Thermally Induced Gelation of Chicken Myosin Isoforms

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Thermally induced gelation of one white muscle myosin (pectoralis) and two red muscle myosins (iliotibialis and gastrocnemius) from chicken was investigated using small-strain oscillatory rheology. In dynamic heating conditions (25−75 °C at 1 °C/min), pectoralis myosin gelled at an onset temperature 5 °C lower and developed a greater storage modulus (G') than red muscle myosins. Gel curing at 75 °C for 3 h after dynamic heating increased in G' values, but the relative magnitudes in G' remained the same for all myosins. The isoform-associated rheological differences at 75 °C were lost when gels were evaluated at 25 °C. This was true for G' values determined over a 0.16 s interval and G (shear modulus) values after 1 h of imposed strain. Differences were also noted with isothermic gelation (45, 50, or 55 °C). The pectoralis myosin gelled at 45 °C, but the two red muscle myosins did not. The G' values for pectoralis and iliotibialis myosins gels were not significantly different at 50 °C; however, they were significantly greater than values for gastrocnemius myosin gels. There was no significant differences among the G' values for gels at 55 °C. These results indicate that the dynamics of gelation and temperature sensitivity of intramatrix forces are different among myosin isoforms. Therefore, any relative evaluation of rheological properties must be under temperature conditions that reflect those typical of the meat product application.

Keywords: *Myosin; gelation; rheology; muscle protein*

INTRODUCTION

Gelation has been used as a model reaction to understand molecular mechanisms of meat product texture and water-holding properties (Acton and Dick, 1989; Foegeding and Hamann, 1992). Myosin has been recognized as the main gelling protein of muscle foods (Samejima et al., 1969; MacFarlane et al., 1977), and many studies have been done to characterize the gelation of myosin in the last 20 years (Acton and Dick, 1989; Ziegler and Foegeding, 1990).

The gelation properties of myosin are related to the species and muscle source of myosin. Asghar et al. (1984) evaluated chicken myosin gelation and found that white muscle myosin gels had greater rigidity at 65 °C than red muscle myosin gels. A later study (Morita et al., 1987) found the same general results but had different pH optimums for red and white muscle myosin gel rigidities. The authors suggested the difference between the investigations was due to types of muscles used. Morita et al. (1987) used whole breast and leg muscles whereas Asghar et al. (1984) used specific muscles from the breast and leg. Engelandsdal et al. (1985) and Fretheim et al. (1986), using bovine myosins, found that white muscle myosin had a lower gelation onset temperature and formed gels with higher storage modulus (G') values than red muscle myosin. These investigations show a consistent trend of white muscle myosins gelling at lower temperatures and forming more rigid gels than red muscle myosins. These observations were based on relative differences rather than statistical analyses.

Differences in myosin gelation have been attributed to sequence-specific effects of myosin isoforms. There are light chain and heavy chain families of genes that code for myosin (Emerson and Bernstein, 1987). Myosin isoforms follow functional (fast or slow twitch) and developmental (embryonic, neonatal, and adult) programs (Emerson and Bernstein, 1987; Stockdale and Miller, 1987; Bandman, 1992). Thus, the function of the muscle and age of the animal will determine the myosin isoform distribution.

Thermally induced protein gelation is a multistep process of denaturation, aggregation, and formation of a gel structure. In a separate study (Liu et al., 1996), we reported on the denaturation and aggregation of myosins extracted from one white (pectoralis) and two red (iliotibialis and gastrocnemius) chicken muscles. These muscles were chosen because they were the largest muscles in chicken parts utilized by the meat industry; pectoralis is located in the breast, iliotibialis in the thigh, and the gastrocnemius in the leg. Each myosin showed unique patterns in denaturation and aggregation which could not be simply grouped according to red or white muscle. The goal of this investigation was to characterize the thermally induced gelation of these chicken myosin isoforms. This was accomplished by determining rheological transitions during gelation and evaluating the viscoelastic properties of formed gels.

