

THE ROLE OF SERIES ELASTIC STRUCTURES IN PRESTRETCH-INDUCED WORK ENHANCEMENT DURING ISOTONIC AND ISOKINETIC CONTRACTIONS

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Summary

The influence of series elastic structures on the dynamics of the contractile machinery was examined in the gastrocnemius medialis (GM) of five male Wistar rats, with respect to enhancement of work of a muscle–tendon complex after active stretch. Imposed isotonic and isokinetic contractions were preceded by either an isometric phase (PI) or an active stretch (PS). The effects of fibre length differences at the onset of shortening, due to differences of extension of tendinous structures, were studied. For the isotonic experiments fibre length and shortening velocity were estimated 30 ms after release and compared with the PI length–velocity curve determined at the same force level. For shortening above the optimum length, about half of the enhanced shortening found after prestretch could be explained by PS–PI fibre length differences. Below the optimum length, PS shortening velocity was somewhat lower than expected on the basis of length–velocity characteristics. Enhancement of work output due to stretch was different for isokinetic and isotonic shortening. In isokinetic shortening, following prestretch, fibre work was limited because of enhanced shortening of the tendinous structures.

In stretch–shortening cycles imposed on a muscle–tendon complex, the length of the complex affected all prestretch effects, i.e. potentiation of the contractile element, contractile element interaction with the tendinous structures, and elastic energy release.

It is concluded that, besides potentiation effects and enhanced elastic energy release, the influence of series elastic structures on fibre dynamics determines active stretch-induced work enhancement. The contribution by these mechanisms to this work enhancement depends largely on the type of stretch–shortening cycle.

Introduction

In skeletal muscle, fibres are connected in series with elastic structures. Much

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attention has been focused on the importance of these structures for muscle functioning, particularly with reference to storage and release of elastic energy (for references see Close, 1972; Cavagna, 1977). Generally speaking, the dynamics of the contractile element (i.e. shortening velocity and length) are determined not only by the dynamics imposed on the muscle-tendon complex but also by the dynamics of the series elastic structures, which depend on exerted force and elastic characteristics (Hof *et al.* 1983; Bobbert *et al.* 1986*b,c*; Avis *et al.* 1986; Alexander, 1988). Consequently, this is also the case for work output of the contractile machinery. Such an influence of the series elastic structures on the behaviour of the contractile machinery may be of great importance for muscle functioning, particularly during stretch-shortening contractions, because of a strong muscle force enhancement induced by stretch, resulting in an increased lengthening of the series elastic structures (e.g. Cavagna, 1977; de Haan *et al.* 1989; Ettema *et al.* 1990). These phenomena may be crucial for *in vivo* stretch-shortening movements (Asmussen and Bonde-Petersen, 1974; Hof *et al.* 1983; Komi, 1984, 1986; Avis *et al.* 1986; de Graaf *et al.* 1987). For example, Avis *et al.* (1986) found a negative effect of a counter movement (i.e. prestretch) on the work output of the contractile element during maximal leg extension movements: shortening of the series elastic element was increased by the counter movement, and therefore the shortening range of the contractile element was limited. In other types of movements this effect may also be positive.

In the literature, enhancement of work output induced by stretch is usually explained by two mechanisms: (1) an enhanced recoil of elastic energy because of higher peak forces; (2) a so-called potentiation of the contractile machinery (i.e. changes in force-velocity characteristics of the contractile machinery caused by stretch) (Cavagna and Citterio, 1974; Cavagna, 1977; Edman *et al.* 1978; Sugi and Tsuchiya, 1981). Furthermore, changes in the elastic characteristics of the series elastic component were reported as one of the causes of work enhancement (Cavagna and Citterio, 1974; Cavagna, 1977; Cavagna *et al.* 1981; Sugi and Tsuchiya, 1988), but these changes may reflect extra energy absorption and release by the cross-bridges (Cavagna *et al.* 1981) and they therefore seem to be closely related to the potentiation phenomenon. The aim of the present study was to examine the interaction between the dynamics of series elastic (tendinous) structures and those of the contractile machinery (i.e. muscle fibres) as an additional mechanism of stretch-induced enhancement of work. Within this scope we examined the effects of prestretch on subsequent isotonic and isokinetic concentric contractions. Isotonic and isokinetic results were compared; the influence of the series elastic structures was expected to be different for the two conditions since different parameters were controlled externally (muscle force *versus* muscle length and shortening velocity, respectively). Contractions preceded by an active stretch will be referred to as prestretch or PS contractions, and contractions starting from an isometric state as pre-isometric or PI contractions. The influence of differences in muscle fibre length, given a certain muscle-tendon complex length, in PS and PI contractions was tested for the isotonic experiments.

