CONNECTIVE TISSUE AND MEAT QUALITY

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INTRODUCTION

Muscles of meat animals have a well-developed connective tissue system to support the tissue and to transmit the force of contraction to the skeleton. Connective tissues therefore must have considerable strength to ensure the forces are transmitted without loss of energy. Muscle connective tissue can be distinguished morphologically as three separate hierarchies (Fawcett 1968), the epimysium or outer muscle sheath, the perimysium or the intramuscular connective tissue binding the bundles of muscle fibres, and the endomysium or individual muscle fibre sheath. The major component of these connective tissue domains is collagen, the minor components including elastin, large proteoglycans and specialised glycoproteins.

Meat can therefore be considered as a 'two component' system being composed of the complex intracellular contractile apparatus and the compositionally minor extracellular connective tissue. The contractile muscle proteins contribute the major element of meat texture whilst the connective tissue which comprise less than 2% of most skeletal muscles have long been associated with more subtle textural effects. However, if collagen only provides this so-called 'background' toughness, then the effect of age of the animal and the effect of conditioning on connective tissue would not bring about such dramatic changes in the overall toughness.

A role for collagen in the texture of meat was made as long ago as the beginning of the century (Lehman 1907), but correlations with a single parameter, for example, the total amount or solubility of collagen (Ramsbottom et al. 1945), only gave partial or conflicting relationships. This lack of understanding of the fundamental properties of collagen presented considerable difficulties in developing a rationale for the role of collagen in determining the texture of cooked meat. However, from our work during the 1970s it became clear, based primarily on a basic study of the crosslinks and their crucial role in determining the changes in properties with age and with heat-denaturation of the fibre, that it was the 'quality' of the collagen, not the quantity, that was critical. Based on these specific properties, a rationale for the role of collagen in determining the texture of meat can be presented.

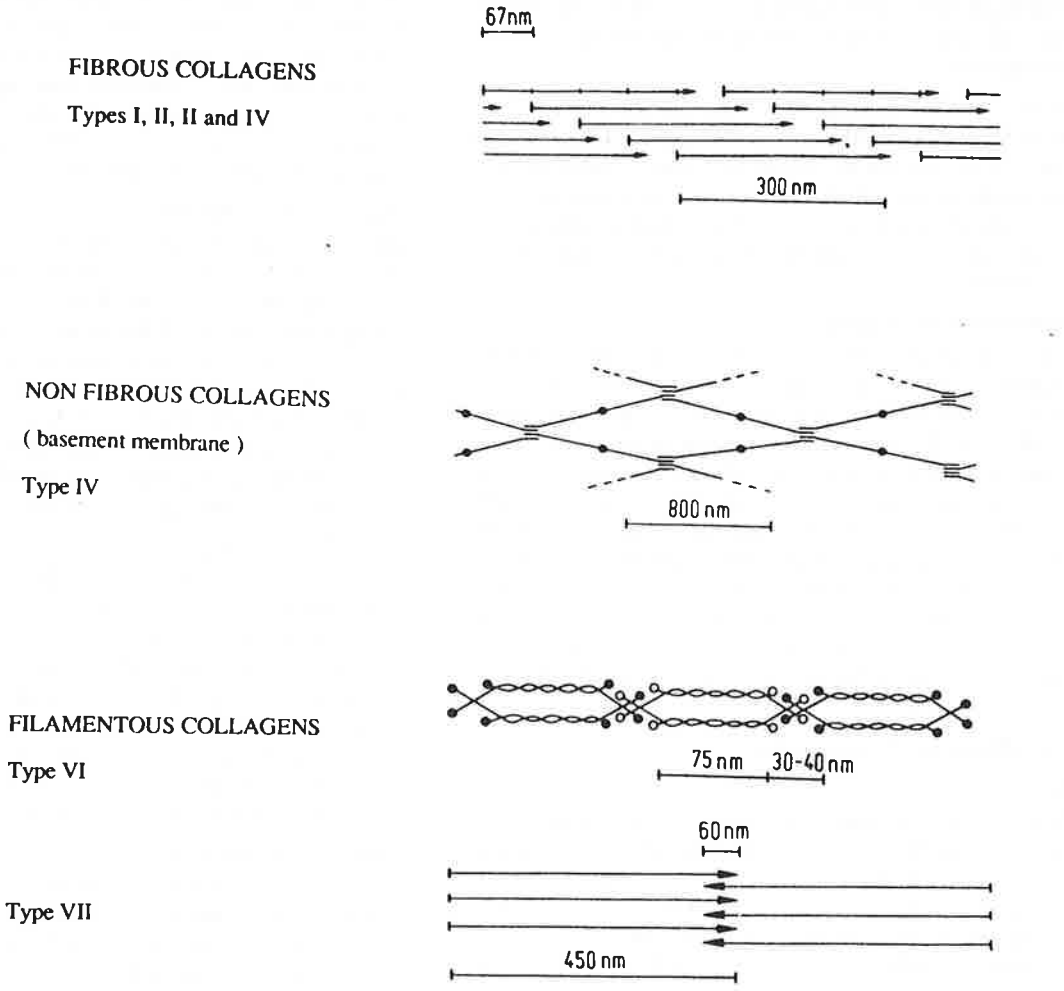

Fig.1. Molecular organisation of the different types of collagen molecules in (a) fibrous collagen, (b) basement membranes, and (c) filamentous collagen.

