EFFECTS OF PRESTRETCH AT THE ONSET OF STIMULATION ON MECHANICAL WORK OUTPUT OF RAT MEDIAL GASTROCNEMIUS MUSCLE–TENDON COMPLEX

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Summary

Work output of rat gastrocnemius medialis (GM) muscle (N=5) was measured for stretch–shortening contractions, in which initiation of stretch occurred prior to the onset of activation, and for contractions with an isometric prephase. Duration of the active prephase (prestretch and pre-isometric) varied from 20 to 200 ms. Subsequent shortening (from optimum length+4 mm to optimum length−2 mm) lasted 150 ms. Stretch velocities of 5, 10 and 20 mm s\(^{-1}\) were used, and the shortening velocity was 40 mm s\(^{-1}\). The effects of several combinations of active stretch duration and active stretch amplitude were compared. Using force–compliance characteristics, the work of the contractile element (CE), elastic energy storage and release of the undamped series elastic component (SEC) were distinguished. During shortening, an extra amount of work output was produced, induced by active stretch, of which the largest contribution (70–80 %) was due to higher elastic energy release. Enhancement of the storage and utilization of elastic energy during the stretch–shortening cycle, caused by higher transition-point forces (i.e. force at onset of shortening), increased with active stretch amplitude and was associated with a net loss of work, probably due to cross-bridge detachment during active stretch. Net work over the stretch–shortening cycle remained positive for all prestretch contractions, indicating that when a muscle performs this type of contraction, it is able to contribute to work performance on body segments. It is concluded that, in stretch–shortening movements of rat GM muscle, maximal positive work output is incompatible with maximal net work output. Consequences for complex movements in vivo are discussed.

Introduction

In many complex movements, muscle–tendon complexes undergo stretch–shortening cycles during activity (e.g. Hof et al. 1983; Komi, 1986; Gregor et al. 1988). During locomotion (e.g. hopping and running) active muscles are stretched to decelerate body mass when landing. Potential and kinetic energy are stored by the elastic structures in the stretched muscle–tendon complexes (Cavagna et al.

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Therefore, active stretch increases the muscle’s ability to perform positive work during subsequent shortening because of enhanced recoil of elastic energy, but also by so-called muscle potentiation (i.e., an enhancement of the ability of the contractile machinery to produce mechanical work) (Cavagna, 1977). It has been proposed that these effects of active stretching just prior to subsequent shortening might explain the relatively high mechanical efficiencies reported for running, jumping and hopping (e.g., Asmussen and Bonde-Petersen, 1974; Cavagna, 1977; Taylor and Heglund, 1982; Bosco et al. 1987).

Protocols used for studying the effects of eccentric contractions on the behaviour of isolated muscle during subsequent active shortening were usually such that stretch was imposed with the muscle already fully active and exerting maximal isometric force (e.g., Cavagna et al. 1968, 1981, 1985; Cavagna and Citterio, 1974; Edman et al. 1978). As a consequence, in these experiments total net work over the entire stretch–shortening cycle was negative. In particular, during actions such as running, net work production of a stretch–shortening cycle should be positive, since muscles that are responsible for storage and utilization of elastic energy (i.e., performing stretch–shortening cycles) have to compensate for energy losses by internal friction, by air friction and by frictional losses during the contact with the ground (e.g., Williams and Cavanagh, 1983; Webb et al. 1988). Especially in running against the wind or in uphill running, such a requirement for positive net work is obvious, not only for hip extensors but also for knee extensors and plantar flexors. As net work has to be produced, it will be a disadvantage if net work output in a prestretch contraction results in a much lower net work output compared to a contraction without prestretch.

In natural movements, the onset of stretching probably does not occur while the muscles are exerting maximal isometric force. For example, in locomotion this would mean that the muscles that are lengthened during the landing phase would be already fully active before contact with the ground. A more realistic situation is one in which activation starts at, or after, the onset of the stretch period to initiate deceleration of the body (Hof et al. 1983).

