined FT-IR microspectroscopy and ¹H NMR relaxometry study. *J Agric Food Chem*. 2006;54:8589-97. <https://doi.org/10.1021/jf061576w>
 84. Colle MJ, Nasados JA, Rogers JM, Kerby DM, Colle MM, Van Buren JB, et al. Strategies to improve beef tenderness by activating calpain-2 earlier postmortem. *Meat Sci*. 2018;135:36-41. <https://doi.org/10.1016/j.meatsci.2017.08.008>
 85. Abdullah AY, Qudsieh RI. Effect of slaughter weight and aging time on the quality of meat from Awassi ram lambs. *Meat Sci*. 2009;82:309-16. <https://doi.org/10.1016/j.meatsci.2009.01.027>
 86. Kim YHB, Frandsen M, Rosenvold K. Effect of ageing prior to freezing on colour stability of ovine longissimus muscle. *Meat Sci*. 2011;88:332-7. <https://doi.org/10.1016/j.meatsci.2010.12.020>
 87. Pouzo LB, Descalzo AM, Zaritzky NE, Rossetti L, Pavan E. Antioxidant status, lipid and color stability of aged beef from grazing steers supplemented with corn grain and increasing levels of flaxseed. *Meat Sci*. 2016;111:1-8. <https://doi.org/10.1016/j.meatsci.2015.07.026>
 88. Lee SH, Kim HY. Analysis of quality and color properties according to the gas composition (modified atmosphere packaging) of pork sous-vide ham preserved in natural brine. *Food Sci Anim Resour*. 2023;43:580-93. <https://doi.org/10.5851/kosfa.2023.e20>
 89. Kim YHB, Stuart A, Rosenvold K, MacLennan G. Effect of forage and retail packaging types on meat quality of long-term chilled lamb loins. *J Anim Sci*. 2013;91:5998-6007. <https://doi.org/10.2527/jas.2013-6780>
 90. Kim HJ, Kim HJ, Kim KW, Lee J, Lee SH, Lee SS, et al. Effect of feeding alfalfa and concentrate on meat quality and bioactive compounds in Korean native black goat loin during storage at 4°C. *Food Sci Anim Resour*. 2022;42:517-35. <https://doi.org/10.5851/kosfa.2022.e21>
 91. Ma D, Kim YHB, Cooper B, Oh JH, Chun H, Choe JH, et al. Metabolomics profiling to determine the effect of postmortem aging on color and lipid oxidative stabilities of different bovine muscles. *J Agric Food Chem*. 2017;65:6708-16. <https://doi.org/10.1021/acs.jafc.7b02175>
 92. Descalzo AM, Rossetti L, Sancho AM, García PT, Biolatto A, Carduza F, et al. Antioxidant consumption and development of oxidation during ageing of buffalo meat produced in Argentina. *Meat Sci*. 2008;79:582-8. <https://doi.org/10.1016/j.meatsci.2007.10.020>

93. Yu HH, Yi SH, Lim SD, Hong SP. The effect of vacuum films on physicochemical and microbiological characteristics of Hanwoo (Korean native cattle). *Food Sci Anim Resour.* 2023;43:441-53. <https://doi.org/10.5851/kosfa.2023.e8>
94. Mottram DS. Flavour formation in meat and meat products: a review. *Food Chem.* 1998;62:415-24. [https://doi.org/10.1016/S0308-8146\(98\)00076-4](https://doi.org/10.1016/S0308-8146(98)00076-4)
95. Spanier AM, Flores M, McMillin KW, Bidner TD. The effect of post-mortem aging on meat flavor quality in Brangus beef. Correlation of treatments, sensory, instrumental and chemical descriptors. *Food Chem.* 1997;59:531-8. [https://doi.org/10.1016/S0308-8146\(97\)00003-4](https://doi.org/10.1016/S0308-8146(97)00003-4)
96. Aung SH, Abeyrathne EDNS, Hossain MA, Jung DY, Kim HC, Jo C, et al. Comparative quality traits, flavor compounds, and metabolite profile of Korean native black goat meat. *Food Sci Anim Resour.* 2023;43:639-58. <https://doi.org/10.5851/kosfa.2023.e25>
97. Utama DT, Jang A, Kim GY, Kang SM, Lee SK. Distinguishing aroma profile of highly-marbled beef according to quality grade using electronic nose sensors data and chemometrics approach. *Food Sci Anim Resour.* 2022;42:240-51. <https://doi.org/10.5851/kosfa.2021.e75>
98. Dashdorj D, Amna T, Hwang I. Influence of specific taste-active components on meat flavor as affected by intrinsic and extrinsic factors: an overview. *Eur Food Res Technol.* 2015;241:157-71. <https://doi.org/10.1007/s00217-015-2449-3>
99. Nishimura T, Rhue MR, Okitani A, Kato H. Components contributing to the improvement of meat taste during storage. *Agric Biol Chem.* 1988;52:2323-30. <https://doi.org/10.1080/00021369.1988.10869028>
