THE FLEXIBILITY OF THE COLLAGEN COMPARTMENT OF MUSCLE

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INTRODUCTION

The connective tissue network of skeletal muscle, consisting predominantly of the protein collagen, forms a structural matrix which provides form and support for the cellular components of muscle and a means of transmitting and absorbing force generated by muscle contraction. An alignment of collagen molecules that allows both fibril formation and their stabilization by covalent crosslinks confers tensile strength on the collagen matrix and is a factor contributing to the texture of meat.

There are three morphologically distinct collagen depots in muscle: the epimysium, the connective tissue sheath surrounding individual muscles; the perimysium, a three dimensional collagen network surrounding large and small bundles of muscle fibers, and which contains lipid deposits (marbling) and muscle vasculature; and the endomysium, a layer of connective tissue encircling individual muscle fibers. The collagen concentration in most muscles is low compared to other tissues, 2-6 percent of total dry weight (DRANSFIELD, 1977). The epimysium is generally easily separated from the body of the muscle and need not be considered as a factor in meat texture. Perimysium and endomysium, connective tissues not practically separated from meat, comprise the intramuscular connective tissue (IMC). Perimysium comprises the vast bulk of IMC, about 90% (LIGHT AND CHAMPION, 1984), and is generally held to be the main contributor to variations in connective tissue-related meat quality (LIGHT et al., 1985). The role endomysium plays in alterations in meat texture is less well understood (LIGHT et al., 1985). However, significant changes in muscle cell diameter and expression of fluid upon heating have been attributed to shrinkage of the endomysium and associated basement membrane (BENDALL AND RESTALL, 1983).

A basis for the role collagen plays in determining cooked meat texture was suggested initially by the observations of DAVEY and GILBERT (1975) which documented a biphasic increase in the toughening of meat as temperature increased. In a series of elegant histological and mechanical experiments, BENDALL and RESTALL (1983) demonstrated step-wise, temperature-dependent increases in tension development and shrinkage which occurred in both single muscle fibers (endomysium) and muscle fiber bundles (perimysium). The factors responsible for development of force, tension, compression and toughening in cooked meat, include variable amounts of collagen (DRANSFIELD, 1977) and collagen crosslinking (BAILEY, 1989). The importance of collagen characteristics, termed collagen quality, in determining the eating properties of meat are widely recognized (BAILEY, 1988). Less well-understood are factors which influence the molecular and biochemical processes responsible for variations in muscle collagen characteristics. This brief review focuses on aspects of collagen biosynthesis and experimental data which indicate the collagens of muscle possess a remarkable capacity for plasticity.

COLLAGEN BIOSYNTHESIS AND COLLAGEN PROTEIN

Collagen, like all proteins, is synthesized intracellularly; however, newly synthesized collagen molecules are secreted from the cells in which they were produced and function extracellularly. Collagen biosynthesis is, thus, divided into events which occur intracellularly and those which happen outside the cell (for review see NIMNI and HARKNESS, 1988). Sequentially, major

intracullular events include a) expression of discrete collagen genes followed by synthesis of specific mRNA for the diff procollagen alpha chains; b) message translation and subsequent enzymatic hydroxylation of selected proline and lysine residues glycosylation of specific hydroxylysine residues; c) molecule folding and triple helix formation and d) proteolytic excision o terminal propeptides as the processed collagen molecule is transported through the cell membrane to the extracellular space. Syn and modifying steps result in a triple helical molecule, flanked by short non-helical regions, with a repeating GLY-X-Y sequ where X or Y is often proline or hydroxyproline. Fibrillar collagens are about one-third glycine and one-quarter proline hydroxyproline with a molecular weight of about 300,000. Once in the extracellular space, collagen molecules align themselves microfibrils, in quarter stagger array; crosslinking is initiated and larger diameter fibrils are formed either by the additi microfibrils or by association with other fibrils. Covalent crosslinking continues as fibers grow and age. It is apparent that coll biosynthesis is a complicated process which entails extremely complex post-translational processing of molecules.

PHENOTYPIC COMPOSITION OF MUSCLE COLLAGENS

Fourteen collagen types, the alpha chains of which are the products of at least 25 discrete genes, have so far been iden (VAN DER REST and GARRONE, 1991). The fibril-forming collagen types I and III comprise the vast bulk of IMC col (BAILEY et al., 1979; LIGHT and CHAMPION, 1984) with small amounts of type V collagen also associated with the fi Basement membrane consists primarily of type IV collagen and likely some type VII collagen occurring as "anchoring fi connecting the basement membrane to the overlying endomysium (TIMPL, 1989). The role that the quantitatively "minor colla i.e., types IV, V and VII, play in meat texture remains obscure. The variation in proportion of types I and III collagen in m and its relationship to meat texture has been investigated, although results are not conclusive and often contradictory.