MATERIALS AND METHODS

Myosin. Myosin was extracted from the pectoralis, iliotibialis, and gastrocnemius muscles of adult Hubbard-type chickens by following the procedure outlined in Liu et al. (1996). Myosin buffer used for all experiments contained 0.6 M NaCl, 10 mM sodium phosphate, and 0.02% sodium azide (pH 6.0). Myosin was held at 4 °C, and all measurements were obtained within 1 week after isolation.

Myosin concentration (mg/mL) was calculated on the basis of A_{280} readings (UV-240, Shimadzu Corp., Tokyo, Japan), using an extinction coefficient of 0.52 cm^2/mg (Quass and

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Briskey, 1968). Stock solutions of 10 mg/mL were prepared for each myosin and degassed for 30 min under vacuum.

Rheological Measurements. Gels were formed from 10 mg/mL myosin solutions. Rheological properties were measured dynamically by oscillatory shearing and statically by stress relaxation. A Bohlin Rheometer (Bohlin Rheology A/B, Lund, Sweden) equipped with a C-14 concentric cylinder fixture was used for all experiments. The cup inner diameter was 15.4 mm and the bob's diameter was 14 mm. All dynamic data were obtained in the oscillatory mode using a 1.757 g cm torsion bar, a fixed frequency of 1.0 Hz (0.16 s per measurement), and a constant strain of 0.0206. A heating and cooling rate of 1 °C/min was used in all dynamic experiments. The rheometer software uses torque and phase angle values to calculate G' (storage modulus, a measure of elastic rigidity) and G'' (loss modulus, a measure of the viscous rigidity). The gelation onset temperature corresponded to temperature at the first G' reading followed by a rapid increase in G' values.

Myosin solutions were gelled under dynamic conditions by heating from 25 to 75 °C and then cooling to 25 °C, or heating from 25 to 75 °C, holding at 75 °C for 3 h, and subsequent cooling to 25 °C. Myosin solutions were also gelled by static heating at 45, 50, or 55 °C for 1 h and then cooling the gel to 25 °C. For the constant-temperature heating, the bob was inserted halfway into the cup and allowed to equilibrate at the desired temperature for 10 min before the myosin solutions were added. The time needed to add the myosin solutions and the start of the rheometer program was less than 1 min.

Viscoelastic properties were determined for all gels at 25 °C by stress relaxation. A constant strain of 0.0213 was applied and stress was measured every min for 1 h. The data was modeled as a single Maxwell element in series with a spring, and the relaxation time (τ) was determined using the following equation.

$$G_{rt} = G_{ae} + (G_i - G_{ae})1/e \quad (1)$$

G_{ae} is the apparent equilibrium shear stress, which was the final stress after 1 h of imposed strain, G_i is the initial stress after a strain rise time of 0.1 s, and G_{rt} is the stress value used to determine the corresponding relaxation time (Steffe, 1992). The relaxation time (τ) is an indication of the viscous property, and G_{ae} is an indication of the inherent elastic property of a viscoelastic material.

Statistical Analysis. Three myosin extractions were performed, and each was used as a replication. For each extraction, four birds were euthanized and the muscles were pooled. Significant differences were determined by analysis of variance using the PROC VARCOMP procedure (SAS Institute Inc., 1990), with the replication as a random variable and muscle myosin as a fixed variable. Where differences between the means were found using the F test, mean differences were evaluated using the Duncan test (Steel and Torrie, 1980).

RESULTS

All myosin gels were very elastic, making G' values much greater than the G'' values; therefore, only G' values are reported. Representative data for all three myosins for heating from 25 to 75 °C and cooling to 25 °C are shown in Figure 1, and means obtained by statistical analysis are presented in Table 1. Onset of the storage modulus for the pectoralis myosin occurred 5 °C lower than the iliotibialis and gastrocnemius myosins, which were not significantly different from each other. The shape of the heating curves (0−50 min) were different between the red and white muscle myosins (Figure 1). The G' values for pectoralis myosin gels reached a plateau between 45 and 50 °C and then rapidly increased after 50 °C, whereas the red muscle myosin gels developed rapidly without an initial plateau. At 75 °C, the pectoralis myosin gels had significantly higher G' values than the iliotibialis and gastrocnemius myosin gels, which were not significantly different than each other (Table 1). Differences in the onset temperatures and G' values at 75 °C for white and red muscle myosins were also found with bovine myosins (Egelandsdal et al., 1985; Fretheim et al., 1986).

