SKELETAL MUSCLE STIFFNESS IN STATIC AND DYNAMIC CONTRACTIONS

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Abstract—Series elastic stiffness of rat gastrocnemius medialis muscle was determined by means of sinusoidal movements (180 Hz, 0.25% of muscle length) for various contraction conditions. The effects of muscle length, activation level, velocity, prestretch, and temperature on the force–stiffness relationship were investigated. All force–stiffness curves were transformed to a linear force–a curve (Ettema and Huijing, 1993; Morgan, 1977) to distinguish mathematically two series elastic components; a force dependent and force independent compliance. For all isometric conditions a typical force–stiffness curve was found, where stiffness increased with force, and this increase levelled off at higher forces. Stiffness in dynamic shortening and lengthening contractions is related to force in a completely different way than in isometric condition. An increase in temperature caused a decrease in muscle stiffness for a given force, and the effects of muscle length, activation level, and prestretch were small. It was concluded that the series elastic component of skeletal-muscle-tendon complex is probably located in more than two morphologically identifiable elements. Furthermore, we concluded that using a single series elastic element in muscle modelling is not appropriate to describe muscle behaviour under all conditions that occur during in vivo activation.

INTRODUCTION

Elasticity of skeletal muscle is an important factor in the fields of motor control (Nichols and Houk, 1976) and energetics of locomotion (Alexander, 1988, Biewener and Blickhan, 1988; Cavagna, 1970, 1977). Regarding this elasticity, two different types of elasticity should be distinguished. First, muscle force strongly depends on muscle length and velocity of length change. The stiffness (i.e. ratio of force change and length change) of the muscle is determined by the interaction of all muscle components. Thus, this stiffness refers to a property of the entire muscle–tendon entity. Another type of stiffness relates to the properties of the so-called series elastic component (SEC) of the muscle. The SEC is a component of a phenomenological muscle model, and is located in series with the contractile machinery of the muscle (e.g. Cavagna, 1977; Hill, 1970; Proske and Morgan, 1987). The SEC is believed to be located mainly in the tendinous structures and cross-bridge attachments of the muscle–tendon complex (Ettema and Huijing, 1993; Morgan, 1977). The stiffness of SEC is often referred to as short-range stiffness, because SEC stiffness equals muscle stiffness in small (and rapid) movements. In such conditions, sliding of the myofilaments caused by cross-bridge cycling does not occur, and all length changes of the muscle are taken up by SEC, including elasticity of the cross-bridges (i.e. sarcomeres may show elastic length change). SEC stiffness plays an important role in the energetics of muscle contraction, since it is a passive structure, which can take up and release mechanical energy without any chemical energy turn over (see Cavagna (1977) for a review). It should be noted that to take up elastic energy, resistance has to be provided, which under in vivo condition would require metabolic energy from the organism. In other words, the origin of the stored elastic energy is metabolic. Furthermore, the role of SEC in motor control must be recognised (Proske and Morgan, 1987).

The problem of location of parts of SEC in separate morphological structures has been attended to in the literature (e.g. Ettema and Huijing, 1993; Morgan, 1977; Proske and Morgan 1987). Stiffness of tendinous structures and cross-bridges related to force differently; tendon stiffness depends on force in a unique non-linear way, whereas cross-bridge stiffness is primarily related to the number of attached cross-bridges, and thus only indirectly to muscle force. Therefore, the distinction between tendinous and cross-bridge elasticity has major implications for the overall behaviour and function of SEC. Even though it is generally known that the force–stiffness curve in isolated muscle fibres depends on the cross-bridge dynamics (see Pollack and Sugi (1984) for details), in many models of the muscle–tendon entity a single SEC force extension curve is implemented. The question is whether or not a single element can describe SEC behaviour, with such an accuracy that the model output is not seriously affected by this simplification (i.e. that the simplification does not cause artefacts) Ettema and Huijing (1993) showed that, to explain their results in rat
gastrocnemius with tendinous structures of about 2
times the length of muscle fibres, about 30% of series
elastic compliance had to be located within the cross-
bridges. Thus, we hypothesise that cross-bridge dy-
namics will seriously affect stiffness of an entire
muscle–tendon complex. Therefore, to be able to
assess this hypothesis appropriately, a good under-
standing of the tendon–cross-bridge distinction is
needed.