For example, in studies with cattle, increased proportions of type III collagen in the IMC have been associated in instances with tougher muscles (BAILEY et al., 1979), in others with more tender muscles (BURSON and HUNT, 1986), and i others with no change in meat texture (LIGHT et al., 1985; LIGHT, 1987). Intuitively, one would expect decreasing prop of type III collagen to be associated with increased muscle toughening. Type III collagen is generally considered the embryo precursor form in fibrillar collagens consisting of types I and III. Fetal or neonatal tissues are rich sources of type III collage in most tissues including skeletal muscle, there is a general shift with chronological aging to increased proportions of type I co (KOVANEN and SUOMINEN, 1989). Type III collagen fibrils are likewise smaller in diameter than type I collagen fibrils sug they should pose less resistance to shear force (BAILEY, 1988). However, type III collagen also possesses a few disulfide (unlike the other fibrillar collagens) and in cooked meat is apparently less heat soluble than type I collagen (BURSON and H 1986b), factors which may in part account for its association with negative textural changes in muscle.

Our present inability to elucidate the relationships between phenotypic variations in IMC and meat texture are certainly to only rudimentary understanding of fibril composition. Most tissues, including muscle, contain more than one collagen ty recently has it become evident that collagen fibrils themselves (termed heterotypic fibrils) may contain mixtures of collage Molecules of different collagen types associate in mixed fibrils via reducible and non-reducible lysine aldehyde-derived cr For example, in cartilage, a tissue containing fibrils composed of types II, IX and XI collagens, the proportions of reducible reducible crosslinks vary with collagen molecule type and crosslink location (WU and EYRE, 1989). Evidence that

crosslinking pattern, i.e., degree of maturation of reducible to non-reducible crosslinks, depends upon the specific association of different collagen species within a fibril has been reported (ROBINS and DUNCAN, 1983). Biochemical, as well as immunofluorescence studies, indicate that type I and III collagens also occur together in the same fibril (RAMSHAW, 1986; KEENE et al., 1987; FLEISCHMAJER et al., 1990). Lysine aldehyde-derived covalent crosslinks linking types I and III molecules in human leiomyoma and calf aorta have been documented (HENKEL and GLANVILLE, 1982). Concerning the connective tissue of muscles, attempts to relate phenotype composition to textural attributes are limited by the absence of data indicating how these collagens associate within the fibrils, and how extensively crosslinked they may be. We have observed a significant increase in the proportion of type III collagen in the longissimus dorsi muscle of growing rams compared to wethers, an increase which was also correlated with significantly higher crosslink concentrations and shear force scores for the rams (MAIORANO et al., 1992). On the other hand, decreasing amounts of type III collagen have been associated with increased crosslinking in the skeletal muscles of rats (KOVANEN and SUOMINEN, 1989; KOVANEN, 1991). Variation in IMC phenotype composition is a poor predictor of meat tenderness or toughness because there can be either a positive or a negative correlation with crosslink concentration in the same muscle.

CROSSLINK BIOSYNTHESIS

Structural, biochemical and physiological aspects of collagen crosslinking are detailed in several comprehensive reviews (EYRE et al., 1984; YAMAUCHI and MECHANIC, 1988; REISER et al., 1992). Crosslinking is initiated by the oxidative deamination via the enzyme lysyl oxidase of specific lysines or hydroxylysines which produces peptidyl aldehydes, termed allysine or hydroxyallysine, respectively. The head-to-tail lateral alignment of collagen molecules in a quarter-stagger array allows the aldehyde functions to react with other peptidyl aldehydes or unmodified lysine or hydroxylysine residues on adjacent alpha chains. The initial condensation products form reducible crosslinks, so named because they contain Schiff base double bonds which can be reductively labelled. There are two major pathways by which crosslinks form: the first, the allysine pathway which is based on lysine aldehydes and produces aldimine crosslinks; the second, the hydroxyallysine pathway, produces crosslinks arising from hydroxylysine aldehydes. Amadori rearrangement of the initial aldimine crosslinks formed between lysine and hydroxylysine aldehydes can produce ketoamine derivatives (EYRE et al., 1984). The reducible crosslinks vary in their stability, with ketoamine crosslinks being heat stable and aldemine crosslinks heat labile (ALLAIN et al., 1978). Crosslinking in collagen is a progressive process, and the reducible crosslinks undergo further reactions and are replaced with mature non-reducible crosslinks. In the hydroxyallysine pathway a mature non-reducible crosslink which has been identified is hydroxypyridinium (HP).