For these reasons, we aimed to gain more insight into the effects of active stretch on muscle behaviour in stretch–shortening cycles by ensuring that the onset of stretch preceded the onset of stimulation; this is closer to the conditions actually observed in complex movements (e.g., Hof et al. 1983). The influence of active stretch amplitude, as one of the major parameters determining the effects of prestretch on a consecutive contraction (e.g., Edman et al. 1978; Cavagna et al. 1986), was examined in this study. Since in our experiments stretch was imposed during the onset of stimulation, active stretch duration was also considered as a possible parameter determining stretch effects.

**Materials and methods**

_Surgery and experimental protocol_

The experiments were performed on the gastrocnemius medialis (GM) muscle—
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tendon complex of the rat. Five young adult male Wistar rats (body mass 295–350 g) were anaesthetized with pentobarbital (initial dose 10 mg 100 g\(^{-1}\) body mass, intraperitoneally). The GM was freed from its surrounding tissues leaving muscle origin and blood supply intact. The distal tendon and part of the calcaneus were looped around a steel wire hook, tightly knotted with a suture, and glued with tissue glue (Histoacryl). 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 made at an ambient temperature of 25°C on a multipurpose ergometer (Woittiez et al. 1987). The muscle was excited by supramaximal stimulation of the distal end of the severed nerve (square wave pulses; 0.4 ms duration, 3 mA, 100 Hz). The optimum length of the muscle–tendon complex (\(l_o\)), defined as that length at which active isometric muscle force was highest (\(F_o\)), was determined to within 0.5 mm. Using compasses and a dissecting microscope, the lengths of muscle fibres and series-elastic structures (distal tendon and proximal aponeurosis) were measured at \(l_o\). Force–compliance characteristics of the series elastic component were determined using quick length decreases of 0.2 mm within 3 ms during isometric tetanic contractions (Bobbert et al. 1986a) at different muscle–tendon complex lengths, and thus for a wide range of force levels. Compliance (\(C\)) was calculated as the ratio of length to force change of the muscle–tendon complex during the quick release.

We examined active stretch amplitude and active stretch duration effects by comparing stretch–shortening contractions with different values of stretch velocity, stretch amplitude and stretch duration (Fig. 1).

Prestretch (PS) experiments were conducted in the following way. The muscle was lengthened at velocities of 5, 10 or 20 mm s\(^{-1}\) for 250 ms. The moment of onset of stimulation, during lengthening, was varied to alter the duration of stretch of active muscle: for 5 mm s\(^{-1}\) stretches, active stretch periods of 20, 80 and 150 ms were imposed; for 10 mm s\(^{-1}\) stretches, active periods of 20, 50, 80, 110, 150 and 200 ms; for 20 mm s\(^{-1}\) stretches, periods of 20, 50, 80 and 150 ms. In this way, combinations of active stretch duration, active stretch amplitude and stretch velocity were obtained. After lengthening, a concentric contraction of 150 ms at a shortening velocity of 40 mm s\(^{-1}\) was imposed. Stimulation continued until 100 ms after the end of the shortening phase.

Pre-isometric (PI) experiments were made using a similar procedure. The lengthening period occurred 1 s earlier, so that stimulation started after termination of stretch, with the muscle–tendon complex kept at a constant length. The sequence of the measurements was such that PS and PI contractions with similar active prephase durations (which were to be compared) were performed in succession. All measurements were made at a muscle–tendon complex length at which the length at the end of stretch, and during isometric prephase, was \(l_o+4\) mm, whereas shortening stopped at \(l_o-2\) mm. This length range was chosen because active stretch has greatest effects on force enhancement at muscle lengths above optimum length (Edman et al. 1978). After each block of about eight contractions \(F_o\) was measured. If a deviation of more than 10% from the initially
Fig. 1. Diagram of changes in the length of the muscle-tendon complex from its optimum length \((l-l_0)\) as a function of time. The pre-isometric condition (PI) as well as the prestretch conditions (PS) at different velocities \((5, 10 \text{ and } 20 \text{ mm s}^{-1})\) are indicated. All pre-conditions were followed by an identical shortening phase. Vertical arrows indicate times of excitation \((-20, -50, -80, -110, -150 \text{ and } -200 \text{ ms})\) and end of stimulation \((250 \text{ ms})\). Triangles indicate the times when the preparation was stimulated in the different experiments.

measured value of \(F_o\) was observed, the muscle was excluded from further experiments.