Morgan (1977) developed a simple method to dis-
tinguish mathematically these two components. This
method, the alpha- method, is based on two assump-
tions. The first one is that tendinous stiffness is
constant above about 20% of maximal isometric force
exerted by the muscle (we disagree with this assump-
tion, see below). The second assumption concerns a
linear force–extension relationship of the elastic com-
ponent within a single cross-bridge (Ford et al., 1977),
and the direct relation between the number of attach-
ed, force exerting cross-bridges and the total muscle
force. (Again, the second part of this assumption
cannot be supported generally for all muscle contrac-
tion conditions, see below). Morgan (1977) described
the relationship between total muscle compliance (i.e.
stiffness$^{-1}$) and force as follows:

\[ C = C_t + a_0/F \tag{1} \]

or

\[ \alpha = C^* F = C_t^* F + a_0, \tag{2} \]

where \( C \) is the SEC compliance, \( F \) is the muscle force,
\( C_t \) is the tendinous compliance and \( a_0 \) is the elastic
extension with the cross-bridges (which is the same for
all isometric forces); \( a_0/F \) is the elastic cross-bridge
compliance. Thus, by performing a linear regression
analysis on \( \alpha - F \) data, compliance of tendon and cross-
bridges could be distinguished. For a detailed discus-
sion of the method we refer to Morgan (1977) and
Ettema and Huijing (1993). Linear relationships of
experimental \( \alpha - F \) data were found by several investi-
gations (Ettema and Huijing, 1993; Morgan, 1977;
Morgan et al., 1978). However, Ettema and Huijing
(1993) showed that the linearity of the \( \alpha - F \) curve is not
a validation of the assumption of constant tendon
compliance, and they, and others (e.g. Benedict et al.,
1968), further demonstrated that tendon stiffness in-
creases with force, even at levels of maximal isometric
force. Ettema and Huijing (1993) concluded that a
part of the calculated \( a_0 \) should be apportioned to the
tendinous structures. Furthermore, experiments on
isolated frog fibres show that considerable part of
sarcomere compliance may reside outside the cross-
bridges, e.g. in the myofilaments (Blangt et al., 1985;
Jung et al., 1992), which would appear in the \( C_t \)
component (equation 2) of series elasticity.

In other words, although the \( \alpha - F \) curve has been
found to be linear, we do not \textit{a priori} support the
morphological distinction of tendinous and cross-
bridge compliance according to eq. (2). However, the
method can be used to distinguish mathematically two
different components of SEC: a force dependent and a
force independent (i.e. constant) component. There-
fore, we propose to rewrite equation (2) as

\[ \alpha = C^* F + a_0, \tag{3} \]

where the subscripts \( i \) and \( d \) represent elements of the
series elastic component of which stiffness is independ-
ent of and dependent on force, respectively. Note that
equations (2) and (3) are mathematically identical but
differ in their morphological interpretation.

The purpose of this particular study was to measure
stiffness of activated muscle under various conditions,
and compare the force–stiffness results for these condi-
tions. This way, we wanted to test if a single and
unique force–stiffness relationship exists for SEC of a
muscle–tendon entity, independent of the way active
force is generated. We also aimed to test whether or
not equation (3) holds as a simple model for a
muscle–tendon complex. By using equation (3), a more
detailed comparison is possible than by exclusively
comparing the original force–stiffness curves. Analysis
according to equation (3) for different contraction
conditions may yield understanding regarding the
morphological location of different parts (\( C_i \) and \( a_d \)) of
SEC: is the distinction of \( C_i \) and \( a_d \) exclusively math-
ematical or does it have a morphological basis? The
factors affecting muscle force and SEC stiffness that we
studied were muscle length, contraction velocity, ac-
tivation level, temperature, and muscle activation
history (prestretch).