Before developing such a hypothesis it would be sensible to briefly review the recent advances in connective tissue research relevant to meat science.

STRUCTURE AND PROPERTIES OF CONNECTIVE TISSUES

Collagen

The collagens are, in fact, a family of closely related proteins, possessing a basic structure of three polypeptide chains with a -Gly-X-Y- repeat forming tightly bound triple helices which subsequently aggregate to form various types of supporting structures (Piez and Reddi 1985; Mayne and Burgeson 1987; Bailey and Light 1988). The family can be subdivided into three classes; the fibrous collagens which are the commonest, the non-fibrous basement membrane collagens, and the filamentous collagens which are present in much smaller amounts but play a crucial role in specific tissues (Fig.1).

The fibrous collagens

The collagen molecules in this group self-assemble to form fibres with a characteristic band pattern with a periodicity of 67 nm, identifiable in the electron microscope. The collagen types in the group are Types I, II, III and the minor collagens V and XI. Type I and III collagens are the major collagens of the epi- and perimysium (Bailey et al. 1979), whilst Type v is a minor component (Linsenmayer et al. 1983). Small amounts of Types III and V are present in the fibrous part of the endomysium.

The non-fibrous collagens

The only member of this group is Type IV collagen, and these molecules self-assemble to form a 'chicken wire' network structure which acts as the basic framework for all basement membranes. Type IV collagen is the major collagen of the basal lamina of the endomysium (Bailey et al. 1979).

Filamentous collagens

A number of recently identified minor collagens have variable molecular lengths and form a variety of filamentous structures. Some of these collagens are tissue specific, but the only ones of interest in meat are Types VI and possibly Type VII. Type VI is observed as a loosely packed filamentous structure with an axial repeat of 100 nm and is formed by anti-parallel alignment of the individual molecules. Type VII microfibres underlie some basement membranes acting as anchoring fibrils between the membrane and the underlying matrix. Type VI has been located in the perimysium of muscle (Linsenmayer et al. 1986), and Type VII may be located in the endomysium.

Non-collagenous Components

Elastin

Elastin is a fibrous protein which, in complete contrast to collagen, is highly elastic (Sandberg et al. 1977). The role of elastin in the texture of meat has been neglected since it wag assumed that it was present in small quantities, that is, less than 10% of the collagen, and was mainly associated with the blood vessels (Bendall 1967). Recent histological studies have suggested that its role might have been overlooked since it appears in significant quantities, 40% of the collagen, in semitendinosus muscle (Rowe 1986). Elastin is unaffected by heat treatment and if a significant proportion were present in muscle this could provide an increase in resistance to shear resulting in tougher meat. However, most muscles contain much less elastin and its role in the semitendinosus cannot necessarily be extrapolated to other muscles.

Proteoglycans

The role of proteoglycans which, in contrast to collagen and elastin, do not possess mechanical strength and are thermally labile, would not be expected to play a role in the texture of meat. However, they could play an indirect role. For example, the proteoglycans can be located at specific points along the fibre (Scott 1980) and may therefore be important in registering the alignment of the fibres particularly under stress, hence their modification or loss during conditioning could lead to a change in mechanical properties. It has been demonstrated in vitro that proteoglycans can increase the shrinkage temperature of collagen fibres, but whether the concentrations are sufficient in vivo is doubtful.

ORIGIN OF THE MECHANICAL AND THERMAL PROPERTIES OF COLLAGEN

The properties of collagen relevant to the meat scientist are not easy to follow in intact muscle, primarily because Of the small amount present but also because of its organisation. However, there are simple model systems of pure fibrous collagen, such as tendons for the epi- and perimysium, and placenta or lens capsules as models of pure non-fibrous collagen for the endomysium. Using these models it has been possible to understand many of these properties and to subsequently apply them to meat.

Mechanical properties

The high mechanical strength of collagen is brought about through the formation within the fibres of intermolecular crosslinks (Bailey et al. 1974; Eyre et al. 1984). These chemical bonds are covalent in nature and result from specific structural features of the collagen molecules, and of their precisely organised alignment in the fibre. In the absence of these crosslinks the collagen fibre has no mechanical strength and is soluble in neutral salt solutions, as illustrated by the disease lathyrism, in which the crosslinking is specifically inhibited.

Crosslink precursors

The crosslinks are formed by the oxidation of specific lysyl, and hydroxylysyl residues in the globular terminal region of the collagen molecules. Oxidative deamination is achieved by the enzyme lysyl oxidase whose binding site on the helical part of the molecule Hyl-Gly-His-Arg is conserved throughout the collagen family (Fietzek et al. 1977). This binding site is aligned in the fibre directly opposite the lysine in the globular region of another molecule, which is then converted to lysine-aldehyde.