_Treatment of data_  

All calculations concerning compliance and mechanical work were corrected for equipment compliance \((0.014 \text{ mm N}^{-1})\). Work performed on and done by the muscle-tendon complex was calculated by numerical integration of force-length data for the prestretch phases and the shortening phase. A simple two-element Hill-type model \((\text{Hill, 1938})\) was used to distinguish work delivered by the contractile element (CE) from that of elastic energy storage in and release from the undamped series elastic component (SEC). Visco-elastic behaviour of a damped part of the SEC and associated energy losses during dynamic contractions were not considered, because the damped elastic element is probably small compared to the undamped part \((\text{Hatze, 1977; van Ingen Schenau et al. 1988})\). The following function was fitted to the force-compliance data of the series elastic component:

\[
C = a F^b ,
\]

where \(F\) is mean force level during the quick release, and \(a\) and \(b\) are fitting constants.

By means of this force-compliance relationship, work stored in and released
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from the SEC was calculated for the entire stretch–shortening cycle and shortening period. Therefore, from the total muscle–tendon complex work ($W_{\text{cmpx}}$), the work done by the contractile element ($W_{\text{ce}}$) and the work done by the SEC ($W_{\text{sec}}$) could be distinguished. Since stimulation was not terminated at the end of shortening, and active force was still generated, some elastic energy was stored in the SEC at the end of the cycle and dissipated as heat during relaxation. In most in vivo movements all elastic energy stored will be released during shortening, since final force levels equal zero. In other words, in such movements a balance of elastic energy input and output is obtained for the entire stretch–shortening cycle. To obtain such a balance in our calculations, the amount of elastic energy stored at the end of shortening was added to elastic energy release calculated over the shortening period.

Use of a Hill-type CE–SEC model implicitly assumes that a single force–extension relationship for the SEC exists, regardless of contraction dynamics. Apparently this is not the case for two reasons. (1) Muscle fibre force–stiffness characteristics change due to stretch (Cavagna and Citterio, 1974; Cavagna, 1977; Cavagna et al. 1981; Sugi and Tsuchiya, 1988). However, only a minor part of the SEC of rat GM (expressed in extension at $F_o$ about 15%) is located within the muscle fibres (G. J. C. Ettema and P. A. Huijing, in preparation). Therefore, for GM these changes will be relatively small compared to total SEC stiffness (fibre and tendinous structures). (2) The length of the aponeurosis (tendon plate or intramuscular tendon) as part of the SEC is dependent not only on force but also on muscle length (Huijing and Ettema, 1988/89; Ettema and Huijing, 1989). It must be pointed out that only force–dependent, i.e. elastic, properties of the aponeurosis as part of the SEC are considered in the present study. Consequently, muscle-length-dependent length changes of the aponeurosis were included in CE length changes. Using a single force–compliance relationship, van Ingen Schenau et al. (1988) found reliable simulations of force output during dynamic contractions, despite the possible influence of contraction dynamics on SEC characteristics. Therefore, we believe that to distinguish contractile work from elastic energy storage and release, it is reasonable to use unique SEC characteristics.

The influence of the parallel elastic component (PEC) was neglected, since only contractions at similar muscle–tendon complex lengths, and thus similar passive force, were compared. Maximal passive force (at $l_o+4\text{mm}$) was about 5% of $F_o$. In fact, work done by the PEC is included in $W_{\text{ce}}$.

Statistics

Differences of PS and PI values were tested using two-tailed Student's $t$-test for paired observations. Significance was set at $P<0.05$.