Materials and methods

The experiments were performed *in situ* on the gastrocnemius medialis (GM) muscle–tendon complex of the rat. Five young adult male Wistar rats (body mass 228–246 g) were anaesthetized with pentobarbital (initial dose 10 mg 100 g⁻¹ body mass intraperitoneally). The GM muscle–tendon complex was freed from its surrounding tissues, leaving muscle origin and blood supply intact. The distal tendon was tightly knotted and glued (Histoacryl Blau) to a steel wire, just behind the calcaneus bone, leaving the major part of the distal tendon intact. All measurements were performed at an ambient temperature of the muscle of 25°C on a multipurpose ergometer (Woittiez *et al.* 1987). The muscle was activated by supramaximal stimulation of its severed nerve (square wave pulses; 0.4 ms, 3 mA, 100 Hz).

Experimental protocol

Force–compliance characteristics of the series elastic component were determined using quick length decreases (0.2 mm within 3 ms) during isometric tetanic contractions at different muscle–tendon complex lengths (Bobbert *et al.* 1986a). Optimum length of the muscle–tendon complex (l_o), defined as that length at which experimentally determined isometric muscle force was highest (F_o), was determined with an accuracy of 0.5 mm during these combined length–force and compliance measurements. Length–velocity characteristics around l_o of the muscle–tendon complex were determined for a force level of 67 % of F_o by means of isotonic afterload contractions, preceded by a period of isometric force development of 140 ms.

Prestretch experiments were performed in the following way. The muscle was stretched at a velocity of 20 mm s⁻¹ during the first 140 ms of activation. After this lengthening, the muscle was released at an afterload of 67 % of F_o for 200 ms. Pre-isometric experiments were performed using a similar procedure, except that the lengthening period occurred 1 s earlier (i.e. prior to onset of activation), so that stimulation started with the muscle–tendon complex at constant length. PI contractions were identical to the contractions used for obtaining length–velocity characteristics, but were performed directly after the PS contractions, to exclude the influence of alterations of muscle characteristics with time.

Prestretch and pre-isometric experiments were also performed under isokinetic conditions. Shortening speeds during the first 140 ms after release of the isotonic PS and PI contractions were estimated during the experiments. Isokinetic shortening velocity was chosen such that it was comparable to the average of the estimated isotonic PS and PI shortening velocities. This procedure allowed a reliable comparison to be made between the influences of prestretch on subsequent isotonic and isokinetic shortenings.

On the basis of the fibre length–force curve, different prestretch effects were expected at lengths above and below l_o : above l_o , muscle fibres were expected to act closer to their optimum length in the PS than in the PI condition, whereas

below l_0 , a reversed situation was expected. Therefore, measurements were performed at a muscle-tendon complex length at which peak length at the end of stretch and during the isometric prephase amounted to l_0+4 mm and l_0 , respectively.

After each block of about eight contractions F_0 was determined. If a deviation of more than 10% from the initial measured value of F_0 was observed, the muscle was excluded from further experiments.

Using dividers, the lengths of the distal muscle fibre and its in-series connected tendinous structures were measured at l_0 at the end of the experiments.

Treatment of data

Tendon compliance

All calculations concerning compliance, mechanical work and muscle fibre length were corrected for equipment compliance (0.014 mm N^{-1}).

To obtain values of compliance of the tendinous structures (C_t), the measured compliance of the muscle-tendon complex was corrected for series elasticity located within the muscle fibres (elastic elongation within the fibre at isometric force level is 1.5% of muscle fibre length; G. J. C. Ettema and P. A. Huijing, in preparation). The following function was least-square fitted for these corrected force-compliance data:

$$C_t = aF^b, \quad (1)$$

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

Length and velocity of the muscle-tendon complex and the muscle fibre

Extension of the tendinous structures was derived from equation 1 by integration with respect to force. Using these force-extension characteristics, fictive length of the muscle fibres (l'_f) was estimated by subtracting the extension of the tendinous structures from the length of the muscle-tendon complex. Fictive optimum fibre length (l'_{f0}) is defined as l'_f at l_0 with force being equal to F_0 . This way, the real difference between actual fibre length and actual optimum fibre length ($\Delta l_f = l'_f - l'_{f0}$) could be calculated. It should be noted that, as a consequence, values of Δl_f include the influence of muscle fibre rotation, responsible for part of the muscle length changes (Huijing and Woittiez, 1984, 1985; Otten, 1988; Zuurbier *et al.* 1989). The shortening velocity of the fibres was calculated as the length change with time. Visco-elastic effects were neglected because they are considered to be very small (Hatze, 1977; van Ingen Schenau *et al.* 1988).