**METHODS**

The experiments were performed on the gastrocne-
mius medialis (GM) muscle–tendon complex of the
rat. Ten young adult male Wistar rats (body mass
241–304 g) were anaesthetised with pentobarbital (ini-
tial dose 10 mg/100 g body mass ip.). The GM was
freed from its surrounding tissues leaving the muscle
origin and blood supply intact. The distal tendon and
part of the calcaneus were looped around a steel wire
hook, tightly knotted with suture and glued with
tissue glue (Histoacryl Blau, Melsungen). The steel
wire was connected to a strain gauge force transducer.
This procedure left the major part of the distal tendon
intact. All measurements were done within a time span
of 4 h. Ambient muscle temperature was controlled at
27°C by means of feedback-system-controlled infra-
red light heat source. Two thermocouples were placed
in a support table so that they were in direct contact
with the lower surface of the muscle, while the heat
source was positioned above the muscle. The muscle
was excited by stimulation of the distal end of the
severed nerve (square wave pluses; 0.4 ms duration,
3 mA, 100 Hz). Optimal length of the muscle–tendon
complex (\( l_0 \)), defined as that length at which active
isometric muscle force was highest (\( F_0 \)), was deter-
mined with an accuracy of 0.5 mm (around \( l_0 \) iso-
metric contractions were performed with 0.5 mm
length increments).
Stiffness of the muscle was measured by imposing 180 Hz sinusoidal length changes of 0.1 mm peak to peak, i.e. approximately 0.25% of muscle–tendon complex length, during muscle contractions (Ettema and Huijing, 1994). The total contraction time amounted to 300 ms, whereas the vibrations lasted 100 ms and were imposed after 150 ms contraction time, unless otherwise stated (see below).

Three groups of muscles were studied.

(A) In four muscles we studied the effects of muscle length, nerve stimulation current, and isokinetic velocity on stiffness. Muscle stiffness was determined under three different settings:

(i) Isometric contractions at different muscle lengths (ML). Muscle length ranged from 70% l0 to 105% l0 (1 mm increments, i.e. \(\sim 2.3\% \ l_0\)) to obtain a force range from near zero to \(F_0\),

(ii) Isometric contractions with different stimulation current at \(l_0\) (SC). In these experiments stimulation current varied from \(\sim 0.05\) to 3 mA (i.e. supramaximal) to obtain a similar force range as in the ML experiments.

(iii) Isokinetic contractions with different velocities through \(l_0\) (IK). Isokinetic velocities were +10, +15, 0, -5, -10, -20, -30, -40, and -50 mm s\(^{-1}\) (10 mm s\(^{-1}\) \(\approx 0.23\ l_0\ s^{-1}\), positive value is defined as lengthening). A 150 ms isometric contraction period preceded the isokinetic period, which lasted 100 ms. Optimum muscle length was reached in the middle of the isokinetic period. The starting muscle length and amplitude of movement were determined by the set velocity. A 50 ms period of 180 Hz vibrations was imposed 25 ms after onset of the isokinetic period. A total contraction time was 300 ms (50 ms of isometric contraction occurred at the end of the isokinetic period).

In addition to their experimental purpose, the ML-100% \(l_0\), SC-3 mA, and IK-0 mm s\(^{-1}\) conditions also served as control experiments to monitor the condition of the muscle preparation, as they all measure \(F_0\) . The largest difference in \(F_0\) during the experiments amounted to 6.5% of the maximal value of \(F_0\) obtained (this maximal value appeared to occur randomly in time).