Initial studies by BAILEY and co-workers (BAILEY, 1989) demonstrated the presence of reducible crosslinks in IMC, and the relationship of toughening in cooked muscle to the concentration of heat resistant ketoamine crosslinks. We have most frequently utilized the mature non-reducible crosslink HP to follow variations in muscle collagen crosslinking. HP residues apparently arise from the condensation of two ketoamine crosslinks (EYRE et al., 1984), a mechanism of formation which is confirmed by the stoichiometric relationship between the disappearance of ketoamine molecules and the appearance of HP (LAST et al., 1989). Further, because the reducible crosslinks are transient, their concentration in tissue diminishes as collagen ages or matures. Thus, an inverse relationship can, and often does exist between degree of mature crosslinking and the measured concentration of reducible crosslinks. Unlike other tissues such as lung (LAST et al., 1989), the progression of crosslink formation along the hydroxyallysine pathway in skeletal muscle

is rapid. As illustrated in table 2, in IMC from young steers (McCORMICK et al., unpublished data) and goats (HORGAN et al. 1991), when both reducible (dihydroxylysinonorleucine, DHLNL; hydroxylysinonorleucine, HLNL) and non-reducible (HP) crosslinks were determined, the proportion of HP to its ketoamine precursor (DHLNL) was higher in animals just one year of age.

TABLE 1. Reducible (DHLNL, HLNL) and non-reducible (HP) crosslink concentration in biceps femoris and LD IMC from steers and goats one year of age[a].

	DHLNL	HLNL	HP
Goats[b]	0.067	0.106	.180
Steers[c]	0.173	0.200	.400

[a]Crosslinks expressed as mole per mole of collagen.
[b]Data from HORGAN et al. (1991).
[c]Data from ORIA (1990) and McCORMICK et al. (unpublished data).

Relatively little is know about factors which may affect crosslinking patterns in muscle collagens (REISER et al., 19... Variations in lysyl oxidase activity could play a role in determining total number of crosslinks although this has not been dir... investigated in muscle tissues. Lysyl oxidase requires copper for activity; in studies with severely copper-deficient swine we ... unable to demonstrate an effect of copper deficiency on crosslink concentrations in IMC (LARSEN et al., 1991). It is possible ... in muscle tissue, as in skin (ROMERO-CHAPMAN et al., 1991), the concentration of lysyl oxidase far exceeds the min... requirements for crosslink formation and, thus, even large variations in activity may not affect crosslinking. Levels of hy... hydroxylation apparently influence crosslinking patterns in some tissues, including proportions of HP to its ketoamine precu... (HENKEL et al., 1987) and the ratio aldimine to ketoamine crosslinks (LAST et al., 1990). There is variability in levels of hy... hydroxylation among collagen types and among different tissues (REISER et al., 1992). Fluctuations in muscle collagen hy... hydroxylation have not been examined.

The progressive nature of collagen crosslink biosynthesis does not mean, however, that in every muscle there is a ge... irreversible progression of lysine aldehyde-derived crosslinks from less mature to mature forms. While there is a good corre... between maturation of muscle collagen crosslinks and chronological age, it is also apparent that rate of crosslink formation ... directional shifts in the concentration of mature crosslinks, irrespective of age, can be altered.

AGE, GROWTH AND ADAPTATION

There is remarkably little variation in the collagen concentration of a skeletal muscle with growth and aging. In gen... variations in skeletal muscle collagen concentrations are relatively slight indicating that synthesis, accretion and turnover of co... and extracellular proteins in muscles remain in equilibrium over much of the life span of the animal. Some exceptions are the pro... collagen concentrations in the muscles of very young animals compared to larger, more mature animals (ANDERSEN et al., ... and diminished collagen concentration in the muscles of double-muscled cattle (BAILEY et al., 1982). Collagen concentration ... slightly increased in the muscles of intact males compared to castrates (SEIDEMAN et al., 1982 MILLER et al., 1989).