Intermediate crosslinks

The lysyl-aldehyde formed condenses with the hydroxylysine in the enzyme binding site to form a Schiff base or aldimine bond dehydro-hydroxy-lysinonorleucine (dehydro-HLNL). If the precursor is hydroxylysine-aldehyde the aldimine initially formed undergoes a spontaneous Amadori rearrangement to

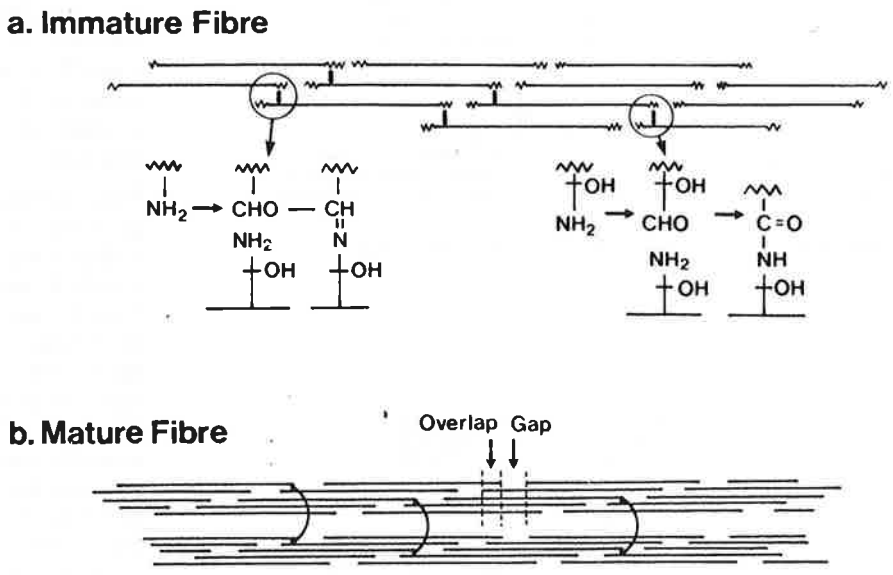

Fig.2. (a) Structure and location of the reducible aldimine and keto-imine crosslinks in immature fibres. (b) Location of the transverse mature crosslinks linking microfibrils in register.

form a keto-imine bond dehydro-dihydroxylysinonorleucine (dehydro-DHLNL). These two crosslinks are precisely located in the fibre linking the molecules head-to-tail to form an infinite polymer.

In contrast to the fibrous collagens, the location of these crosslinks in the non-fibrous collagens is still debatable. Crosslinks have been located in the anti-parallel amino-terminal region, but the mode of binding of the globular C-terminal domains has not yet been elucidated (Bailey et al. 1984).

Mature crosslinks

The collagen family of proteins possess an extremely long biological half-life compared to most proteins, and therefore has the ability to change in properties with age. As collagen ages the fibres become progressively stronger' and more rigid, less susceptible to enzymic degradation and to swelling by acids. This maturation of the fibres is achieved by further reaction of the intermediate crosslinks to form multivalent crosslinks capable of crosslinking several molecules. We have proposed that the reaction occurs via molecules in register which must therefore be from adjacent 'microfibrils', thus dramatically increasing the stability of the fibre (Light and Bailey 1980). Based on this proposal crosslinking can be considered to take place in two stages. The initial end-overlapped molecules are polymerised by longitudinal head-to-tail crosslinks, which is then followed by interaction of these intermediate crosslinks to form transverse crosslinks between these long polymers (Fig.2).

Several compounds have been isolated and proposed as mature crosslinks but only three are supported by convincing evidence. The relative contribution of each of these mature crosslinks has not yet been elucidated, but clearly they have a critical effect on the properties of collagen.

The first compound identified in mature dermal collagen was hydroxyaldolhistidine (Housley et al. 1975), but its structure and mode of formation (involving aldehydes in the helix) was dubious. Recently its structure has been re-evaluated as histidino-hydroxylysinonorleucine (Yamauchi et al. 1987). This may be the major mature crosslink in tissues in which the precursor is lysine-aldehyde. Pyridinoline was later isolated and characterised by Fujimoto et al. (1977). It is a fluorescent cyclic compound and derived from hydroxylysine-aldehyde. The structure and location of these compounds are shown in Fig.3.

It has therefore been suggested that two pathways exist. If the tissue contains the crosslink precursor lysine- aldehyde then histidino-hydroxylysinonorleucine is the mature crosslink but if hydroxylysine-aldehyde is the precursor then pyridinoline is the mature crosslink (Eyre 1980). On the other hand, we have isolated a compound (M) that is present in both types of tissue which may therefore be a universal mature crosslink (Barnard et al. 1986). As yet its structure and mode of formation is unknown, although it is clearly derived from the intermediate divalent crosslinks.