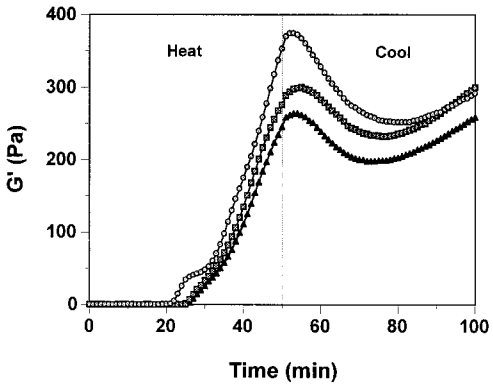

Figure 1. Effect of heating from 25 to 75 °C and cooling to 25 °C on the G' values of pectoralis (circles), iliotibialis (squares), and gastrocnemius (triangles) myosin dispersions/gels. The data are for the replication that was closest to the mean values of the three replications.

Table 1. Rheological Attributes for Gelation (100 min) of Pectoralis, Iliotibialis, and Gastrocnemius Myosins

	myosin		
attribute	pectoralis	iliotibialis	gastrocnemius
Dynamic Measurements[c]			
onset temp (°C)	45.4[b]	50.1[a]	51.1[a]
G' at end of heating (Pa)	364[a]	287[b]	234[b]
G' at end of cooling (Pa)	324[a]	291[a]	245[a]
temp at G' min in cooling (°C)	44.8[a]	48.5[a]	50.3[a]
Stress Relaxation[d]			
relaxation time (τ) (min)	1.0[a]	2.8[a]	1.5[a]
G_i (Pa)	388[a]	338[a]	285[a]
G_{ae} (Pa)	242[a]	218[a]	176[a]
$G_i - G_{ae}$ (Pa)	146[a]	120[a]	109[a]

[a,b] Means within a row with different superscripts are significantly different ($P < 0.05$). [c] Myosin solutions were heated from 25 to 75 °C and then cooled to 25 °C at a rate of 1 °C/min. [d] A constant strain of 0.0213 was applied, and stress was measured every 1 min for 1 h.

All of the myosin gels had a decrease and then a slight increase in G' values upon cooling (Figure 1). The temperature at which the lowest G' values occurred was not found to be significantly different for the myosins. This point occurred at a temperature which was close to the onset temperature (Table 1). The G' values at the end of cooling to 25 °C were not significantly different among the myosins (Table 1).

The similar physical properties among gels at the end of cooling is further shown in the viscoelastic properties determined by stress relaxation analysis (Table 1). There were no significant differences among myosin gels in τ, G_{ae}, or $G_i - G_{ae}$.

The significantly ($P < 0.05$) larger G' values of the pectoralis myosin gels at the end of the heating from 25 to 75 °C could be due to a kinetic limitation in G' development for red muscle myosin gels. The heating time was extended to determine if this was what caused lower G' values in iliotibialis and gastrocnemius myosin gels at 75 °C. The same regime of heating, cooling, and stress relaxation was done, but after heating to 75 °C, the gels were held at 75 °C for 3 h prior to cooling. All the myosins had the same statistical trends for transi-

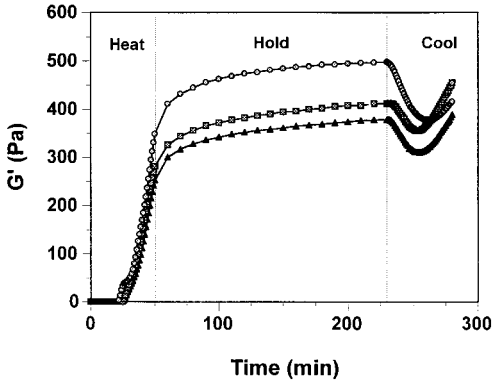

Figure 2. Effect of heating from 25 to 75 °C, holding at 75 °C for 3 h, and cooling to 25 °C on G' values of pectoralis (circles), iliotibialis (squares), and gastrocnemius (triangles) myosin dispersions/gels. The data are for the replication that was closest to the mean values of the three replications.