The well-known textural changes that occur in meat as animals grow and mature are most directly correlated to the pro... maturation of muscle collagen. Table 2 summarizes variations in HP concentration in different muscles from several species

function of age. It is immediately apparent that mature collagen crosslink concentrations increase with age for all species. Where more complete data are available, for example for sheep and deer, it is obvious that the non-reducible crosslink concentration of animals less than a year old are already 50 percent or more of values obtained for mature animals five to seven years old. HORGAN et al. (1991) documented similar findings in the muscles of goats one day to 13 years of age. Crosslink concentrations are similar for the meat-producing species with larger variation apparent in older animals. HP values for sheep and goats (HORGAN et al., 1991) tend to be lower than for cattle and pigs. HP values for rat skeletal muscle, as well as for other organs such as heart (THOMAS et al., 1992), are quite low relative to those found in the larger species.

The steady increase in mature collagen crosslinking is due to progressive and ongoing crosslinking reactions that occur within fibrillar collagen with the slowing of collagen synthesis rates as animals reach maturity. Less collagen synthesis and turnover provide existing fibrillar collagen time to progressively crosslink or mature. A muscle effect on crosslink concentration is also apparent. In general, muscles with considerably higher concentrations of collagen such as biceps femoris or soleus, which also tends to be slow-twitch, possess higher reducible and non-reducible crosslink concentrations than muscles of lower collagen concentration (SHIMOKOMAKI et al., 1972; LIGHT et al., 1985; HORGAN et al., 1991). There are exceptions such as semitendinosus which has relatively high levels of collagen (DRANSFIELD, 1977) yet moderate or low levels of ketoamine or HP crosslinks (LIGHT et al., 1985; HORGAN et al., 1991). These data emphasize the difficulties in attempting to determine the contribution that muscle collagen concentration makes to meat texture, particularly when different muscles are compared.

Although a steady increase in crosslink concentration in muscles with aging is typical, the properties of extracellular collagen

Table 2. **Non-reducible crosslink concentrations from different species and muscles of varying age[a].**

Species (muscle)	Age (years)				
	≤ 1	1-3	4	≥ 5	Reference
Sheep (wethers) (LD)	0.20	0.31	-	0.38	McCormick, 1989
Cattle (steers) (LD)	0.29	0.33	-	-	Oria, 1990; McCormick et al. (unpublished data)
(BF)	0.39	0.57	-	-	
White-tailed deer (does) (LD)	-	0.31	0.42	0.64	Vijayakumar and McCormick (unpublished data)

	Age (months)					
Rats	3	5	12	22	26	30	Reference
(GA)	-	0.04	.054	0.10	0.20	0.34	Kovanen et al., 1991; Zimmerman et al., 1992
(S)	-	0.035	0.13	0.196	0.31	0.45	
Pigs (barrows) (LD)	0.21	0.28	-	-	-	-	Andersen et al., 1992
(BF)	0.33	0.41	-	-	-	-	

[a]Moles of hydroxypyridinoline per mole of collagen; LD is longissimus dorsi, BF is biceps femoris; GA is gastrocnemius; S is soleus.

of muscle, including crosslinking profile, are extremely adaptable. In middle-aged and senescent rats subjected to exercise tr for 10 weeks, we documented a 58 and 76% reduction, respectively, in the mature crosslink concentration of the soleus m compared to untrained counterparts. Crosslinking concentration in gastrocnemius, a fast-twitch muscle, was not altered by tr (ZIMMERMAN et al., 1992). Again using rats, exercise-induced hypertrophy of the heart muscle (a tissue whose collagen comp closely resembles skeletal muscle in concentration, type and crosslink profile) resulted in a 50% reduction in crosslinking in old r animals relative to their sedentary cohorts (THOMAS et al., 1992). In both instances, the impetus for the dramatic s crosslinking was undoubtedly related to exercise-induced increases in collagen synthesis in these muscles. These observations s that the potential for significantly altering and, indeed, reversing the usual aging-associated maturation of collagen crosslinks in exists.

GROWTH RATE: RAPID VERSUS SLOW

The effects of growth rate on muscle collagen characteristics, whether mediated by variable plane of nutrition or endog hormones such as testosterone, have been studied extensively and have resulted in a great deal of confusion and some contra findings (McCORMICK et al., 1989). Slaughtering animals after a period of rapid growth is generally thought to produce mea collagen characteristics conducive to tenderness because newly synthesized collagen dilutes the older, existing muscle co (ETHERINGTON, 1987). The observation that growth and new collagen synthesis results in muscle with less mature colla certainly valid in some circumstances. However, the complex relationship between collagen synthesis and muscle co characteristics (particularly crosslinking) cannot be satisfactorily explained solely by a dilution effect that newly synthesized co molecules may have on existing fibrillar collagen. By considering two different situations, first, the relatively slow or mo fluctuations in muscle growth achieved by varying energy intakes, and second, the rapid muscle accretion typical in intac castrate) males or meat animals administered growth hormone, some relationships between growth and muscle collagen vari become apparent.