100. Xu L, Liu S, Cheng Y, Qian H. The effect of aging on beef taste, aroma and texture, and the role of microorganisms: a review. *Crit Rev Food Sci Nutr.* 2023;63:2129-40. <https://doi.org/10.1080/10408398.2021.1971156>
101. Martins SIFS, Jongen WM, van Boekel MAJS. A review of Maillard reaction in food and implications to kinetic modelling. *Trends Food Sci Technol.* 2000;11:364-73. [https://doi.org/10.1016/S0924-2244\(01\)00022-X](https://doi.org/10.1016/S0924-2244(01)00022-X)
102. Watanabe A, Kamada G, Imanari M, Shiba N, Yonai M, Muramoto T. Effect of aging on volatile compounds in cooked beef. *Meat Sci.* 2015;107:12-9. <https://doi.org/10.1016/j.meatsci.2015.04.004>
103. Wang Q, Zhao X, Ren Y, Fan E, Chang H, Wu H. Effects of high pressure treatment and temperature on lipid oxidation and fatty acid composition of yak (*Poephagus grunniens*) body fat. *Meat Sci.* 2013;94:489-94. <https://doi.org/10.1016/j.meatsci.2013.03.006>
104. Sylvestre MN, Feidt C, Brun-Bellut J. Post-mortem evolution of non-protein nitrogen and its peptide composition in growing lamb muscles. *Meat Sci.* 2001;58:363-9. [https://doi.org/10.1016/S0309-1740\(01\)00029-8](https://doi.org/10.1016/S0309-1740(01)00029-8)
105. Bauchart C, Rémond D, Chambon C, Patureau Mirand P, Savary-Auzeloux I, Reynès C, et al. Small peptides (<5kDa) found in ready-to-eat beef meat. *Meat Sci.* 2006;74:658-66. <https://doi.org/10.1016/j.meatsci.2006.05.016>
106. Moya VJ, Flores M, Aristoy MC, Toldrá F. Pork meat quality affects peptide and amino acid profiles during the ageing process. *Meat Sci.* 2001;58:197-206. [https://doi.org/10.1016/S0309-1740\(00\)00152-2](https://doi.org/10.1016/S0309-1740(00)00152-2)
107. Claeys E, De Smet S, Balcaen A, Raes K, Demeyer D. Quantification of fresh meat peptides by SDS-PAGE in relation to ageing time and taste intensity. *Meat Sci.* 2004;67:281-8. <https://doi.org/10.1016/j.meatsci.2003.11.001>
108. Ogasawara M, Katsumata T, Egi M. Taste properties of Maillard-reaction products prepared from 1000 to 5000 Da peptide. *Food Chem.* 2006;99:600-4. <https://doi.org/10.1016/j.foodchem.2005.08.040>

109. Ishii K, Tsuchida M, Nishimura T, Okitani A, Nakagawa A, Hatae K, et al. Changes in the taste and taste components of beef during heating at a low temperature for a long time. *J Home Econ Jpn.* 1995;46:229-34. <https://doi.org/10.11428/jhej1987.46.229>
110. Okumura T, Yamada R, Nishimura T. Sourness-suppressing peptides in cooked pork loins. *Biosci Biotechnol Biochem.* 2004;68:1657-62. <https://doi.org/10.1271/bbb.68.1657>
111. Henriksen AP, Stahnke LH. Sensory and chromatographic evaluations of water soluble fractions from dried sausages. *J Agric Food Chem.* 1997;45:2679-84. <https://doi.org/10.1021/jf960792>
112. Yamasaki Y, Maekawa K. A peptide with delicious taste. *Agric Biol Chem.* 1978;42:1761-5. <https://doi.org/10.1271/bbb1961.42.1761>
113. Noguchi M, Arai S, Yamashita M, Kato H, Fujimaki M. Isolation and identification of acidic oligopeptides occurring in a flavor potentiating fraction from a fish protein hydrolysate. *J Agric Food Chem.* 1975;23:49-53. <https://doi.org/10.1021/jf60197a003>
114. Pereira-Lima C, Ordoñez JA, García de Fernando GD, Cambero MI. Influence of heat treatment on carnosine, anserine and free amino acid composition of beef broth and its role in flavour development. *Eur Food Res Technol.* 2000;210:165-72. <https://doi.org/10.1007/PL00005506>
115. Liu Y, Xu XL, Zhou G. Changes in taste compounds of duck during processing. *Food Chem.* 2007;102:22-6. <https://doi.org/10.1016/j.foodchem.2006.03.034>
116. Gianelli MP, Flores M, Toldrá F. Interactions of soluble peptides and proteins from skeletal muscle on the release of volatile compounds. *J Agric Food Chem.* 2003;51:6828-34. <https://doi.org/10.1021/jf0303666>
117. Ishibashi N, Sadamori K, Yamamoto O, Kanehisa H, Kouge K, Kikuchi E, et al. Bitterness of phenylalanine- and tyrosine-containing peptides. *Agric Biol Chem.* 1987;51:3309-13. <https://doi.org/10.1080/00021369.1987.10868574>
118. Mottram DS. Some aspects of the chemistry of meat flavour. In: Shahidi F, editor. *Flavor of meat and meat products*. Boston, MA: Springer; 1994. p. 210-30.