Results

Table 1 shows morphological data for the gastrocnemius medialis (GM) muscles studied. Imposed stretch velocities were about 0.4, 0.8 and 1.6 fibre lengths s$^{-1}$
Table 1. Morphological data and maximum isometric muscle force ($F_o$) for the five gastrocnemius muscles used

<table>
<thead>
<tr>
<th>Length (mm)</th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Muscle-tendon complex</td>
<td>39.9±2.2</td>
</tr>
<tr>
<td>Distal fibre</td>
<td>12.1±0.7</td>
</tr>
<tr>
<td>Tendinous structures</td>
<td>27.5±1.3</td>
</tr>
<tr>
<td>Muscle mass (g)</td>
<td>0.77±0.04</td>
</tr>
<tr>
<td>$F_o$ (N)</td>
<td>10.26±0.35</td>
</tr>
</tbody>
</table>

Values are mean±s.E.M.

(for stretches of 5, 10, 20 mm s$^{-1}$, respectively), and shortening velocity was about 3.3 fibre lengths s$^{-1}$. Minimal and maximal active stretch amplitudes were less than 1% and about 25% of the fibre length, respectively.

A typical example of experimental length and force tracings, as well as calculated CE length changes, is shown in Fig. 2 for three prestretch contractions of differing durations of muscle activation at a stretch velocity of 10 mm s$^{-1}$ and for three corresponding pre-isometric contractions. If the active muscle–tendon complex is stretched for only 20 ms (Fig. 2A), the CE shortens continuously, despite stretch of the muscle–tendon complex (bottom panel). This occurs because the SEC accommodates all complex lengthening, as well as some CE shortening. The CE continuously performs work on the SEC. Net work production is somewhat higher in PS condition (PS–PI=+0.40±0.09 mJ). A somewhat longer active stretch duration (50 ms, Fig. 2B) leads to a small isometric phase at the level of CE at the end of stretch, where no work is done by the CE, and net energy production is somewhat smaller than in the PI condition (PS–PI=−0.79±0.07 mJ). This occurs mainly because the CE cannot deliver as much work during the prestretch as during the pre-isometric phase. A longer active stretch period (200 ms, Fig. 2C) results in CE lengthening after initial shortening at the onset of force development. Energy is taken up by the CE and it is not totally regained as mechanical work in the subsequent shortening period (PS–PI=−13.88±0.85 mJ). This can also be seen in Fig. 3, which shows length–force tracings of the same experiments for the muscle–tendon complex and CE. For PS contractions with short active stretch durations (Fig. 3A,B), the tracing during lengthening lies below the tracing during shortening for the same length range. In other words, for these particular stretch–shortening cycles, net work production is already positive at the moment when the muscle reaches the length at which active stretch was started. For the contraction with longer stretch duration (Fig. 3C), a hysteresis curve was encountered for the initial part of the cycle, i.e. loss of mechanical work occurs; for this entire PS contraction, net work is positive, because the muscle was allowed to shorten more than it was stretched. It should be noted that positive (shortening) and negative (lengthening) phases of work performance for the CE and entire muscle–tendon complex are not synchronized: during (part of) the active stretch of the muscle–tendon complex,
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Fig. 2. Typical examples of results obtained for muscle-tendon complex length changes relative to optimum length ($\Delta l_{oc}$) (upper panel), force (middle panel) and calculated contractile element length changes ($\Delta l_{ce}$) (lower panel). Results for pre-isometric as well as prestretch (stretch velocity 10 mm s$^{-1}$) conditions are presented for a prephase duration of 20 ms (A), 50 ms (B) and 200 ms (C). CE length was calculated as: $\Delta l_{ce} = (l_i - l_o) - [E(F_i) - E(F_o)]$, where $l_i$ and $F_i$ are the length of the complex and force, respectively, and $E$ is the extension of the series elastic component as a function of force. Onset and termination of excitation are indicated by upward- and downward-directed arrows, respectively, in the upper panel. Active prephase periods are outlined by vertical dotted lines. Dashed curves indicate estimated CE patterns of length changes, after correcting for aponeurosis length shift (0.2 mm per 1 mm muscle length change). Prestretch (PS) and pre-isometric (PI) tracings are indicated in C.

the CE performs positive work on the SEC, while external work is performed on the muscle–tendon complex.