Thermal properties

During the cooking of meat the collagen is denatured and because of its partially crystalline nature it shrinks at about 65°C to form insoluble gelatin. The fibre is converted from an inextensible highly organised fibre to a randomly organised elastic fibre. It is the nature of the crosslinking that will determine its solubility, the extent of shrinkage and the tension generated on shrinkage. We have shown that the tension generated under isometric conditions in tissues crosslinked by dehydro-HLNL does not achieve its potential due to the thermal instability of this crosslink, and that above maximum tension the crosslinks are increasingly ruptured leading to a dramatic loss of tension (Bailey and Lister 1968; Allain et al. 1978). In tissues crosslinked by the thermally stable dehydro-DHLNL maximum tension is achieved with little loss of the crosslink, and on further heating there is only a small relaxation of the tension. With increasing age the formation of the multivalent transverse crosslinks there is a dramatic increase in the tension generated and a reduction in the relaxation of that tension at higher temperature (Fig.4). The residual tension maintained means that the fibre still has a significant mechanical strength despite being denatured. This can readily be explained by the heat stability of the increasing number of mature crosslinks maintaining some strength in the denatured fibre.

Analysis of collagen in muscle

Based on our current knowledge of the properties of collagen it should be possible to consider the inadequacies of the methods generally employed in

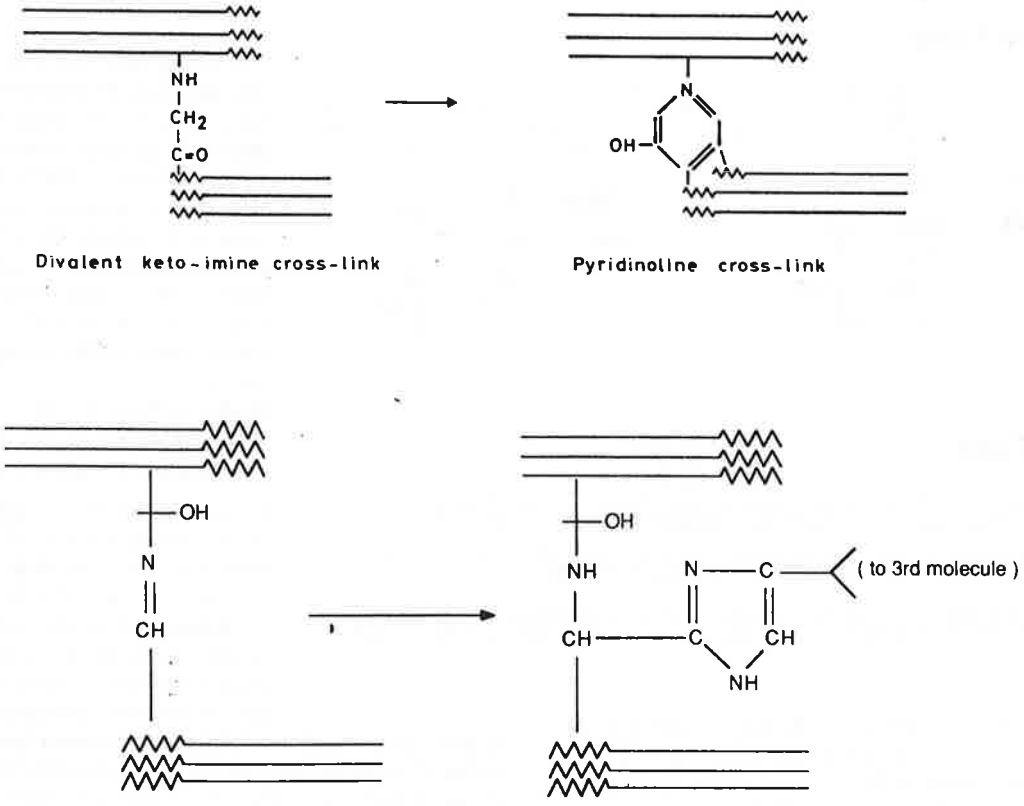

Fig.3. Structure and location of two mature crosslinks: (a) hydroxypyridinoline linking two molecules, (b) histidino-hydroxylysinonorleucine crosslinking linking three molecules.

attempts to correlate collagen and the tenderness of meat.

Determination of the total amount of collagen in relation to texture has generally been shown to be contradictory and of little value (Ramsbottom et al. 1945; Field et al. 1970; Dransfield 1977). This is best illustrated by the extreme case of identical muscles from a calf and adult animal where there is a negative correlation of collagen content and texture. Naturally, when the quality of the collagen is the same in different muscles then the amount of collagen becomes important.

The determination of the solubility of collagen, since it changes with age, should provide a better correlation with texture but is again conflicting (Hill 1966; Williams and Harrison 1978; Jeremiah and Murray 1984). The reasons for differences in solubility are complex and the correlation is not sufficiently reliable for use as a predictor of texture. This is due to the fact that the divalent crosslink dehydro-DHLNL can confer insolubility, but the proportion of mature crosslinking has a larger effect on the tension generated on shrinkage and residual strength than solubility.

The size of the fibres may also play a role since the larger the fibre the higher the mechanical strength and resistance to enzymes, but no correlation between fibre size and texture could be found. Rowe (1981) showed that there was a less dense layer of fine perimysial fibres where it joined the endomysium and Carroll et al. (1978) suggested cleavage occurred at this junction.