119. Lee HJ, Choe J, Kim M, Kim HC, Yoon JW, Oh SW, et al. Role of moisture evaporation in the taste attributes of dry- and wet-aged beef determined by chemical and electronic tongue analyses. *Meat Sci.* 2019;151:82-8. <https://doi.org/10.1016/j.meatsci.2019.02.001>
120. Kim YHB, Kemp R, Samuelsson LM. Effects of dry-aging on meat quality attributes and metabolite profiles of beef loins. *Meat Sci.* 2016;111:168-76. <https://doi.org/10.1016/j.meatsci.2015.09.008>
121. Koutsidis G, Elmore JS, Oruna-Concha MJ, Campo MM, Wood JD, Mottram DS. Water-soluble precursors of beef flavour. Part II: effect of post-mortem conditioning. *Meat Sci.* 2008;79:270-7. <https://doi.org/10.1016/j.meatsci.2007.09.010>
122. Iida F, Miyazaki Y, Tsuyuki R, Kato K, Egusa A, Ogoshi H, et al. Changes in taste compounds, breaking properties, and sensory attributes during dry aging of beef from Japanese black cattle. *Meat Sci.* 2016;112:46-51. <https://doi.org/10.1016/j.meatsci.2015.10.015>
123. Kim DG, Lee SH, Kim GH, Ko KB, Ryu YC. Meat quality changes in aged pork loin using Jeju volcanic scoria earthenware. *Food Sci Anim Resour.* 2023;43:901-13. <https://doi.org/10.5851/kosfa.2023.e46>
124. Toldrá F, Flores M. The role of muscle proteases and lipases in flavor development during the processing of dry-cured ham. *Crit Rev Food Sci Nutr.* 1998;38:331-52. <https://doi.org/10.1080/10408699891274237>
125. Oh J, Lee HJ, Yoon JW, Choe J, Jo C. Electrical resistance and mold distribution on beef surface as indicators of dry aging. *J Food Process Eng.* 2019;42:e13122. <https://doi.org/10.1111/jfpe.13122>

- p>org/10.1111/jfpe.13122
126. Lee HJ, Yoon JW, Kim M, Oh H, Yoon Y, Jo C. Changes in microbial composition on the crust by different air flow velocities and their effect on sensory properties of dry-aged beef. *Meat Sci.* 2019;153:152-8. <https://doi.org/10.1016/j.meatsci.2019.03.019>
127. Kim SG, Kim HY. Effect of the types of starter on microbiological and physicochemical properties of dry-cured ham. *Food Sci Anim Resour.* 2023;43:454-70. <https://doi.org/10.5851/kosfa.2023.e9>
128. Zhan H, Hayat K, Cui H, Hussain S, Ho CT, Zhang X. Characterization of flavor active non-volatile compounds in chicken broth and correlated contributing constituent compounds in muscle through sensory evaluation and partial least square regression analysis. *LWT.* 2020;118:108786. <https://doi.org/10.1016/j.lwt.2019.108786>
129. Hwang YH, Ismail I, Joo ST. Identification of umami taste in sous-vide beef by chemical analyses, equivalent umami concentration, and electronic tongue system. *Foods.* 2020;9:251. <https://doi.org/10.3390/foods9030251>
130. Joo ST, Choi JS, Hur SJ, Kim GD, Kim CJ, Lee EY, et al. A comparative study on the taste characteristics of satellite cell cultured meat derived from chicken and cattle muscles. *Food Sci Anim Resour.* 2022;42:175-85. <https://doi.org/10.5851/kosfa.2021.e72>
131. Kwon JA, Yim DG, Kim HJ, Ismail A, Kim SS, Lee HJ, et al. Effect of temperature abuse on quality and metabolites of frozen/thawed beef loins. *Food Sci Anim Resour.* 2022;42:341-9. <https://doi.org/10.5851/kosfa.2022.e9>
132. Calkins CR, Hodgen JM. A fresh look at meat flavor. *Meat Sci.* 2007;77:63-80. <https://doi.org/10.1016/j.meatsci.2007.04.016>
133. Zhao J, Wang T, Xie J, Xiao Q, Cheng J, Chen F, et al. Formation mechanism of aroma compounds in a glutathione-glucose reaction with fat or oxidized fat. *Food Chem.* 2019;270:436-44. <https://doi.org/10.1016/j.foodchem.2018.07.106>
134. Ba HV, Park KM, Dashmaa D, Hwang I. Effect of muscle type and vacuum chiller ageing period on the chemical compositions, meat quality, sensory attributes and volatile compounds of Korean native cattle beef. *Anim Sci J.* 2014;85:164-73. <https://doi.org/10.1111/asj.12100>