Table 2. Rheological Attributes for Gelation (280 min) of Pectoralis, Iliotibialis, and Gastrocnemius Myosins

attribute	myosin		
	pectoralis	iliotibialis	gastrocnemius
Dynamic Measurements[c]			
onset temp (°C)	45.4[b]	50.3[a]	51.1[a]
G' at end of heating (Pa)	371[a]	288[b]	240[b]
G' at end of additional isothermal heating (Pa)	547[a]	413[b]	362[b]
G' at end of cooling (Pa)	518[a]	428[a]	383[a]
temp at G' min in cooling (°C)	46.3[a]	50.8[a]	50.1[a]
Stress Relaxation[d]			
relaxation time (τ) (min)	0.8[a]	1.5[a]	1.2[a]
G_i (Pa)	648[a]	533[a]	479[a]
G_{ae} (Pa)	456[a]	375[a]	332[a]
$G_i - G_{ae}$ (Pa)	192[a]	158[a]	147[a]

[a,b] Means within a row with different superscripts are significantly different ($P < 0.05$). [c] Myosin solutions were heated from 25 to 75 °C at 1 °C/min, held at 75 °C for 180 min, and then cooled to 25 °C at a rate of 1 °C/min. [d] A constant strain of 0.0213 was applied, and stress was measured every 1 min for 1 h.

tion temperatures and rheological values (Table 2) as in the first gelation experiment (Table 1) without the 3 h curing period at 75 °C. During the 3 h hold at 75 °C, there was a decrease in the rate of G' increase for all myosins, and the red muscle myosin gels did not reach G' values that were similar to those of pectoralis myosin gels (Figure 2). The G' values of pectoralis myosin gels at the end of the 3 h hold were significantly ($P < 0.05$) greater than those for red muscle myosin gels, which were not significantly different from each other (Table 2). Thus the differences in G' values seen in the 100 min heating/cooling regime were not due to a kinetic limitation imposed on the gelation reaction. Holding times >3 h were not attempted; however, the rate of increase in G' over the last 1 h of holding at 75 °C showed that the rate of pectoralis myosin was 13 Pa/h, whereas the rates for iliotibialis and gastrocnemius myosin were 10 and 11 Pa/h, respectively. It appears that the red muscle myosins would not be able to reach the same storage modulus if a longer holding time was used.

Myosin gelation was also investigated under static heating conditions (Figures 3−5). The two red muscle myosin solutions showed no increase in G' values during heating and cooling at 45 °C, so only the pectoralis myosin data are shown in Figure 3. At 45 °C, the pectoralis myosin had a rapid increase in G' values within the first 20 min and then began to level off.

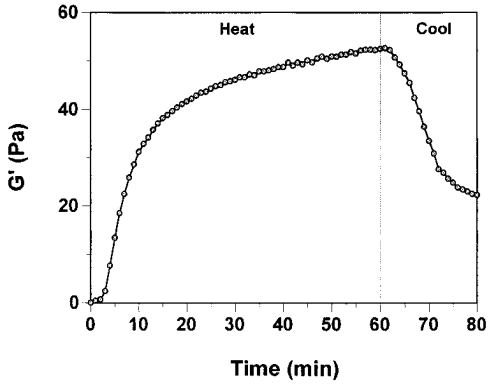

Figure 3. G' values for isothermal heating at 45 °C for a pectoralis myosin dispersion/gel. The data are for the replication that was closest to the mean value of the three replications.