To determine whether the calculations of fibre length based on force-compliance data were reliable for the purposes of the present study, PS and PI contractions were filmed in one muscle using a high-speed camera ($100 \text{ frames s}^{-1}$). Markers were inserted into the muscle-tendon complex at the muscle origin, the distal end of the muscle belly, the distal end of the proximal aponeurosis (i.e. the proximal end of the distal fibre), and at the distal end of the

Achilles tendon. Film data were smoothed (Butterworth low-pass fourth-order filter, cut-off frequency 20 Hz). Muscle-tendon complex length, and the lengths of the distal muscle fibre and of the tendinous structures (tendon and aponeurosis) were determined with an accuracy of 0.05 mm. Furthermore, the angle between the muscle fibre and the line of pull was calculated and used to calculate the length of the muscle fibre projection on the line of pull. Length changes of this fibre projection were compared with fibre length changes calculated on the basis of force-compliance data. The differences of projection of the muscle fibre length on the line of pull between prestretch and pre-isometric contractions, obtained from high-speed film and from calculations using compliance data of the tendinous structures, were compared for isotonic and isokinetic contractions. PS-PI differences were not equal, but qualitatively similar results are obtained for both methods (maximal difference during shortening was 0.5 mm). This indicates that using a simple muscle-tendon complex model of a series elastic component and contractile element connected in series gives reasonable results for the purposes of this study.

Statistics

Differences between PS shortening velocity and expected velocity on the basis of length-velocity characteristics and differences between PS-PI differences of mechanical work output during isokinetic and isotonic shortening were tested using Student's *t*-test for paired comparison, two-tailed, $P < 0.05$.

Results

Table 1 shows morphological and force data measured at l_o . Prestretch velocity

Table 1. *Morphological and force data measured at the optimum length of the muscle-tendon complex, as well as peak forces at the end of prephase (average of isokinetic and isotonic experiments)*

	Mean (S.E.M.)
Length (mm)	
Muscle-tendon complex	38.6 (0.5)
Distal fibre	12.3 (0.2)
Proximal aponeurosis	20.4 (0.2)
Tendon	7.8 (1.2)
Force (N)	
F_o	10.37 (0.13)
Passive force	0.07 (0.008)
Peak force (N)	
PI at $l_o + 4$ mm	7.91 (0.21)
PS at $l_o + 4$ mm	17.0 (0.40)
PI at $l_o + 0$ mm	10.27 (0.31)
PS at $l_o + 0$ mm	14.61 (0.67)

Values are mean and (S.E.M.), $N=5$.

(20 mm s^{-1}) was $1.6 \text{ fibre lengths s}^{-1}$. Peak force levels at the end of prestretch amounted to about 1.6 times F_0 for experiments above l_0 and about 1.4 times F_0 at l_0 .

Isotonic contractions

Fig. 1 shows typical examples of changes of muscle-tendon complex length and force and calculated changes of muscle fibre length as a function of time during isotonic PS and PI contractions. At the onset of release, muscle-tendon complex length is equal for PS and PI contractions (Fig. 1, upper panel). However, because of higher force levels (Fig. 1, middle panel), tendinous structures are lengthened more in PS conditions. As a consequence, fibres act at shorter lengths (Fig. 1, lower panel). During the quick release, i.e. before isotonic conditions are obtained, almost all shortening is taken up by the tendinous structures. This means