In terms of nutritional effects, a number of studies have compared young cattle fed high or low energy diets, and e palatability traits, collagen concentration, collagen solubility and thermal transition temperatures. These studies have confirm sensory traits and collagen characteristics of muscle are improved by high energy feeding (ABERLE et al., 1981; FISHELL 1985). On the other hand, results from studies with young cattle fed under similar conditions are inconsistent (HALL and F 1982), and include reports of negative correlations between high energy diets and connective tissue-related tenderness (CROUSE et al., 1985). Differences in the physical characteristics of collagen and the palatability traits of meat from ani high or low energy diets can, in part, be accounted for by variation in mature muscle crosslinking. In studies wi (McCORMICK, 1989), and cattle (ORIA, 1990), we have documented growth rate-dependent shifts in muscle collagen cross In both instances variations in growth rate resulted in alterations in crosslink concentration in the muscles sampled; howe directional shift in crosslink concentration was dependent upon the magnitude of the change in growth rate. Thus, young wethers on a high energy diet had less crosslinked IMC than those on a lower plane of nutrition. However, compensatory induced by feeding a high energy diet to a second group of wethers previously fed maintenance level rations resulted in rapid accompanied by high IMC crosslink concentrations. In steers slaughtered after 60, 85 or 142 days on either high or low energy

diminished HP concentration in biceps femoris muscle followed periods of more rapid growth; elevated crosslink concentration followed periods of slower average daily gain irrespective of animal age. These shifts in crosslinking occurred for animals receiving either high or low energy diets. There were no shifts in type III collagen proportions and collagen concentrations remained constant throughout the study. Significant variations in mature crosslinking concentration could be detected between groups of cattle differing by no more than 25 days in age. It would appear that, irrespective of level of energy intake, variation in average daily gain influenced muscle crosslinking profile. The demonstrable variations in crosslinking within the high and low energy groups at different time points may explain some of the inconsistent findings related to plane of nutrition, collagen characteristics and meat palatability. Groups of steers fed either the high or the low energy diet for the entire 142 days had identical muscle crosslink concentrations, suggesting that typical dietary regimens may ultimately have little effect on muscle collagen characteristics.

The anabolic effects of testosterone on collagen synthesis (CUTRONEO, 1987), collagen solubility (CROUSE et al., 1985; MILLER et al., 1989) and muscle toughening (SEIDEMAN et al., 1982) are well known. Decreased muscle tenderness in pigs administered somatotropin has also been reported (MILLER et al., 1991). Markedly elevated IMC crosslink (HP) concentrations without an increase in collagen concentrations in both the muscles of rams compared to wethers (MAIORANO et al., 1992), and in muscles of young, growing pigs administered somatotropin compared to untreated animals (ANDERSEN et al., 1992), provide a plausible explanation for previous findings documenting increased shear force and lower sensory scores in both models of rapid muscle growth.

As regards possible relationships between increased collagen synthesis, immature collagen deposition and resulting meat texture, it is significant that the fraction of IMC that is soluble is usually the same or greater in intact males compared to castrates (CROUSE et al., 1985; MILLER et al., 1989). We observed that, although HP concentrations were 40% greater in IMC of rams than wethers, the absolute and relative size of the soluble and insoluble collagen pools did not differ, this in spite of the fact that type III collagen proportion was greater in rams, indicating new collagen synthesis and accumulation (MAIORANO et al., 1992). It would, thus, appear that muscle accretion accompanied by increased collagen synthetic activity and accumulation of substantial amounts of immature collagen can, at the same time, be associated with accelerated crosslinking in a fraction of extracellular collagen.

CONCLUDING REMARKS

Significant advances have been made in elucidating the role collagen, and in particular collagen crosslinking, plays in determining the texture of meat. The plasticity of collagen in muscle tissues is established. Future goals should be directed towards understanding mechanisms which produce both desirable and undesirable changes in muscle collagen. For example, the role that altered collagen synthesis rates play in influencing crosslink formation and maturation is poorly understood. Likewise, how different fibrillar collagen types in muscle associate and its relationship to crosslinking patterns is unclear. In summary, our ability to promote desirable changes in collagen and improved meat quality by management practices, especially by those which promote rapid growth and muscle accretion, remains a challenge.

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