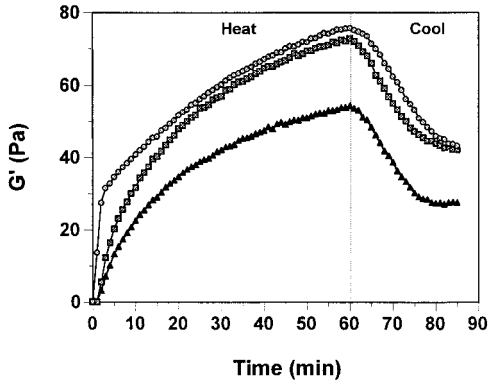

Figure 4. G' values for isothermal heating at 50 °C of pectoralis (circles), iliotibialis (squares), and gastrocnemius (triangles) myosin dispersions/gels. The data are for the replication that was closest to the mean values of the three replications.

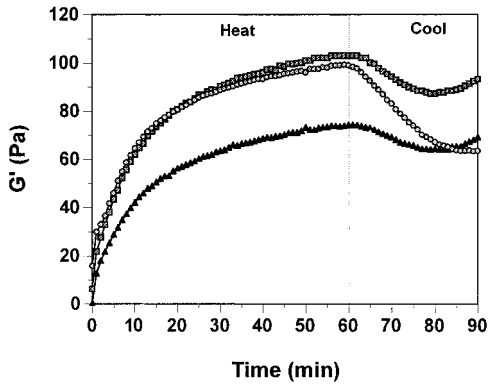

Figure 5. G' values for isothermal heating at 55 °C of pectoralis (circles), iliotibialis (squares), and gastrocnemius (triangles) myosin dispersions/gels. The data are for the replication that was closest to the mean values of the three replications.

During cooling there was a decrease in G' values; however, G' did not have an increase at the lower temperatures as seen in the dynamic heating experiments.

When myosins were heated at 50 °C for 1 h, there was no significance difference between the G' values for pectoralis and iliotibialis myosin gels, but their values were significantly higher than that of gastrocnemius myosin gels (Figure 4 and Table 3). These differences were also found when the gels were cooled to 25 °C. During cooling, all myosin gels decreased with no subsequent increase in G' values, which was similar to

Table 3. Effects of Isothermal Heating on Storage Modulus and Stress Relaxation Parameters for Pectoralis, Iliotibialis, and Gastrocnemius Myosins

		dynamic measurements			stress relaxation[c]			
temp (°C)	muscle myosin	G' at end of heating (Pa)	G' at end of cooling (Pa)	temp at G' min in cooling (°C)	relaxation time (τ) (min)	G_i (Pa)	G_{ae} (Pa)	$G_i - G_{ae}$ (Pa)
45	pectoralis	57.5	27.1	25.0	2.7	37.7	12.0	25.7
	iliotibialis	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	gastrocnemius	0.0	0.0	0.0	0.0	0.0	0.0	0.0
50	pectoralis	72.6[a]	44.4[a]	25.0[a]	13.4[a]	56.9[a]	26.5[a]	30.4[a]
	iliotibialis	74.6[a]	44.5[a]	25.0[a]	14.6[a]	48.1[a]	24.8[a]	23.2[a]
	gastrocnemius	49.6[b]	24.7[b]	25.0[a]	16.2[a]	31.9[a]	12.6[a]	19.3[a]
55	pectoralis	98.6[a]	68.8[a]	25.0[a]	8.3[a]	88.1[a]	56.3[a]	31.8[a]
	iliotibialis	110.2[a]	88.8[a]	29.7[a]	3.0[a]	113.7[a]	77.0[a]	36.7[a]
	gastrocnemius	70.4[a]	62.2[a]	31.0[a]	7.5[a]	76.6[a]	37.6[a]	39.0[a]

[a,b] Means within a column for each temperature with different superscripts are significantly different ($P < 0.05$). [c] A constant strain of 0.0213 was applied, and stress was measured every 1 min for 1 h.

the pectoralis myosin gels formed at 45 °C. There was no significant difference among myosin gels for any of the parameters determined from stress relaxation at 25 °C (Table 3).

