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EFFICIENCY OF RAT MEDIAL GASTROCNEMIUS MUSCLE IN CONTRACTIONS WITH AND WITHOUT AN ACTIVE PRESTRETCH

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Summary

The efficiency of positive work was measured for rat medial gastrocnemius muscle at 25°C during repeated contractions. Six muscles were stimulated to perform concentric contractions preceded by an active prestretch (PS contractions) and six muscles made to give concentric contractions from an isometric state (PI contractions). Both lengthening and shortening of the muscles (distance: 6 mm) occurred at a constant velocity of 20 mm s^{-1} (1·5 fibre lengths s^{-1}). Stimulation was started 150 ms prior to the onset of concentric contraction for both types of contraction. For the PS contractions this meant that the active state was developed during the last 2·4 mm of the lengthening.

Energy consumption (calculated from high-energy phosphate consumption) appeared to be equal for both types of contraction, although positive work output was 39·4 % higher in the PS contractions than in the PI contractions. The efficiency of positive work was 36·8 ± 3·5 % in the PS contractions and 26 ± 2·0 % in the PI contractions. In contrast to results of previous studies, the positive work done by the muscle in the PS contractions was much larger than the negative work done on the muscle during stretch owing to the applied stimulation protocol which was intended to simulate *in vivo* conditions during running. The efficiency of positive work in the PS contractions is too low to explain the efficiencies of 40–70 % reported for human and animal running.

Introduction

Although a large number of measurements of the efficiency of total body movements have been reported, data on the efficiency of isolated muscles are relatively scarce. Knowledge of muscle efficiency [which is defined as the quotient of mechanical power (or work) output and metabolic power (or work) input], however, is required to explain the efficiencies reported for total body movements. In particular, for larger animals (including man) efficiencies of positive

Key words: running efficiency, stretch–shortening cycle, stimulation, mammalian muscle.

power production during walking, hopping and running (Margaria, 1968; Pugh, 1971; Williams & Cavanagh, 1983; Heglund *et al.* 1982) are far in excess of the muscle efficiency, which is generally assumed to be lower than 30 % (Stainsby *et al.* 1980; Astrand & Rodahl, 1977). This value is calculated from the product of phosphorylative coupling efficiency e_p and contraction coupling efficiency e_c (Alexander & Goldspink, 1977; Astrand & Rodahl, 1977). The e_p is assumed to be of the order of 60 % whereas e_c is estimated to be about 50 % (Whipp & Wasserman, 1969; Stainsby *et al.* 1980). Most authors explain the relatively high gross efficiency found in walking, running and hopping by storage and release of mechanical energy in elastic structures of the muscle–tendon complexes (Cavagna *et al.* 1964; Taylor & Heglund, 1982; Alexander *et al.* 1982; Alexander, 1984, 1988; McMahon, 1985). Elastic structures in a muscle–tendon complex can store potential energy when they are stretched. The capacity to store elastic energy is a function of the applied force and the compliance of the muscle–tendon complex. From the relatively low compliances reported in the literature (Walmsley & Proske, 1981; Morgan *et al.* 1978; Morgan, 1977; Van Ingen Schenau *et al.* 1988) it can be concluded that the role of storage and release of elastic energy is often highly overestimated (Van Ingen Schenau, 1984). Alternative explanations for the high efficiencies found in total body movements involve either the storage and release of mechanical energy by a nonelastic mechanism in the contractile machinery, as shown by Cavagna *et al.* (1985), or a muscle efficiency higher than 30 %. The latter explanation is based on uncertainties in the estimation of the free energy, ΔG, or the total enthalpy for *in vivo* conditions in mammalian muscles (Astrand & Rodahl, 1977; Morel, 1981) which means that the magnitude of e_p is open to discussion. Moreover, the often-cited value of $e_c = 49\,\%$ (Whipp & Wasserman, 1969) is based on the gross efficiency in human cycling. Much higher values (up to $e_c = 75\,\%$) are reported for slow animal muscles (Alexander & Goldspink, 1977). So there seem to be no decisive thermodynamic arguments against a muscle efficiency considerably higher than 30 %.

During running, many muscles of the lower extremities (in particular the knee extensors and the calf muscles) appear to be actively stretched before they are allowed to shorten. The purpose of the present study was to measure muscle efficiency in comparable stretch–shortening contractions. Even though much attention has been paid to enhancement of force and work due to an active stretch (e.g. Cavagna *et al.* 1968; Edman *et al.* 1978), only one study (Heglund & Cavagna, 1987) has reported data on muscle efficiency in contractions immediately preceded by stretching of the active muscle. However, in all these previous studies of mechanical or energetic effects of prestretching the contracting muscle, the stimulation protocols led to an unrealistic balance between negative work (work done on the muscle) and positive work (work done by the muscle). Stimulation was started at or prior to the onset of the stretch phase. As can easily be deduced from the force and length tracings presented by Cavagna *et al.* (1968) and Heglund & Cavagna (1987) such protocols lead to an amount of negative work which is more than four times larger than the subsequent positive work output. Even in

level walking and running, however, the mean net work output of the muscles of the lower extremity has to be larger than zero since these muscles will have to compensate for the losses of mechanical energy due to active deceleration of body segments, deformations of the foot and work done against the environment (mainly air friction). As shown by Hof *et al.* (1983), the positive work done by human calf muscles during walking is much larger than the negative work done on the muscles during the eccentric phase of this stretch–shortening cycle. This positive net work output appears to be achieved by activating the muscle shortly before the onset of the concentric phase. This activation condition was simulated in the present *in situ* experiments.