In the above considerations, the influence of aponeurosis characteristics (Huijing and Ettema, 1988/89; Ettema and Huijing, 1989) that affect possible length shifts of aponeurosis length–force curves depending on muscle length, are not taken into account. To obtain a rough estimate of the possible effects of such an aponeurosis length shift, a linear relationship between change of muscle length and aponeurosis length shift with a rather high slope of 0.2 mm aponeurosis shift per 1 mm muscle length change (Huijing and Ettema, 1988/89) was assumed. CE
Fig. 3. Length–force tracings of muscle–tendon complex (upper panel) and CE (lower panel) from the experimental results shown in Fig. 1: prephase durations are 20 ms (A), 50 ms (B) and 200 ms (C). Length is plotted relative to optimum length. Arrows indicate direction of movement. Different phases of the stretch–shortening cycle are indicated in the upper panel of C: o, onset of stimulation; p, isometric prephase; p', prestretch; s, shortening; i, isometric force redevelopment after shortening; e, end of stimulation; r, relaxation.

lengths were calculated for a PS and PI contraction with a 200 ms prephase duration. Results are shown in Figs 2C and 3C (bottom diagram, dashed lines). From Fig. 3 it can be deduced that the aponeurosis shift mainly causes a reduction of CE length changes, because some of the length changes of the muscle–tendon complex are taken up by this shift. Because this effect occurred for all PI and PS contractions, no qualitative differences were found between the original calculations on prestretch effects and the calculations including the aponeurosis shift.

Fig. 4 shows net work for the entire stretch–shortening cycle and Fig. 5 shows work production during the shortening phase, as a function of prephase duration, for PI contractions and PS contractions with a stretch velocity of 10 mm s⁻¹. Note that for PS contraction net work decreases with increasing prephase duration (Fig. 4). Most of the work performed during shortening originates from the contractile element in both conditions: more than 90% for small-amplitude
stretches and 70–80% for large-amplitude stretches (Fig. 5A,B). However, for almost all active stretch durations, extra work performed after prestretch is mostly (about 80%) a result of extra elastic energy release (PS–PI, Fig. 5C). On average, the CE produces a rather small but significant amount of extra work after prestretch (PS–PI: 0.53±0.06 mJ, all conditions, N=63; see Fig. 8).

Net work of the SEC was almost zero; only a small net release was calculated for all PS and PI contractions (0.15±0.01 mJ, N=92) because of passive force levels at the start of contraction. In the following considerations this will be neglected and net $W_{cmps}$ will be taken to be equal to net $W_{ce}$. Slightly more work is produced in PS than in PI conditions only for the shortest active prephase duration (0.24±0.12, 0.4±0.09 and 0.44±0.12 mJ for 20 ms stretches at 5, 10 and 20 mm s$^{-1}$, respectively). At longer active stretch durations PS net work production decreases rapidly but remains positive. This positive net work was found for every PS contraction. Only for the stretch–shortening cycle with an active stretch of 150 ms at 20 mm s$^{-1}$ was net work reduced to zero (0.38±1.24 mJ; Fig. 10).

For more detailed analysis, mean PS and PS–PI values of work and force levels at the transition from prephase to shortening phase are plotted against active stretch duration and amplitude for the three stretch velocities used (Figs 6–10).
Fig. 5. Mean work output during the shortening phase by gastrocnemius muscle-tendon complex (■, solid line), contractile element (○, dotted line) and series elastic component (▲, dashed line) presented as a function of prephase duration. (A) Pre-isometric condition; (B) prestretch condition with stretch velocity of 10 mm s⁻¹; (C) the differences between these conditions. S.E.M. is indicated by vertical bars (N=5).