All myosin gels were similar when formed by heating at 55 °C for 1 h (Figure 5, Table 3). When the gels were cooled to 25 °C, G' values of pectoralis myosin gels decreased with no subsequent increase, similar to transitions seen at 45 and 50 °C. G' values of red muscle myosin gels decreased with a subsequent increase as the temperature approached 25 °C, similar to cooling curves obtained with the dynamic heating experiments.

DISCUSSION

This investigation and earlier studies (Engelandsdal et al., 1985; Fretheim et al., 1986) found that, under dynamic gelation conditions, white muscle myosin gels had higher G' values than red muscle myosin gels. There was no difference between the red muscle myosins. White muscle myosin began to gel at least 5 °C lower than the red muscle myosins during isothermal and dynamic heating. Engelandsdal et al. (1985) and Fretheim et al. (1986) showed that bovine white muscle myosin gels at a lower temperature than red muscle myosin; however, the difference was much less than seen in this study with chicken myosins. The shape of G' curves for chicken white and red muscle myosins in this study are similar to those for corresponding white and red bovine myosins (Engelandsdal et al., 1985; Fretheim et al., 1986). These observations support previous investigations that have shown greater similarities within twitch speed isoform types among species than between isoform types within species (Stabursvik and Martens, 1980). Pectoralis myosin started gelling at a lower temperature than the red muscle myosins; therefore, the total network formation time was longer for pectoralis myosin. However, the greater G' values for pectoralis myosins gels at 75 °C were not due to kinetic limitations for red myosin gelation, as adding a 3 h holding period at 75 °C did not alter the relative magnitudes.

The first two reactions in thermally induced gelation of proteins are unfolding and aggregation. All of the myosins were found to begin unfolding (T_o) at 33−36 °C and had similar initial transition (T_{m1}) temperatures of 48−49.5 °C (Liu et al., 1995). However, only the pectoralis myosin was found to aggregate (Liu et al., 1995) and gel when heated isothermally at 45 °C. This indicates that the calorimetry-detected transitions in the structure of red myosins at temperatures ≤45 °C are insufficient to cause intermolecular aggregation.

Ferry (1948) suggested that thermally induced protein gelation is due to association of polypeptide chains at attractions that act along the entire molecular length. This type of association makes the gel matrix structure aggregation rate dependent. The aggregation rates for the three muscle myosins were not different when heated at a constant 50 °C; however, the red muscle myosins (iliotibialis and gastrocnemius) formed more particles and/or larger particles than pectoralis myosin (Liu et al., 1996). This difference in aggregation patterns did not produce coinciding rheological difference at 50 °C. The pectoralis and iliotibialis myosins formed gels with similar G' values that were significantly higher ($P < 0.05$) than those of the gastrocnemius myosin gels. Gels formed at 55 °C had similar rheological properties; however, there were differences in the aggregation rates. Gastrocnemius myosin had a significantly higher ($P < 0.05$) aggregation rate than the pectoralis and the iliotibialis muscle myosins at 55 °C (Liu et al., 1995). These observations lead to the conclusion that the close link between aggregation rate and gel network formation suggested by Ferry (1948) was not seen in myosin gelation. However, the type of aggregates formed may be related to rheological properties. Gastrocnemius myosin consistently had the highest turbidity values (Liu et al., 1996) and lowest G' values (Table 3) at the end of heating at 50 and 55 °C. While these differences were not always significant at the 95% level, the trend suggests that an increase in the average aggregate size causes a decrease in matrix rigidity.

Rheological transitions in the initial heating and holding phases are associated with the formation of a gel matrix and addition of dispersed molecules as the gel cures. In contrast, G' transitions associated with cooling are assumed to reflect interactions of a "formed" matrix, i.e., one with a constant degree of polymerization. Specific to our experimental conditions, changes in G' values seen in cooling reflect interactions that do not relax within the 0.16 s testing period. These could be interactions affecting intrastrand stiffness or interstrand cross-links. Within the temperature range 25−75 °C, hydrophobic interactions and entropy (rubber) elasticity increase with temperature (Privalov and Gill, 1988; Mark, 1984), whereas hydrogen bonds decrease. These temperature dependencies allow one to make some general conclusions regarding the predominant forces responsible for mechanical properties of the gel matrix. The pectoralis myosin gels were more rigid at 75 °C than the iliotibialis and gastrocnemius myosin gels; however, this difference was not present once the gels were cooled to 25 °C. Figures 1 and 2 show that