Determination of the genetic type of collagen has also been carried out, since Type I generally forms thick fibres, Type III forms fine reticulin type fibres, whilst Type IV is non-fibrous. Using immunohistological techniques followed by biochemical analysis it was shown that the epimysium contains a high proportion of Type I, the perimysium a high proportion of Type III and the endomysium basal lamina predominantly Type IV (Bailey et al. 1979; Light and Champion 1984). It is possible that the fine Type III in the perimysium could lead to a reduction in tensile properties. On the other hand Type III contains disulphide bonds in addition to the lysine derived crosslinks which could generate a high tension on heating. This is illustrated by the insolubility (Deethardt and Tuma 1971), resistance to enzymes (Wu et al. 1982) and high strength of denatured reticulin fibres, which are primarily Type III (Nowack et al. 1976). More recently Burson and Hunt (1986) have reported the decreased solubility of Type III compared to Type I collagen in intramuscular collagen.

Studies of the amounts of Type III in the perimysium in an attempt to relate these to texture have provided equivocal answers. In several muscles a reduction in Type III content provided a good correlation with increasing tenderness, but there were significant exceptions to this correlation (Bailey and Sims 1977; Light et al. 1984; 1985). Similarly, Burson et al. (1986) could find no difference in the proportions of Types I and III in collagen from bulls and steers, suggesting other factors are more important in determining the less tender muscle of bulls.

The role of Type IV collagen may well be significant. Type IV is the major framework collagen of basal lamina (Timpl et al. 1981) and is present in the endomysium (Bailey et al. 1979). The endomysium is a composite tissue of a thin basal lamina (15-30 nm) and an overlying fibrous (reticular) layer. The endomysium is very thin (approximately 15-30 nm) but has an appreciable

strength, although this is partly due to the underlying fibrous collagen. The intact endomysium certainly has the strength to resist swelling of the myofibrils (Wilding et al. 1986; Offer et al. 1987) and the ability to contract on heating thereby generating a tension. Unfortunately it is difficult to distinguish the properties of the basement membrane collagen from the fibrous supporting collagen. We have therefore used lens capsule as a model since it does not possess the associated fibrous collagen. The Type IV in this basement membrane has been shown to possess considerable strength and to shrink at about 50-550 (Kent and Bailey 1988). A 'chicken wire' network type of structure has been proposed (Timpl et al. 1981) but our recent studies by x-ray diffraction (Barnard et al. 1987) and differential scanning calorimetry (Kent and Bailey 1988) suggest that there is some lateral alignment of the molecules to form a non-striated fibrous structure rather than a uniform network. The endomysium shrinks at the higher temperature 55-65°C presumably due to the associated fibrous collagen. The tension generated clearly could play a role in the overall shrinkage of the connective tissue in muscle.

The role of the minor collagen Types V and VI have not yet been determined. Type V is primarily located in the perimysium (Linsenmayer et al. 1983) and forms part of the fine fibrous network overlying the basal lamina of the endomysium. Type VI is also present in the perimysium (Linsenmayer 1986), but only in small quantities and unless it plays a role in stabilising the much more abundant Types I and III fibres is unlikely to make a significant contribution.

Attempts have also been made to define a relationship between the crosslinks and texture based on the thesis that the crosslinks determine the tension generated during thermal shrinkage (Bailey and Sims 1977; 1981). Initial studies demonstrated the perimysium generally possessed a higher content of the relatively heat-stable oxo-imine crosslink than the epimysium. As anticipated, the best correlation was found with the content of the heat stable crosslink DHLNL of the perimysium, but a few muscles, for example psoas major, possessed a high content of DHLNL yet produces tender meat (Shimokomaki et al. 1972; Light et al. 1984). Clearly the relationship is complex. It is certainly possible to have a collagenous tissue of high DHLNL content, which is consequently very insoluble in acid but is incapable of generating a significant tension on shrinkage. An extreme case is the low tensile strength of cuverian tubules despite a high proportion of DHLNL making the fibres insoluble Bailey et al. 1982a). The obvious answer is that both the intermediate and the mature crosslinks need to be determined.

These analyses of different parameters, and their partial correlation with texture, together with the fundamental studies on the connective tissues have allowed a rational description of the role of collagen in meat texture to be developed over the past few years. The hypothesis has developed such that