**Force and the series elastic component**

The difference of force level at the transition point from prephase to shortening (known as the transition-point force) between PS and PI contractions was taken to indicate the amount of force enhancement due to stretch. The PS–PI values of transition-point force (Fig. 6B vs 6D) and consequently positive $W_{sec}$ (Fig. 7B vs 7D) are clearly determined by active stretch amplitude rather than by active stretch duration. Considering the absolute PS values yields a more complex situation. For a given amplitude of stretch, a lower stretch velocity brings about higher transition-point forces (Fig. 6A), resulting in higher elastic energy release during shortening (Fig. 7A). The higher transition-point force is probably due to the longer time of activation, which allows a more complete build-up of force in
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Fig. 6. Mean transition-point force levels, presented as a function of active prestretch amplitude (A and B) or duration (C and D) for three different stretch velocities 5 (■, solid line), 10 (▲, dashed line) and 20 m s⁻¹ (●, dotted line). Prestretch results are presented in A and C, and differences between prestretch and pre-isometric conditions in B and D. Maximal S.E.M. is indicated by vertical bars (N=5).

The contractile element

For the contractile element the situation is different from that of the SEC: the small amount of extra work produced in the concentric phase due to prestretch is not fully determined by either active stretch duration or amplitude (Fig. 8B,D). In contrast, Fig. 8A,C shows that activation time rather than active stretch amplitude determines the absolute amount of $W_{ce}$ performed in PS shortening. Note, however, the highly limited range of the y-axis scale in these figures, i.e. the differences in Fig. 8 are relatively small. A similar negative dependence of work performed during the concentric phase on active prephase duration was also found in PI contractions (Fig. 5A).

Positive work of the muscle–tendon complex after prestretch is clearly determined by active stretch amplitude (compare Fig. 9A with Fig. 9C). Apparently, differences between the effects of amplitude on $W_{sec}$ and $W_{ce}$ during the...
shortening period (Figs 7A and 8A) compensate each other. This may be related to the interaction between the SEC and the CE: if shortening of the SEC is enhanced due to a large decrease in force, this will automatically lead to a diminished shortening of the CE and, consequently, a lower CE work output (Avis et al. 1986). PS–PI differences of positive muscle–tendon complex work depend on stretch amplitude (compare Fig. 9B with Fig. 9D). This is due to a major contribution by (enhanced) elastic energy release, which is amplitude-dependent (compare Fig. 7B with Fig. 7D).

A striking observation concerning net work production is that only in the case of the shortest active stretch duration (20 ms), with small amplitude, does the PS condition result in a higher net work production than does the PI condition (Figs 4 and 10D). For stretch velocities of 10 and 20 mm s\(^{-1}\) these PS–PI values differ significantly from zero (for 20 ms stretches PS–PI work is 0.48±0.10 mJ at 10 mm s\(^{-1}\) and 0.54±0.13 mJ at 20 mm s\(^{-1}\)). Furthermore, a clear inverse relationship was found between active stretch amplitude (and duration) and net work, indicating large energy losses at longer stretches (Fig. 10). In other words, only very short and small stretches imposed on the muscle–tendon complex induce
extra net work production for the entire cycle. The amount of energy loss is mainly related to active stretch amplitude rather than to active stretch duration (compare Fig. 10A with Fig. 10C). This is in agreement with the suggestion that, when the muscle–tendon complex is subjected to large stretches, CE lengthening, i.e. cross-bridge cycling and thus cross-bridge detachment, occurs. In this way mechanical energy is probably degraded into heat. (Note that short-range stiffness is incorporated in the SEC, which means that any calculated change of the CE is considered to be brought about by cross-bridge cycling.)

**Discussion**

Prestretch of a muscle at the onset of stimulation results in an enhancement of work production during subsequent shortening, which is mainly caused by extra elastic energy release. However, this stretch-induced enhancement of positive work is associated with net loss of work over the entire stretch–shortening cycle. This is because large stretches, which are necessary to enhance elastic energy storage and release, cause extensive CE lengthening, i.e. cross-bridge cycling, of
which cross-bridge detachment forms a part; during cross-bridge cycling in eccentric movements, mechanical energy is stored in the attached cross-bridges, and this work is lost if these cross-bridges detach. Net energy loss occurred when active stretch of the muscle–tendon complex exceeded about 0.5 mm (Fig. 10B), i.e. 4% of the fibre length. Since a considerable part of this stretch is taken up by the tendinous structures, the fibre can be lengthened by only a few percent without the occurrence of loss of work. This is in agreement with the data of G. J. C. Ettema and P. A. Huizing (in preparation), who showed that the short-range stiffness (i.e. extension without cross-bridge detachment) of rat GM fibres is about 1.5% of the fibre length.