this was due to a decrease in G' values of pectoralis myosin gels during the first stage of cooling (75−50 °C), followed by an increase in the G' values of iliotibialis and gastrocnemius myosin gels at the latter stage of cooling (50−25 °C). These trends were also seen in isothermal gelation. Pectoralis myosin gels formed at 45−55 °C never showed an increase in G' with cooling. Red muscle myosin gels showed cooling-associated increases of G' in gels formed at 55 °C. Hydrogen bonding appears to play a more significant role in red muscle myosin gel rigidity, whereas hydrophobic interactions and rubber elasticity dominate white muscle myosin gel rigidity.

The temperature corresponding to the minimum G' seen in cooling was not different among the myosin gels within each experiment and very close to the onset temperature of gelation (Tables 1 and 2). Coinciding temperatures for gelation onset and cooling-induced rheological transitions in the gel matrix suggest that re-formation of "nativelike" hydrogen-bonded structures are responsible for the increase in G'. Clearly, this deduction needs to be verified by experimental evidence.

Dynamic measurements of rheological properties of viscoelastic gels are limited by being frequency dependent. Viscous relaxations which require a longer time to occur than the measuring period remain in-phase with strain oscillations and are calculated as part of G'. Stress relaxation experiments are done statically over longer periods of time (1 h in our experiments), which permits a more accurate analysis of elastic and viscous components. A completely elastic gel would show no decrease in G' during stress relaxation and $G' = G_{ae}$. Gels formed under dynamic heating conditions had G_{ae} values that were 72−88% of the G' values determined dynamically after cooling. Moreover, there was a general trend for an increase in elasticity, as shown by G' representing a higher proportion G_{ae}, as heating temperature (Table 3) or time (Tables 1 and 2) increased. This could be due to addition of dispersed molecules to the gel matrix or an increase in intramatrix interactions that do not relax in 1 h. The relaxation time indicated the period required for 37% of the total (1 h) relaxations to occur. This property was sensitive to isothermal heating temperature (Table 3) but did not show any isoform-associated difference.

This investigation has shown that isoform-associated differences in G' values of myosin gels seen at 75 °C are removed when the gels are compared at 25 °C. The absence of isoform-associated differences has also been seen in fracture properties (i.e., large-strain) of gels determined at 25 °C. Thermally induced gels made from turkey breast and thigh myofibrils have similar stress at fracture and strain at fracture values at 25 °C (Lavelle and Foegeding, 1993; Northcutt et al., 1993). Lavelle and Foegeding (1993) also evaluated G values from the nonfracture region of torsional force−deformation curves. No differences in G values were found between thermally induced breast and thigh myofibril gels which were formed at two pHs (6.0 and 6.4), two salt concentrations (0.5 and 1.0 M NaCl), and two temperatures (55 and 70 °C). Our data on nonfracture rheological properties of myosin gels 25 °C are consistent with both nonfracture and fracture properties of myofibril gels.

CONCLUSIONS

Myosin isoforms from three chicken muscles showed different rheological properties during thermally induced gelation. Pectoralis myosin gelled at a lower temperature and developed a greater G' at 75 °C than red muscle myosins (iliotibialis and gastrocnemius). The ability for pectoralis myosin to gel at lower temperatures is consistent with a lower aggregate temperature than red muscle myosins (Liu et al., 1996). Cooling from 75 to 25 °C causes a decrease in G' of pectoralis myosin gels and a slight increase in G' values of iliotibialis and gastrocnemius myosin gels. The net result of the dissimilar rheological transitions was that there was no difference in viscoelastic properties among chicken myosin gels at 25 °C. Since rheological properties of myosin gels depend strongly on gel temperature, experimental conditions should reflect the temperature relevant to the meat property being evaluated.

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