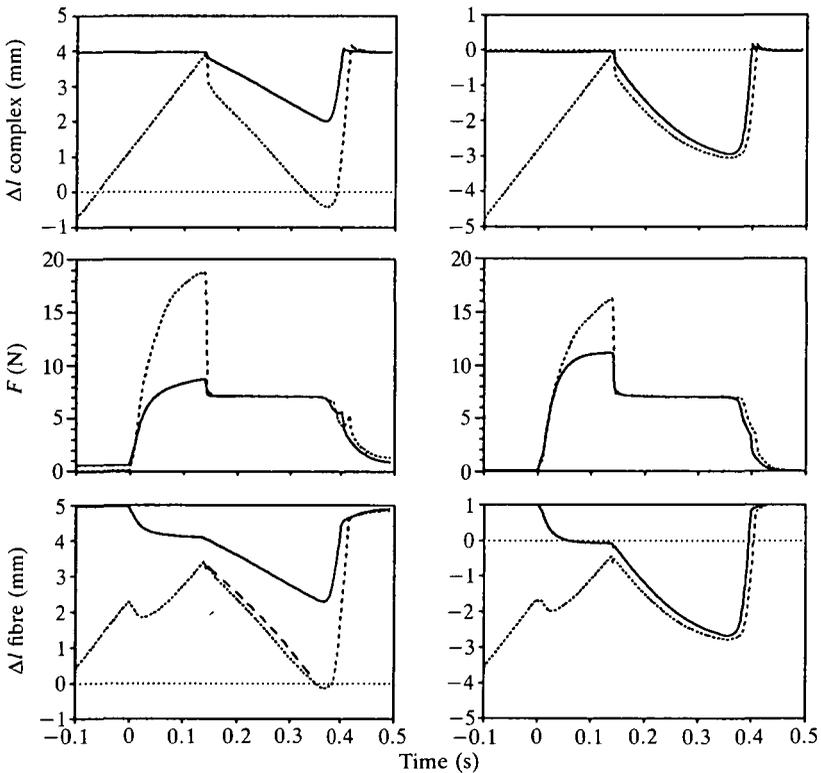


Fig. 1. Experimental results of isotonic contractions for one muscle. Measured muscle-tendon complex length (Δl complex), force (F) (original experimental tracings) and calculated changes in fibre length (Δl fibre) are plotted for PI (solid lines) and PS (dashed lines) contractions. Activation starts at zero time, onset of shortening at 0.14 s. Contractions at peak length of $l_0 + 4 \text{ mm}$ and at l_0 are shown in the left-hand and right-hand figures, respectively. The long-dashed line in the lower left-hand figure indicates the calculated (i.e. simulated) tracing for the same muscle, but with a pre-isometric condition in which the isotonic shortening started at the same length as in the prestretch condition.

that PS–PI differences for fibre length are still present at the onset of the isotonic shortening phase. From this moment on, the fibres follow their basic force–velocity characteristics. Because these characteristics are dependent on fibre length and because the force levels in both situations are equal, different velocities will occur for PS and PI conditions. For contractions above l_o , the fibres act closest to their optimum length in PS conditions. Therefore, in these conditions, fibre shortening velocity must be higher than for PI contractions. Consequently, fibre lengths in PI and PS conditions diverge during the concentric phase. Thus, as long as the muscle fibres are acting above optimum fibre length, PS–PI differences increase with time. For contractions below l_o , the situation is reversed: for PI rather than for PS contractions the fibre is acting closest to its optimum and therefore is shortening with a higher velocity. In this case, fibre lengths for PS and PI contractions converge during muscle shortening.

In the left-hand bottom figure a tracing for fibre length is indicated (long dashes), which was calculated on the basis of the length–velocity relationship for isotonic shortening at $0.67F_o$ (see Fig. 2). That is, we calculated fibre length as a function of time for an imaginary pre-isometric contraction (no potentiation of contractile machinery) in which, 10 ms after the release, the fibre length was equal to the fibre length actually measured in the prestretch contraction at peak length = $l_o + 4$ mm. (From 10 ms after release, shortening was clearly isotonic and the length–velocity curve for $0.67F_o$ could be applied.) The fact that this simulated fibre behaviour diverges from the tracing for the prestretch condition indicates that at a given length the fibre is able to shorten at a higher velocity owing to prestretch. However, as the tracing for the simulation is very close to that of the prestretch contraction, it is also clear that for the current experiment most of the PS–PI differences are due to differences of fibre length between the PS and PI conditions at the onset of shortening. For the experiment shown in Fig. 1, fibre work performed from 150 to 280 ms amounted to 7.5 mJ for the PI condition, 14.7 mJ for the PS condition, and 13.1 mJ for the simulation, which would indicate a potentiation effect of approximately 12%. It should be noted, however, that the difference between prestretch and simulation is not determined exclusively by potentiation of the contractile machinery. For example, halfway through the shortening period, the fibre acts closest to optimum length in the PS condition; this is caused by potentiation but in itself enables the fibre to produce more work. In other words, the difference in work between the PS condition and the simulation is due to potentiation and fibre length differences, which are initially induced by a potentiation of the contractile machinery.