(B) Seven muscles were used to study effects of active prestretch on the force stiffness relationship. In the prestretch experiments (PS) the muscles were stretched by 5 mm at 20 mm s\(^{-1}\) after which muscle length was kept constant (isometric period). Stimulation started 130 ms after the onset of-stretching, i.e. 120 ms prior to the end of the prestretch, and lasted until 300 ms after onset of the isometric period. Sinus vibrations were imposed after 100 ms of the isometric period for a duration of 100 ms. The control, preisometric experiments (PI) were similar to the stretch experiment, with the one difference that the muscle was already brought to the length of the isometric period prior to onset of stimulation. Thus the control experiments resembled the ML experiment, except for the duration of contraction. The PS and PI experiments were performed at lengths in the same region as the ML experiments.

(C) On four muscles the ML experiments were performed at 37°C (T37) and 27°C (T27) ambient muscle temperature, in this respective order. At 37°C we needed a higher stimulation frequency to obtain a fused tetanus (Ranatunga, 1982). We used the lowest possible frequency that was determined in a pilot study at 143 Hz. The T37 at \(l_0\) experiment was repeated as a last measurement for control purposes.

Length and force tracings were A/D converted (2500 Hz, accuracy 2.5 μm and 0.01 N, respectively). The force tracings were corrected for artefacts due to accelerations of the force transducer (Ettema and Huijing, 1994). The signals were filtered, using a Butterworth 25–300 Hz, 16th order band pass filter. Average muscle stiffness was calculated as the ratio of the peak-to-peak force difference and peak-to-peak length difference during the sinusoidal movements. Stiffness was corrected for compliance of the measurement system (0.014 mm N\(^{-1}\)) \([S_{comp} = 1/(1/S_{total} – C_{system})]\). Stiffness was averaged over all but the first couple of sinus movements; the first two complete sinus cycles were excluded from data analysis to allow for preconditioning. Stiffness values were transformed to alpha values according to

\[\alpha = \frac{F}{S},\]

where \(S\) is the stiffness at force level \(F\) (see the introduction section for the interpretation).

Alpha was plotted against muscle force, and linear regression analysis was performed for these data. All data at forces below 15% \(F_0\) (\(\sim 2N\)) were excluded from the fitting procedure because of known deviation from a straight line (Ettema and Huijing, 1993; Morgan 1977). The intercept (\(x_0\)) and slope (\(C_0\)) of the linear regression represent extension of force dependent elasticity and compliance of the force independent elasticity, respectively (see equation 3).

**Statistics**

The two variables \(x_0\) and \(C_0\) were tested for the different experimental conditions as follows. Effects of conditions (ML, SC and IK) were tested for significance by means of a one way ANOVA for repeated measures and a Tukey post hoc test was used to locate possible differences. The IK condition was split into a couple of sinus movements; the first two complete sinus cycles were excluded from data analysis to allow for preconditioning. Stiffness values were transformed to alpha values according to

\[\alpha = \frac{F}{S},\]

where \(S\) is the stiffness at force level \(F\) (see the introduction section for the interpretation).

Alpha was plotted against muscle force, and linear regression analysis was performed for these data. All data at forces below 15% \(F_0\) (\(\sim 2N\)) were excluded from the fitting procedure because of known deviation from a straight line (Ettema and Huijing, 1993; Morgan 1977). The intercept (\(x_0\)) and slope (\(C_0\)) of the linear regression represent extension of force dependent elasticity and compliance of the force independent elasticity, respectively (see equation 3).