Active stretch duration also plays an important role in this matter. For a given active stretch amplitude, a longer active stretch duration (i.e. lower velocity) leads to a higher transition-point force and therefore to a stiffer SEC during the last period of stretch. This means that during such stretches relatively less of the extension of the muscle–tendon complex is taken up by the SEC, causing more CE lengthening and thus energy loss. The higher force levels are probably caused by a longer activation time. This also occurs in the PI condition, but will only influence...
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Fig. 10. Mean net work performed by gastrocnemius muscle–tendon complex during the entire stretch–shortening cycle, presented as a function of active prestretch amplitude (A and B) or duration (C and D) for three different stretch velocities 5 (•, solid line), 10 (▲, dashed line) and 20 mm s⁻¹ (●, dotted line). Prestretch results are presented in A and C, and differences between prestretch and pre-isometric conditions in B and D. Maximal S.E.M. is indicated by vertical bars (N=5).

the amount of positive CE work performed on the SEC during the prephase: in isometric contractions loss of mechanical energy does not occur, since the CE is not stretched (see Fig. 2C). It should be noted that if we speak of loss of mechanical energy by stretch, this does not necessarily mean that this work is (directly) degraded into heat: it may be stored in the muscle in another form of energy. However, in mechanical terms it can be considered loss of energy, since work stored in the muscle during stretch is not released as work during subsequent shortening (i.e. before relaxation of the muscle).

The loss of mechanical energy in PS contractions does not necessarily lead to a negative balance of net work, indicating that such muscle contraction patterns can contribute to external work for in vivo movements.

Extra contractile element work during shortening following prestretch

Stretch-induced CE work enhancement during shortening is small compared to the added release of elastic energy. Apparently, CE work enhancement plays a minor role in complex movements. This is in agreement with results of counter-movement jumps (i.e. jumps in which plantar flexors are stretched before they
induce plantar flexion: prestretch) and jumps in which the knee remains extended (no prestretch) (de Graaf et al. 1987), where enhancement of CE work production apparently did not occur. All the differences caused by a prestretch effect could be explained by extra elastic energy release.

The small enhancement of \( W_{ce} \) following prestretch can be explained mechanically in two ways. (i) CE is potentiated towards a higher energy level during active stretch, resulting in extra work during subsequent shortening (e.g. Cavagna and Citterio, 1974; Cavagna et al. 1985, 1986; Edman et al. 1978). The fact that the level of force remains higher after a prestretch, even during the isometric period after shortening (Fig. 2), also suggests that some form of potentiation of CE did occur. (ii) SEC–CE interaction caused differences of length changes of the CE, possibly leading to differences of CE work output (Avis et al. 1986). Because of differences in force patterns during the shortening period, SEC length and velocity were different for PS and PI conditions, having the opposite effects on CE level (Fig. 2). Therefore, these load differences influenced \( W_{ce} \) after prestretch.

In vivo movements

As mentioned in the Introduction, in repeated movements, such as level walking and running, net work production (irrespective of positive work) is essential. Thus, any loss of mechanical energy due to stretch must be considered a disadvantage for long-duration exercise. Only for active stretches of very short amplitude (and duration) was about the same amount of net work found compared to the pre-isometric contractions, whereas at stretches of larger amplitude a considerable net loss of work occurred due to prestretch. Furthermore, net efficiency in PS contractions (with stretches of 3 mm in 150 ms), in stretch–shortening cycles similar to the ones used in this study, is considerably lower than in PI contractions (de Haan et al. 1989). Therefore, considering these negative effects of prestretch on net work production and net efficiency, it seems reasonable to suppose that if a prestretch phase should occur to decelerate the body mass in movements such as walking and running, it is of short duration and small amplitude, resulting in moderate peak forces with very little or no CE lengthening. This is in agreement with observations on triceps surae action during level walking (Hof et al. 1983). Observations by Biewener et al. (1988) and Biewener and Blickhan (1988) also suggest that, at least at moderate intensity, no CE stretch occurs during these types of movements: they reported peak muscle force levels of about 35% of \( F_o \) in kangaroo rat hopping at preferred hopping speeds.