To distinguish more precisely the amount of stretch-induced enhancement of fibre performance caused by differences of fibre length from that caused by potentiation, fibre shortening velocity (v_f) was determined 30 ms after release for all PS, PI and length–velocity experiments. At 30 ms, isotonic conditions were stable and most prestretch-induced effects were likely to be still present. Shortening velocity in PS contractions was compared to the velocity found using the length–velocity curve for a similar fibre length. This velocity at PS fibre length

was found by means of interpolation of the length–velocity data. PS shortening velocity was corrected with the small deviations of the PI shortening velocity from the length–velocity curve (Fig. 2). Differences in passive force exerted by the parallel elastic structures may have affected PS–PI shortening velocity differences to some extent, as not all force is delivered by the contractile element at lengths above l_0 . However, these effects were not taken into account because of their relatively small contribution to total force: on the basis of the passive length–force characteristics of the GM, the maximal PS–PI difference of passive force was estimated to be about 2% of the isotonic force level. A typical example of fibre length–velocity data is shown in Fig. 2 for the same muscle as that used for Figs 1 and 3. Corrected PS shortening velocity deviates from the length–velocity curve, particularly above l_0 . Table 2 shows results of statistical analysis of this corrected shortening velocity for PI and PS contractions, as well as PS velocity predicted on the basis of fibre length (i.e. corresponding velocity on the length–velocity curve calculated by means of interpolation). Above l_0 , the shortening velocity after prestretch is significantly higher than that predicted on the basis of fibre length, indicating these are fundamental changes in the force–velocity characteristics of the muscle fibre. For these experiments, about half the stretch-induced enhancement of shortening velocity can be explained by fibre length differences. Below optimum length the total PS–PI difference amounts to -1.12 mm s^{-1} , of which -0.38 mm s^{-1} can be explained. This unexplained decrement of shortening velocity is relatively small, but nevertheless significant.

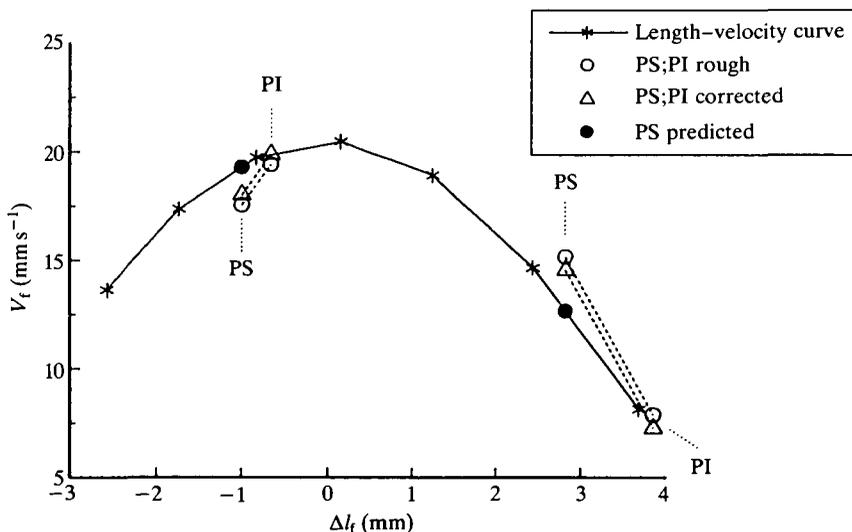


Fig. 2. Length–velocity curve (*, solid line) of the muscle shown in Fig. 1, with original (○) and corrected (△) length–velocity data for PI and PS contractions. Corresponding PI and PS data are connected with dashed line. Predicted PS velocity is indicated by (●). All data are obtained 30 ms after the onset of isotonic release. v_f is shortening velocity of the muscle fibre; Δl_f is difference between the fibre length and its optimum length.

Table 2. Fibre length and fibre shortening velocity 30 ms after release in PI and PS isotonic shortening contractions

	$l_{\text{peak}}=l_0+4\text{ mm}$	$l_{\text{peak}}=l_0$
Δl_f (mm)		
PI	3.99 (0.04)	-0.65 (0.03)
PS	3.02 (0.05)	-0.95 (0.04)
v (mm s^{-1})		
PI	4.51 (1.03)	17.77 (1.06)
PS	13.21 (0.65)	16.65 (1.09)
PS predicted	8.67 (1.26)	17.40 (1.04)
PS-PI	8.70* (0.85)	-1.12* (0.23)
PS-PS predicted	4.54* (1.06)	-0.74* (0.18)

Values are mean (S.E.M.), $N=5$.

PS predicted values are based on calculated fibre length and length-velocity curves.

Significant differences ($P<0.05$) are indicated by *.

Isotonic versus isokinetic work production

Mechanical work was determined for a period of 140 ms during the shortening phase from the onset of release by means of numerical integration of force with respect to length. Using the force-extension characteristics of the tendinous structures, storage and release of elastic energy of the tendinous structures were calculated for the same period. Therefore, within the category of work performed by the muscle-tendon complex (W_{cmplx}), work performed by the muscle fibres (W_f) and tendinous structures (W_t) could be distinguished. It should be noted that for contractions above l_0 a small part of W_f should actually be attributed to passive parallel elastic structures.