**RESULTS**

The most relevant morphological and physiological data of the muscles used are shown in Table 1. Note that the length of tendinous structures is about 2.2 times fibre length, and about 70% of total...
Table 1. Morphological and physiological characteristics of the experimental muscles. Variables: $l_0$ is optimum muscle-tendon complex length; $l_1$ is fibre length, $l_2$ is length of tendinous structures, and $F_o$ is isometric force at $l_0$, respectively.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>ML−SC−IK</th>
<th>PS vs PI</th>
<th>T27 vs T37</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$X$ SE n</td>
<td>$X$ SE n</td>
<td>$X$ SE n</td>
</tr>
<tr>
<td>$l_0$ (mm)</td>
<td>43.00 0.35 4</td>
<td>42.71 1.58 7</td>
<td>46.05 3.21 4</td>
</tr>
<tr>
<td>$l_1$ (mm)</td>
<td>13.75 0.56 4</td>
<td>13.14 0.64 7</td>
<td>14.50 0.71 4</td>
</tr>
<tr>
<td>$l_2$ (mm)</td>
<td>29.88 0.96 4</td>
<td>30.36 1.09 7</td>
<td>31.68 3.08 4</td>
</tr>
<tr>
<td>Muscle mass (g)</td>
<td>0.98 0.03 3</td>
<td>0.84 0.06 7</td>
<td>1.01 0.30 4</td>
</tr>
<tr>
<td>$F_o$ at 27°C (N)</td>
<td>13.34 0.58 4</td>
<td>12.15 0.98 7</td>
<td>11.51 1.77 4</td>
</tr>
<tr>
<td>$F_o$ at 37°C (N)</td>
<td></td>
<td>12.24 2.02 4</td>
<td></td>
</tr>
<tr>
<td>Rat mass (g)</td>
<td>293.25 9.68 4</td>
<td>248.29 4.46 7</td>
<td>364.75 95.81 4</td>
</tr>
</tbody>
</table>

muscle-tendon complex length. Muscle force at optimum length is somewhat higher at 37°C compared to $F_o$ at 27°C (6.2% ± 1.2%), and a considerable increase in isometric force is seen due to active pre-stretch (Fig. 1).

In Fig. 1 typical examples of force-stiffness and force-$\alpha$ results are shown for the ML, SC and IK conditions; the average results for all muscles are presented in Table 2. A significant effect of condition on $\alpha_2$ and $C_i$ was found (one-way ANOVA, $p<0.01$). Both ML and SC data resulted in linear force-$\alpha$ curves, except for forces below 2 N, which data were excluded from linear regression. The correlation coefficients varied from 0.986 to 1.000. The differences between ML and SC conditions are small and not significant. The force-stiffness relationship for IK contraction differs greatly from the ML curve. Particularly, the shape of the curve is typical: in the lower force region (IK-lo), at shortening velocities from $-50$ to $-10$ mm$^{-1}$, the curve is relatively flat with a maximum stiffness at about $-30$ mm$^{-1}$, to become much steeper at higher forces (IK-hi; velocities from $-10$ to $+10$ mm$^{-1}$). This distinction between these two regions of the force-stiffness curve becomes even more apparent when expressed in a $F$-$\alpha$ plot (Fig. 2B).

Whereas linear regression on all IK data resulted in poor fittings, good results were obtained for regression on the two subgroups (correlation coefficients from 0.988 to 0.998 for IK-lo, and 0.515 to 0.998 for IK-hi; the $r=0.515$ was due to an almost horizontal fit with a slope not significantly differing from zero). The two subgroups (IK-hi and IK-lo) both differed from ML regarding $\alpha_2$ and $C_i$. Furthermore, $\alpha_2$ was larger for the IK-hi condition, whereas $C_i$ was larger for the IK-lo condition (Table 2). Thus, although individual data points of the IK experiments may not deviate from the ML and SC curves, the entire IK curves differ significantly from the isometric (ML and SC) curves. These results can be summarised as follows. First, for isometric conditions, changing muscle force by sub-maximal stimulation or by reducing muscle length, has only minor and statistically not significant effects on force-stiffness characteristics. Second, the force-stiffness relationship in isokinetic contractions is totally different from that relationship under isometric conditions.

The results of history and temperature effects are shown in Fig. 3 (typical examples) and Table 3. All $\alpha$-data fitted well to a linear curve, which correlation coefficients from 0.970 to 0.999, and an average of 0.990. Note that the force-stiffness curves do not differ greatly between PI and PS conditions, but that both $\alpha_2$ and $C_i$ differ significantly between conditions. Considerable effects are induced by a change of temperature (Table 3B, Fig. 3C and D), at 37°C, stiffness is decreases about 15% at $F_o$ when compared with the 27°C values. This decrease in stiffness is expressed in an increased $C_i$ and unaltered $\alpha_2$. 