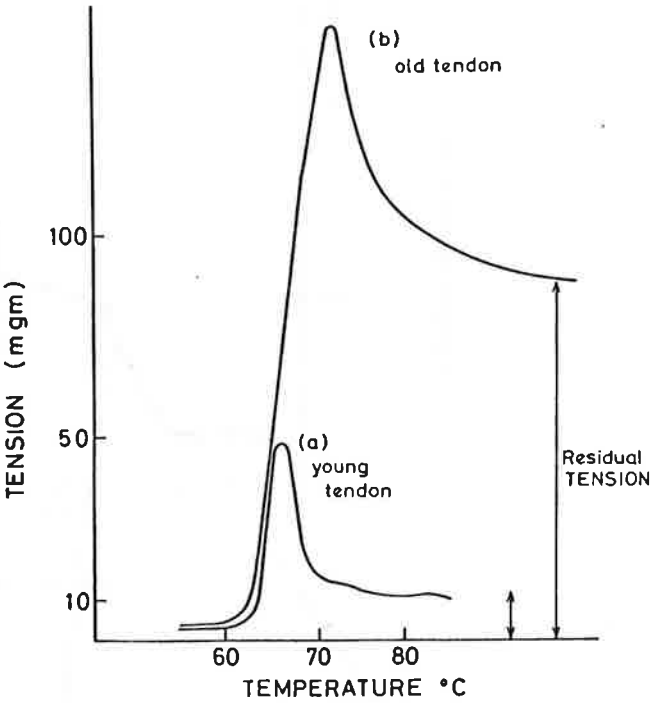

Fig-4. Isometric tension curves for young and adult tendon showing increase in tension generated and residual strength of the tendon after heating with increasing age.

it can be shown that collagen is the major determinant of the texture of cooked meat, and that it is the quality as well as the quantity of the collagen that accounts for the variability in texture.

To illustrate this primary role of collagen consider the nature of the changes taking place in meat as it is cooked (Fig.5). It is obvious that as the temperature is raised the proteins denature, and it is the properties of the denatured proteins that determine the texture of meat.

At temperatures between 40 and 50° there is an increase in toughness (Davey and Gilbert 1975), as determined by shear value, due to the aggregation of the denatured

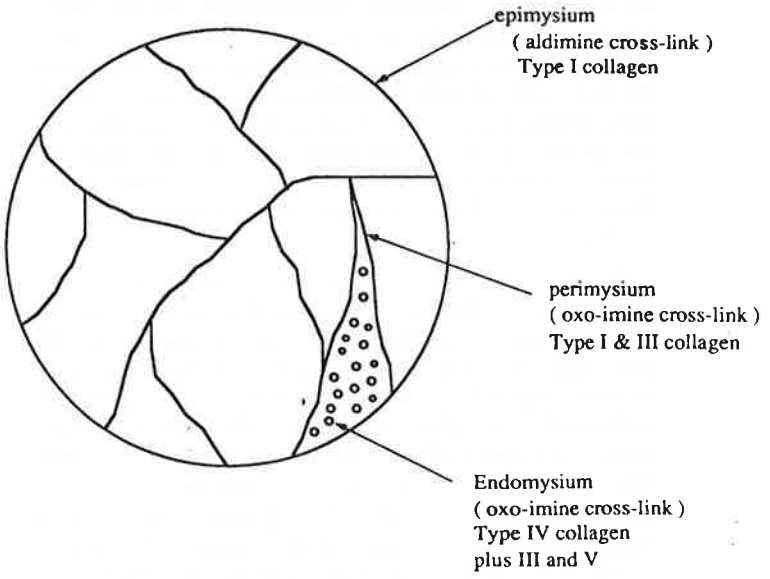

Fig.5. Location of the different types of collagen and types of crosslink present in the intramuscular collagen of the peri- and endomysium.