Table 3A shows PI and PS work, as well as PS-PI differences of work for isotonic and isokinetic experiments. For comparison of isotonic and isokinetic experiments, shortening velocities are shown in Table 3B. During isotonic shortening above l_0 , enhancement of work output due to stretch is caused to a large extent by increased muscle fibre work. In contrast, during isokinetic shortening, a stretch-induced reduction of fibre work occurs. Work of the muscle-tendon complex is increased for PS contractions, because of a much higher release of elastic energy. For contractions with peak length at optimum length, differences between isotonic and isokinetic contractions are qualitatively similar. However, at these muscle lengths fibre work output during isotonic shortening following prestretch is reduced as well. This reduction is smaller than

Table 3. (A) Work (mJ) performed by the muscle-tendon complex and its elements, during 140 ms of shortening. (B) Mean shortening velocity (mm s^{-1}) of a 140 ms shortening period for isotonic and isokinetic contractions

	$l_{\text{peak}}=l_0+4\text{ mm}$			$l_{\text{peak}}=l_0$		
	Complex	Fibre	Tendon	Complex	Fibre	Tendon
A Work						
Isotonic						
PS	20.95 (1.58)	14.10 (1.49)	6.85 (0.23)	19.85 (0.60)	14.24 (0.67)	5.61 (0.14)
PI	5.13 (1.11)	4.69 (0.99)	0.45 (0.12)	16.81 (0.30)	14.65 (0.32)	2.16 (0.11)
PS-PI	15.82† (1.00)	9.42† (1.02)	6.40† (0.18)	3.03† (0.46)	-0.42 (0.44)	3.45† (0.10)
Isokinetic						
PS	10.89* (1.58)	4.62* (1.43)	6.28 (0.21)	11.70* (1.43)	7.45* (1.14)	4.25* (0.36)
PI	7.86* (1.23)	7.09* (1.12)	0.77* (0.13)	11.41* (1.26)	9.77* (1.15)	1.64* (0.13)
PS-PI	3.03†* (0.35)	-2.47†* (0.32)	5.51†* (0.10)	0.28* (0.32)	-2.33†* (0.05)	2.61† (0.34)

Values are mean (s.e.m.), $N=5$.

Significant PS-PI differences are indicated by †.

Isokinetic values differing significantly from corresponding isotonic values are indicated by *.

	$l_{\text{peak}}=l_0+4\text{ mm}$	$l_{\text{peak}}=l_0$
B Shortening velocity		
Isotonic	8.64 (1.01)	13.81 (0.21)
Isokinetic	8.75 (1.35)	11.02 (1.08)

Values are mean (s.e.m.), $N=5$.

Averages of PS and PI contractions are given.

No significant differences were found between isotonic and isokinetic conditions.

that during isokinetic shortening. Prestretch effects due to interactions of tendinous structures and muscle fibres during isotonic shortening have been described above. For an isokinetic experiment, force and length tracings, as well as calculated fibre length changes, are shown in Fig. 3. For a description of such interaction effects on isokinetic fibre work, the force-velocity characteristics of the fibres must be taken into account. The isokinetic shortening velocities of the muscle-tendon complex are about 9 and 11 mm s^{-1} for contractions above and below optimum length, respectively. These velocities are well below the optimum velocity, i.e. the velocity with the highest power output, which is about 2.3 fibre lengths s^{-1} (i.e. $\pm 30 \text{ mm s}^{-1}$) for rat GM muscle (de Haan, 1988a). The