![Fig. 1. Typical example of length force relationships for prestretch and preisometric contractions at 27°C (A), and for standard isometric contractions at 27°C and 37°C.](image-url)
Table 2. Mean and (se) of the $s_d$ and $C_i$ found by regression according to equation (3) for isometric (ML and SC) and dynamic experiments (IK-hi and IK-lo) (n=4). For both variables a significant effects was found (one-way ANOVA, $p<0.01$). Location of significant differences are denoted by * (different from ML, $p<0.01$); † (different from SC, $p<0.05$); ‡ (different from IK-hi, $p<0.01$). (Tukey post hoc test)

<table>
<thead>
<tr>
<th></th>
<th>ML (0.051)</th>
<th>SC (0.009)</th>
<th>IK-hi (0.041)††</th>
<th>IK-lo (0.010)††</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s_d$</td>
<td>0.466</td>
<td>0.531</td>
<td>0.754</td>
<td>0.129</td>
</tr>
<tr>
<td></td>
<td>(0.079)</td>
<td>(0.075)</td>
<td>(0.136)††</td>
<td>(0.041)††</td>
</tr>
<tr>
<td>$C_i$</td>
<td>0.035</td>
<td>0.032</td>
<td>0.014</td>
<td>0.089</td>
</tr>
<tr>
<td></td>
<td>(0.004)</td>
<td>(0.004)</td>
<td>(0.005)††</td>
<td>(0.010)††</td>
</tr>
</tbody>
</table>

Table 3. Mean and (se) of the $s_d$ and $C_i$ found by regression according to equation (3) for (A) prestretch (PS) and pre-isometric (PI) experiments at 27°C (n=7), (B) isometric contractions at 27°C (T27) and 37°C (T37) (n=4). Significant differences are indicated by ↑ ($p<0.01$)

<table>
<thead>
<tr>
<th></th>
<th>A $s_d$</th>
<th>C_i</th>
<th>B $s_d$</th>
<th>C_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS</td>
<td>0.452</td>
<td>0.042</td>
<td>0.305</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>(0.051)</td>
<td>(0.009)</td>
<td>(0.022)</td>
<td>(0.006)</td>
</tr>
<tr>
<td>PI</td>
<td>0.499</td>
<td>0.038</td>
<td>0.307</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td>(0.038)</td>
<td>(0.008)</td>
<td>(0.017)</td>
<td>(0.008)</td>
</tr>
</tbody>
</table>

Fig. 2. Typical example of force-stiffness (A) and force-α (B) data for ML, SC and IK experiments. The symbols represent different conditions. In Figure B and IK data are separated in IK-h (■) and IK-lo (□). The grey markers (F < 2N) indicate data omitted from linear regression. The lines in Fig. A are connecting the data points, in B they represent the linear fittings; the dashed line is the SC fit.

Fig. 3. Typical example of force-stiffness (A) and force-α (B) data for PS-PI experiments at 27°C, and for isometric experiments at 27 and 37°C (C and D). The grey markers, F < 2N, (B) indicate data omitted from linear regression. The lines in Figs B and D are the linear fittings.
DISCUSSION

Our findings indicate that muscle stiffness increases with muscle force, even at levels around $F_0$. These data confirm literature findings (Morgan, 1977; Morgan et al., 1978; Proske and Morgan, 1984, 1987; Ettema and Huijing, 1993). In all isometric conditions, a mathematical distinction in a force dependent and independent series elastic component does apply for forces higher than $\sim 15\% F_0$. In other words, equation (3) is an appropriate fitting equation in this condition. Our present results further indicate that the relationship between muscle stiffness and force is not the same under different types of isometric and dynamic loading. Although this is known for the short-range stiffness residing in the cross-bridges (e.g. Sugi and Tsuchiya, 1988), this fact has not been well established for an entire muscle–tendon entity. Most of the series elasticity of the muscle–tendon complex resides within the tendinous structures (Ettema and Huijing, 1993). However, apparently a significant amount is located in the cross-bridges, such that it influences the force–stiffness relationship of the entire muscle. An alternative explanation may be that tendinous compliance is affected not exclusively by muscle force, but also by the way that force is generated. In that case the aponeurosis is the most likely structure to behave in such a manner: several studies have shown that the aponeurosis does not behave almost exclusively elastically, as the external tendon does; force–elongation curves differ depending on the way force is exerted (Huijing and Ettema, 1988; Ettema and Huijing, 1989; Zuurbier et al., 1994).