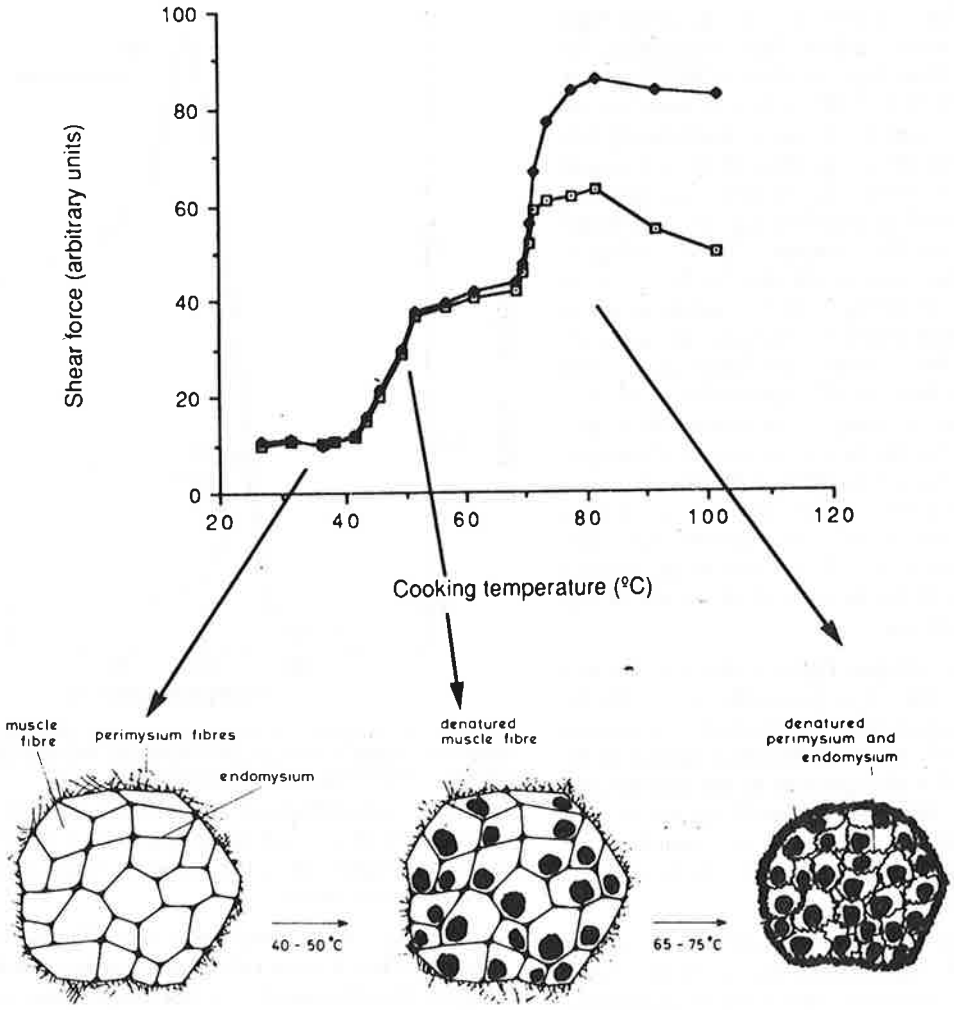

Fig.6. Diagrammatic representation of the changes in the muscle fibres and connective tissues during cooking in a cross-section of muscle related to the change in shear value.

myofibrillar proteins, primarily actomyosin. This denaturation results in the loss of fluid and shrinkage of the muscle fibres within the endomysial sheath. The latter being collagenous is unaffected at this temperature. Presumably the endomysial sheath was under tension in the raw meat but following shrinking of the intracellular proteins this tension is probably released by forcing fluid out of the space between the endomysium and the denatured muscle fibre. In the absence of tension the fluid will not be forced out until the endomysium shrinks at about 50°.

At 60-70° a second increase in shear value occurs due to an additional shrinkage following denaturation of the collagenous endomysium and perimysium. If unrestrained, collagen fibres shrink to about one-quarter of their original length, but the perimysium in meat is restrained in length by the muscle fibres and therefore exerts a tension similar to the isometric tension studies. The extent of the tension generated in this second shrinkage varies considerably depending on the heat stability of the perimysium, which in turn is determined by the nature and extent of the crosslinking (Bailey and Lister 1968; Allain et al. 1978). The older the animal the higher the proportion of heat stable crosslinks and the greater the tension generated on shrinkage (Kopp and Bonnet 1987; King 1987). The pressure exerted on the muscle fibres therefore results in a considerable shrinkage of the muscle, primarily by loss of fluid, with a consequent increase in toughness. The majority of this shrinkage is exerted by the fibrous perimysium, although a small but significant effect may be provided by the shrinkage of the endomysium, both the basal lamina and the underlying fibres. Certainly the combined epimysial-endomysial shrinkage should generate sufficient tension to push fluid out of the fibres and consequently force them closer together. The relative importance of the endo- and perimysium is unknown, but the amount and nature of the basement membrane suggests the contribution of the endomysium is small.

Following shrinkage of both the myofibrillar proteins and the collagenous structures, the muscle fibres are held together by denatured perimysium. The strength of this adhesion is clearly dependent on the residual strength of the denatured collagen, which again is dependent on the proportion of heat stable crosslinks holding the protein chains together. These fibres are weaker in the young animal than the adult animal and the muscle fibres pull apart more easily.

In the third section of the shear value curve there is a decrease as the temperature is increased further. This reduction in toughness could be due to peptide bond cleavage or crosslink rupture of the denatured collagen. The former appears to be the primary effect as we have clear evidence of peptide bond hydrolysis under these conditions. Alternatively, the fall in shear value may be due to breakdown of the myofibrillar proteins. However, it is the denatured collagen fibres that maintain the integrity of the cooked meat by holding the muscle fibres together, hence heat degradation of these fibres would certainly cause a more rapid drop in toughness than random cleavage of the myofibrillar protein. The increased tenderness on prolonged heating is almost certainly primarily due to degradation of the denatured collagen.

The complete reversal of the properties of meat proteins on heating, the myofibrillar proteins denaturing to a more rigid aggregate and the collagen denaturing to a weaker

elastic polymer, leaves the question of which is now the weaker component. The tensile properties of cooked meat are readily observed to be much stronger longitudinally than the force required to separate the fibres transversely. Using the elegant technique of fracture mechanics, Purslow (1985) has demonstrated where the material initially starts to break, how the rupture proceeds, and related this to the tensile strength. If transverse sheets of cooked meat are pulled apart laterally, widespread small cavities appear between fibre bundles near the perimysial-endomysial junction which then join up to produce a tear through the composite material. Further detailed examination of the cleavage site in the scanning electron microscope demonstrated that separation of fibre bundles rather than individual fibres occurs during fracture and that separation occurs near the peri- endomysial junction. Although cleavage has occurred at this site, the perimysial fibres overlying the muscle fibres maintain the structure and these break at a higher load and hence determine breaking strength. Analysis of the lateral versus longitudinal tensile strength revealed the latter was ten times greater. The lateral binding of the muscle fibres is therefore clearly much weaker than the muscle fibres themselves. The relative strength of the perimysium and muscle fibre will vary from muscle to muscle and with age as the quality of the collagen varies, in contrast to the muscle which remains fairly constant. Collagen is therefore a major determinant in the texture of cooked meat.