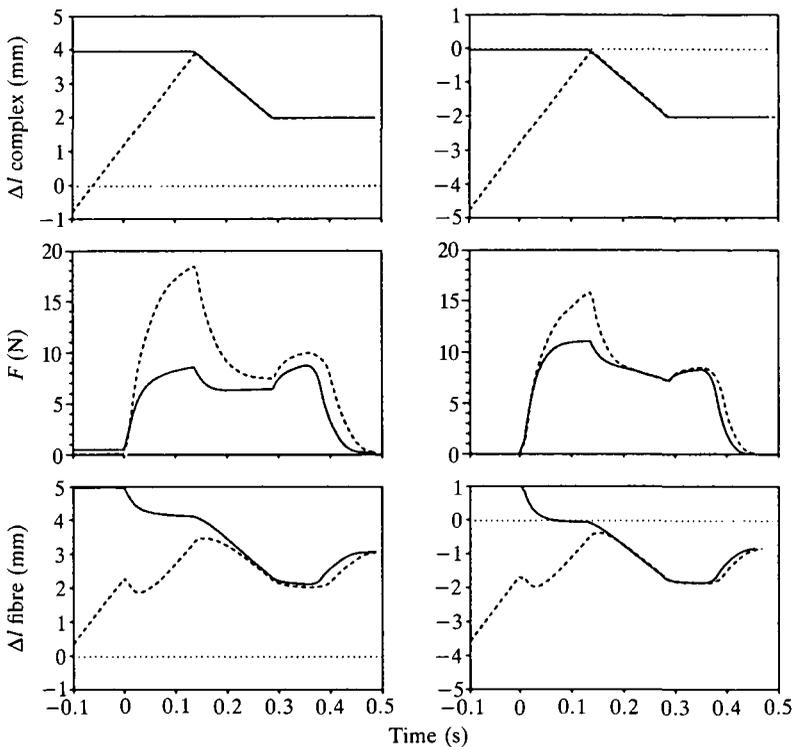


Fig. 3. Experimental results of isokinetic contractions for the muscle shown in Fig. 1. Measured muscle-tendon complex length (Δl complex), force (F) (original experimental tracings) and calculated changes in fibre length (Δl fibre) are plotted for PI (solid lines) and PS (dashed lines) contractions. Activation starts at zero time. Contractions at the peak length of $l_o + 4$ mm and at l_o are shown in the left-hand and right-hand figures, respectively.

shortening velocity of tendinous structures is higher for PS than for PI contractions, because of larger force decrements occurring in the same time. Therefore, for the isokinetic contractions, fibre shortening velocity is lowest when preceded by stretch, and thus attains values further from optimum shortening velocity. This results in a lower power output, and thus in a lower work output over a given period. The influence of extension of the tendinous structures on fibre length, causing the muscle fibres to act closer to their optimum length in PS contractions (Fig. 3, lower panel), is present as well. This would increase fibre work because of the higher force level. However, given the actual reduction of fibre work (Table 3A), this effect is apparently small compared to the influence of reduction of shortening velocity. In shortening starting at l_o , both length and velocity differences, caused by prestretch, affect fibre work output negatively.

Discussion

The results of the present study show that the effects of prestretch on positive

work output are due to three mechanisms: (1) extra elastic energy is released; (2) differences of fibre length and fibre shortening velocity are introduced by different peak forces (interaction between series elastic structures and contractile machinery); and (3) fundamental characteristics of the contractile element are changed (i.e. potentiation of the contractile machinery). All transient effects occurring during the rapid shortening immediately after release were lost at the moment of measurement (30 ms after release) and could not have been detected by our apparatus. The second mechanism can have either negative or positive effects on work output, depending on the type of contraction. But the effects of the other mechanisms may also differ greatly from one type of contraction to another. The potentiation effect of prestretch on work output of the contractile machinery may be totally compensated for, or even exceeded by, a negative effect caused by interaction with the series elastic structures. However, under certain conditions, potentiation may make a considerable contribution to work enhancement owing to prestretch (e.g. expressed in velocity at a given load; see the isotonic experiments at lengths greater than l_0) (Table 2). The relative contribution of extra recoil of elastic energy also depends strongly on the type of contraction. In some conditions it completely explains the work enhancement of the muscle-tendon complex (Table 3A).

Our experiments are merely an example of prestretch effects. Other prestretch variables (velocity, amplitude) will cause different levels of peak force and thus other effects on the interaction between series elastic structures and contractile machinery. The isotonic force level of $0.67F_0$ was chosen merely for pragmatic reasons (i.e. limited capacity of the motor system, which limits the magnitude of force jumps). Other isotonic force levels will certainly show other results, because the length range at which the contractile machinery will operate indirectly depends on the level of force. In order to determine the effects of prestretch on fibre work output during isokinetic shortening, it is crucial to consider if the shortening velocity of the muscle-tendon complex is higher or lower than its optimum shortening velocity.

Potentiation

Enhanced isotonic shortening after prestretch at lengths above optimum cannot be explained completely by differences of muscle fibre length between PS and PI contractions. This means that the force-velocity curve of the contractile element must have been shifted towards higher velocities for a given load. This is in agreement with earlier findings (Cavagna and Citterio, 1974; Edman *et al.* 1978; Sugi and Tsuchiya, 1981) and indicates a potentiation of the contractile machinery. For whole muscle, Cavagna *et al.* (1968) and Bergel *et al.* (1972) used different techniques to obtain equal elastic energy storage at the onset of shortening in PS and PI contractions (by means of regulating force level). This way, they also eliminated PS-PI differences of interaction between series elastic structures and the contractile element at the onset of shortening. Therefore, all excess work

performed after stretch could be attributed to potentiation of the contractile machinery.