Isometric and dynamic stiffness

A large discrepancy in elastic behaviour of SEC is found between isometric and isokinetic contractions. The force–stiffness curves of all isometric experiments (ML, SC, PI, PS, T27, and T37) have an inverse exponential shape, and are consistent with data in the literature on muscular and tendinous stiffness (Butler et al., 1978; Bennett et al., 1986; Proske and Morgan, 1987; Ettema and Huijing, 1989, 1993). The IK curve does not resemble such a relationship, and should actually be described differently for two velocity ranges (see results). This distinction of two parts was confirmed by the alpha analysis. Although the non-elastic behaviour of the aponeurosis (Ettema and Huijing, 1989; Huijing and Ettema, 1988/1989; Zuurbier et al., 1994) should not be ignored, it seems most likely that cross-bridge dynamics are the key to a sound explanation of the isometric–dynamic differences. Our results do not allow a detailed analysis of cross-bridge dynamics. However, a few remarks can be made about whether or not results are in accordance with the current knowledge on cross-bridge dynamics. The clear distinction between IK-lo and IK-hi velocities indicates a difference in cross-bridge dynamics. Qualitative differences exist in cross-bridge dynamics between concentric and eccentric contractions, with the isometric contraction as the transition point (Morgan et al., 1991). In our experiments the velocity at the transition between IK-lo and IK-hi velocities is not zero but between $-5$ and $-10\text{ mms}^{-1}$. However, Zuurbier and Huijing (1992) showed that in rat GM at $I_0$, shortening of muscle fibres is approximately 80–85% of the muscle–tendon complex (caused by a small velocity of tendinous structures and pennation). Thus, in our experiments the transition velocity at the level of the contractile component was probably closer to zero than the externally measured value.

If, for the sake of argument, one would assume the alpha method (Morgan, 1977) as expressed in equation (2) to be correct in principle (see introduction), then the large effect on $C_i$ would indicate involvement of tendinous structures and myofilaments (i.e. non-cross-bridge compliance). We do not have any explanation for this finding, other than a considerable amount of cross-bridge compliance expressed in $C_i$, and thus the morphological distinction cannot be made. At a given muscle force, a higher stiffness (i.e. lower $\alpha$) in shortening contractions was expected than in isometric contractions, caused by a relative higher number of attached cross-bridges (Julian and Morgan, 1981; Julian and Sollins, 1975). Our results confirm this expectation only for the highest shortening velocities ($-50$ to $-30\text{ mms}^{-1}$, Fig. 2). At present we have no explanation for the low stiffness values at the lower shortening velocities.

The stiffness values for the eccentric contractions tend to be a bit higher than was expected on basis of isometric results, which is reflected by lower alpha values (see equation 4, Fig. 2B). This could have been explained by relatively more attached cross-bridges to exert a given force. However, this explanation is in contradiction with results on isolated fibres (Sugi and Tsuchiya, 1988), and thus a more complicated explanation concerning cross-bridge cycling must be sought.

Force production, as well as force enhancement due to prestretch are affected by the distance of previous length change (e.g. Edman, 1975; Ettema et al., 1990, 1992). Thus it is likely that stiffness in dynamic contractions have also been affected by the amount of shortening and lengthening. However, the distance of length change in our experiments was directly related to the velocity of length change, and can therefore not explain the typical shape of the force–stiffness curve.