In contrast, for cat locomotion, stretches of gastrocnemius medialis and soleus muscle were reported which were believed to be beyond the limits of short-range stiffness (Walmsley and Proske, 1981; Gregor et al. 1988). Moreover, Morgan et al. (1978) concluded that some extension possibly occurs within muscle fibres during kangaroo hopping, evoking cross-bridge detachment and energy loss. However, for these movements, lengthening of the fibres may have been overestimated, because elevated compliance levels of the tendinous structures at low force levels were not taken into account in the calculations (G. J. C. Ettema...
and P. A. Huijing, in preparation). Therefore, the muscles involved in cat locomotion and kangaroo hopping may well act within the limits of short-range stiffness (i.e. without cross-bridge detachment).

Clearly, for a sound interpretation of the effects of prestretch, reliable information about the level of activation at the onset of stretch is crucial, as it strongly influences the amount of stretch that can be taken up by the tendinous structures. Moreover, it should be noted that the calculations mentioned above concern the overall length changes during stretch (i.e. differences in CE length at the onset of active stretch and at the end of stretch), whereas in Fig. 2C it is clearly shown that considerable CE lengthening may occur in the last phase of stretch, even though almost no overall CE length change takes place.

The requirements necessary to prevent waste of mechanical energy during CE extension may be in conflict with the requirements for optimizing storage and utilization of elastic energy. In particular, it was argued that during locomotion the ankle plantar flexors should primarily act as force generators allowing their relatively long tendons to store and release elastic energy during stance (Taylor, 1980). The results of the present study show that, in order to prevent mechanical energy degrading into heat during CE extension, the timing of the onset of activation should be such that only small active stretches occur. As a result, no large force enhancement will be achieved, and this limits the amount of elastic energy that can be stored.

For single explosive contractions, such as in jumping and throwing, loss of net work over the entire stretch–shortening cycle is not necessarily a drawback. Here, the amount of positive work determines the level of performance. For example, in jumping a countermovement (active prestretch) improves the performance, because in the push-off phase (muscle shortening) more work is produced (van Ingen Schenau, 1984). High positive work output is obtained by applying large active stretches, inducing high peak forces, and stretching the contractile element. In vivo measurements of jumping movements of the kangaroo rat showed peak force levels (175% of $F_o$) in the ankle extensor muscles, which could only be achieved by means of active CE stretch (Biewener et al. 1988; Biewener and Blickhan, 1988).

Of course one can dispute whether net work production and maximal positive work are essential parameters for the functioning of the gastrocnemius muscle in rat locomotion. Bi-articular muscles, such as gastrocnemius, play a crucial role in the transformation of rotational movements in the joints into translational movements of the body's centre of gravity and in the optimal use of the energy produced by the muscle groups located proximally (van Ingen Schenau et al. 1987; van Ingen Schenau, 1989). In human jumping, for example, the bi-articular gastrocnemius is used to transport energy from the knee-joint (produced by the knee extensors) to the ankle-joint (Gregoire et al. 1984; Bobbert and van Ingen Schenau, 1988). One might consider the possibility that, for some bi-articular muscles, net work is slightly negative, or positive work output is nil, just to carry out this energy transportation function in an optimal way. However, in human
jumping a considerable amount of the positive work around the ankle (about 40%) is delivered by the gastrocnemius (Bobbert et al. 1986b), indicating that high positive work output is an important function for human gastrocnemius in jumping. Even though requirements for a positive net work output with a minimum of energy loss, or maximal positive work output during shortening in complex movements, may not hold for each particular muscle, most major leg muscles will have to be able to fulfill both types of requirements. On the assumption that prestretch effects are basically similar for all skeletal muscles, we conclude that in complex movements maximal positive work output induced by prestretch (as necessary in the long jump and the high jump) requires a completely different timing of activation than in a contraction with maximal net work output (as necessary in long-distance running).

References