Below muscle optimum length, an inverse prestretch effect is seen: a shortening velocity lower than expected was found after prestretch. Interaction between muscle length and stretch effects was demonstrated by Edman *et al.* (1978), who showed that at lower lengths stretch effects were small or even absent. This influence of fibre length on potentiation effects is also shown by the experiments (Figs 1–3) in which potentiation amounts to about 12 %, when expressed as work enhancement for a shortening range from l_o+3 mm to $l_o+0.5$ mm (see results of Fig. 1), and about 26 %, when expressed as enhancement of shortening velocity at l_o+3 mm (30 ms after release).

However, to our knowledge, no negative prestretch effects have been reported in the literature. In the present study, the negative effect on contractile properties apparently has a transient character: it could only be demonstrated to be significant if expressed as fibre shortening velocity at 30 ms after release (Table 2) but not if expressed as work output during 140 ms of isotonic shortening (Table 3A). Therefore, it is possible that, for example, a small visco-elastic component in the tendinous structures may have caused a somewhat higher loss of energy in PS contractions and that this was not accounted for in the calculations. This could occur immediately after the release (i.e. during force transients). Furthermore, small errors may have occurred in the estimation of fibre lengths.

The influence of the tendon on fibre work

For isokinetic shortening at low velocity, a prestretch of the active muscle limits work production by the muscle fibre, because the shortening velocity of the tendinous structures is enhanced. If, as in isokinetic shortening, the shortening distance of the muscle–tendon complex is imposed, prestretch limits not only the shortening velocity but also the amount of shortening of the fibres. This reduction of shortening itself also has a negative effect on fibre work output, especially when a given load has to be displaced (Avis *et al.* 1986). For our experiments, this can be simply demonstrated by calculating work output during isotonic shortening above l_o over a distance of 1 mm. In PS contractions, this still results in a higher work output of the muscle–tendon complex (11.68 mJ for PS vs 7.10 mJ for PI), but in less fibre work (4.34 mJ for PS vs 6.28 mJ for PI). The rate of fibre work (power) is not affected by shortening distance and is much higher for PS than for PI contractions (0.42 J s^{-1} for PS vs 0.06 J s^{-1} for PI).

For isotonic shortening the situation is different from that for isokinetic shortening because the muscle–tendon complex, and thus the muscle fibre, is not limited by the dynamics of the tendinous structures in either the amount or the velocity of shortening. For isotonic shortening, the influence of stretch on fibre work is determined by the effects on the length range at which the fibres act during shortening (potentiation effects not taken into account). For isokinetic shortening this fibre length effect is rather small, because the length of the muscle–tendon complex was controlled and, in time, the force levels tended to converge for PS

and PI conditions. This situation does not allow large differences in length of the muscle fibres (Fig. 3).

Avis *et al.* (1986) concluded that a counter movement reduced contractile element work during maximal leg extension movements because the shortening distance of the contractile element was reduced. This is merely because the subjects were forced to displace a given load over a given distance (see above). However, in the same study, simulation results of a model, in which no potentiation was incorporated, showed that, in addition to work, the power of leg extension preceded by a counter movement was also reduced by the counter movement (Avis *et al.* 1986: their Table 2). As stated above, this reduction of power is not caused by limited shortening of the contractile element, but is probably due to a shift of the length range or of the shortening velocity of the contractile element away from their optimum (possible differences in activation and coordination are not taken into account).

In general, for a proper interpretation of the effects of stretch on work enhancement in stretch-shortening contractions, information about the length ranges of the muscle-tendon complexes involved and their fibres is essential. Also, for interpretations of prestretch-induced effects on energy consumption and on the mechanical efficiency of positive work, the effects of prestretch on fibre length should be taken into account. The relationship between relative load and oxygen uptake during isotonic shortening is influenced by the initial length of shortening (Stainsby and Barclay, 1976). Furthermore, mechanical efficiency seems to be influenced by muscle length, being lower above than at optimum length (de Haan, 1988*b*). Therefore, the increment of mechanical efficiency of positive work of skeletal muscle induced by previous stretch (Komi, 1986; Heglund and Cavagna, 1987; de Haan *et al.* 1989) may be related, at least partly, to differences in fibre length for prestretch and pre-isometric contractions.

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