Temperature

The ambient temperature affected isometric muscle force in a slightly positive way. This is in agreement with what is described for lizard (Bennett, 1985) and cat muscles (Buller et al., 1984).

Muscle stiffness at $F_0$ decreased about 15% when temperature was increased from 27 to $37^\text{C}$. This decrease was expressed in an increased $C_i$ and unaltered $\alpha$. Again, assuming the correctness of the alpha method, our observations indicate that the
decreased stiffness originates in structures other than cross-bridges. The information on temperature effects on tendons and ligaments in the literature is ambiguous (Lam et al., 1990). However, results on the canine medial collateral ligament indicate that stiffness may decrease approximately 10% with a 10°C temperature increase (Woo et al., 1987). Assuming that tendons and ligaments have qualitatively similar mechanical properties, our results are in agreement with these findings. However, Ford et al. (1977) reported $Q_{10}$ value for relative cross-bridge stiffness of 0.7–0.8. Thus, the decreased stiffness most likely originated in the cross-bridges also. In other words, the fact that the temperature only affected $C_i$, indicates the impossibility to allocate $\alpha_d$ and $C_i$ to cross-bridge and non-cross-bridge elasticity, respectively.

**Muscle length and activation level**

The muscle stiffness–force relationships for both ML and SC conditions show great similarities; no statistically significant differences could be demonstrated. Similar results were found in extensor digitorum longus of the rat (Ettema and Huijing, 1993). This is quite surprising given the fact that in isolated fibres at short lengths, stiffness remains elevated despite the fact that force is decreased (Stephenson et al., 1989). In ML condition at short lengths, internal resistance against shortening within the sarcomeres may reduce the external muscle force (Stephenson et al., 1989). Thus, for a given external force below $F_m$ more cross-bridges may be active in force production in ML compared to SC. Apparently, in intact muscle some other mechanisms affecting muscle stiffness, e.g. pennation which decreases stiffness (Ettema and Huijing, 1990), have compensated for this.

**Activation history: prestretch**

An active prestretch enhances muscle force (Edman et al., 1978; Ettema et al., 1992) and stiffness during subsequent isometric contraction. The increase in stiffness is strongly related to the increased force (Fig. 3A). In this respect, our results differ from results on frog muscle fibres (Sugi and Tsuchiya, 1988). They (Sugi and Tsuchiya, 1988) found a lower stiffness for a given force after prestretch. This stiffness was equal to the stiffness in a normal isometric contraction at the same fibre length. Despite the overall similarity of the PI and PS force–stiffness curves, our results illuminate a small difference, represented by a higher $\alpha_d$ and a lower $C_i$ (Table 3A); although the total stiffness hardly changes due to prestretch, the distribution in a force dependent and independent component does change significantly (Fig. 3A and B). This could be explained by small changes in dynamics or properties of the cross-bridge population. Again, our results do not allow any speculation on the mechanisms. Models which include distribution of sacromere and cross-bridge properties, and attachment of a non-random group of cross-bridges under certain conditions (e.g. Morgan, 1990a, b) may be able to explain our results.

**CONCLUDING REMARKS**

For isometric contractions, the force–stiffness relationship of a muscle–tendon complex can be described by a linear model (equation 3), distinguishing a force dependent and independent series elastic compliance, which behave differently from each other as a function of temperature and contraction history. However, the mathematical distinction of a force dependent and independent compliance cannot be backed by a more physiological distinction of cross-bridge and ‘non-cross-bridge’ compliance. The contraction dynamics and temperature have large effects on the relationship between muscle stiffness and force. These effects partially originate within the muscle fibres. Therefore, we conclude that compliance within the muscle fibres is essential for the elastic behaviour of a muscle–tendon entity. Given the magnitude of the effects, we also conclude that using a single model element to describe the series elastic behaviour of skeletal muscle may not always be appropriate, the type and complexity of muscle loading should be considered in designing an SEC model.

**REFERENCES**


Ettema, G. J. C. and Huijing, P. A. (1990) Architecture and elastic properties of the series elastic element of...