In summary, the texture of meat is provided by the denatured myofibrillar proteins, but the expression of that texture is determined by the squeezing together of the muscle bundles and consequent loss of fluid due to the pressure exerted during the contraction of collagen, and the residual strength of the denatured collagen binding the muscle bundles together. These properties of collagen are determined by the nature and extent of the intermolecular crosslinks.

The basic rationale for the role of collagen as the determining factor in the texture of meat is now clear, although further details need to be clarified. For example, confirmation that the cleavage point is the fine fibrils of the endomysial-perimysial junction, the types of collagen present in this region, the precise role of the endomysium, the effect of the orientation of the perimysial fibres, the relative importance of the different mature crosslinks, and their relationship between muscles, with age, and with collagen type. However, the essentials of the hypothesis have been laid.

EFFECT OF PRE- AND POST-SLAUGHTER TREATMENT ON COLLAGEN

Having established the hypothesis it should be possible to use it to predict how pre- and post-slaughter treatments could be utilised to ensure the optimal properties of the collagen to produce tender meat.

The turnover of collagen varies considerably between tissues and the relative growth rates of different muscles result in different levels of maturity of the collagen in a given animal. Similarly, different rates of growth of animals, e.g. bulls and steers and double-muscled animals, result in differences in both the amount of collagen and its maturity in terms of stable crosslinks. Double-muscled Charolais steers possess finer and less mature collagen fibres than controls and taste panels confirmed increased tenderness (Bailey et al. 1982b). The faster growth rate of bulls than steers would suggest increased tenderness from bull meat, but the rate of turnover may well be different and allow maturation of the collagen. This could account for the observed increased toughness of bull meat, but this would need confirming by crosslink determination. High or low energy feeds can affect growth rate and hence maturity of the collagen and consequently the texture of the meat. Certainly it is well known that rapid 'finishing' of animals increases the tenderness, which can be accounted for by the higher proportion of newly synthesised and consequently immature collagen being laid down. The tension generated by this collagen and its 'residual strength' would be reduced resulting in increased tenderness.

Age has the most significant effect on texture. The increase in mature crosslinks with age is now well established and this has been correlated with increased shrinkage tension and residual strength. This leads to increased toughness of the meat despite a lower proportion of collagen. Physical activity also increases the proportion of collagen in fast and slow muscles and this is most marked in the endomysium (Kovanen et al. 1987) but this effect has not been applied to meat texture studies.

Growth promoting agents, anabolic steroids and beta-agonists might at first sight have been expected to increase tenderness due to the higher proportion of newly synthesised collagen in the more rapidly growing animal. However, the mode of action of these agents needs to be understood. Anabolic steroids and growth hormones increase growth rate by increasing both synthesis and, to a lesser extent, degradation. This should lead to an increased proportion of immature collagen. On the other hand, the beta-agonists are believed to cause an increase in growth by reducing the degradation of the protein. In this case the reduction in turnover would allow the additional collagen to mature. This may well account for the increase in toughness of meat from animals treated with beta- agonists. However, as far as I am aware, no studies have been carried out on the proportion of immature and mature crosslinks in the collagen of these animals.

Among post-slaughter treatments the role of collagen in the tenderising effect of conditioning can also be explained. Very limited proteolytic cleavage of the non-helical regions of the collagen molecules possessing the crosslinks would depolymerise the fibre such that the tension generated on shrinkage would be considerably reduced, and hence a reduction in toughness. Such an effect has been observed in comparative isometric tension studies (Kopp and Valin 1981; Mills et al. 1984). Confirmation that some proteolytic cleavage by cathepsins (Etherington et al. 1987) does occur to the collagen, despite little detectable change in solubility, can be shown by 2D-electrophoresis of collagen peptides (Stanton and Light 1988). The limited proteolytic cleavage could be maximised by electrical stimulation

and conditioning temperature. Future methods could involve the stimulation of the catheptic enzymes, or their addition to processing meats. Several myofibrillar proteins are also degraded during conditioning. At a biochemical level proteolysis of myofibrillar proteins is greater than that on collagen, but the latter may be more important in textural terms. Alternatively, the degradation of the myofibrillar proteins may be specific, e.g. the degradation of desmin which could have an effect on the texture. The relative effects may depend on the conditions employed.

It is clear that, despite being a minor component of meat, collagen plays a major role in determining the texture of cooked meat, rather than exercising a subtle background effect. The muscle fibres,provide the texture sensation but its expression is determined by the quality of the collagen. The major factor determining the quality of collagen related to meat texture is the extent of the mature intermolecular crosslinking. Elucidation of the nature of these crosslinks is another example of the importance of fundamental studies in meat science.

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