Materials and methods

The muscle selected for the experiments was the medial gastrocnemius (GM) of adult male Wistar rats. Twelve rats with a mean body mass of 240 ± 7 g were anaesthetized with an initial intraperitoneal dose of 60 mg kg^{-1} pentobarbital. The GMs of both hindlimbs were carefully exposed. The distal tendon of the right GM was connected to the isovelocity system described previously by de Haan *et al.* (1987). Six muscles were allowed to perform repeated concentric contractions starting each contraction from an isometric state (henceforth called preisometric or PI contractions) and the concentric contractions of the remaining six muscles were preceded by a stretch (henceforth prestretch or PS contractions). Owing to the properties of the computerized control system, the imposed length pattern during the PS contractions contained a short (30 ms) isometric plateau between the eccentric and concentric phases. The temperature around the muscle was kept at 25 °C using a diffusing jacket around the muscle through which passed heated water vapour from a nebulizer. The muscles were stimulated with silver electrodes placed on the distal part of the severed sciatic nerve. Muscle optimum length (L_0, the length which gave the highest twitch force) was determined with the blood supply intact. L_0 was identified using 10 twitches at different muscle lengths (one each minute). Maximal isometric force F_0 at L_0 was measured during a short (200 ms) tetanic contraction (60 Hz stimulation frequency). It should be noted that L_0 represents the length of the entire muscle–tendon complex. Muscle belly length and the most distal fibre bundle length were estimated at L_0 using a pair of compasses. After the determination of F_0, the muscle was rested for 10 min and the blood supply was subsequently occluded to minimize aerobic metabolism and to prevent lactate removal during the experiments.

Experimental protocol

A stimulation protocol was chosen which, to a certain extent, is comparable to the activation pattern observed in human calf muscles during walking. It is known that during human walking the calf muscles undergo a pronounced stretch–shortening cycle (Hof *et al.* 1983). Moreover, the activation of these muscles appears to be strongly increased some 100–200 ms prior to the onset of the

concentric phase (Hof *et al.* 1983). A comparable protocol was applied for the present PS contractions. In a pilot study the (tetanic) stimulations were started at different times (70–170 ms) prior to the onset of the concentric phase. The amount of positive power during the concentric phase appeared to reach its highest value when the stimulation started 150 ms prior to the onset of the concentric phase. This interval of 150 ms was chosen for both the PS and the PI experiments. When using this type of stimulation, the muscles used in the pilot study appeared not to be damaged (as judged by repeated force measurements) despite a surprisingly large force enhancement during stretch. The velocity of shortening chosen was relatively low ($20\,mm\,s^{-1}$) to achieve a relatively long-lasting dynamic part of the contraction: the total stimulation time was 450 ms with a concentric phase of 300 ms.

The muscle performed 10 repeated contractions at the rate of $1\,s^{-1}$ (see Figs 1 and 2). In the concentric phase the muscle was allowed to shorten from L_0+3 mm to L_0-3 mm. Stimulation ended immediately at the end of the concentric phase. During PS contractions the muscle subsequently relaxed for 370 ms at L_0-3 mm and was then stretched back to L_0+3 mm at a velocity of $20\,mm\,s^{-1}$. Because the stimulation started 150 ms prior to the onset of the concentric phase and given the isometric plateau of 30 ms, the start of the following stimulation occurred at $L_0+0{\cdot}6$ mm (which is at 60 % of the total stretch distance of 6 mm). The distance of the active stretch was thus 2·4 mm.

In the PI contractions the muscle rested at L_0-3 mm for 200 ms and was subsequently passively stretched to L_0+3 mm in 300 ms (velocity = $20\,mm\,s^{-1}$). After 50 ms at this length the muscle was stimulated and allowed to develop an isometric force for 150 ms followed by the concentric phase. Force and length signals of all contractions were A/D converted and fed into a microcomputer for further analysis.

Immediately after the tenth contraction, the muscle was freeze-clamped and, after weighing, ground in a mortar precooled with liquid nitrogen, and subsequently freeze-dried. The contralateral resting GM was freeze-clamped before the exercise protocol and treated in the same way. After removal of connective tissue the dry muscle powder was stored at −70 °C.

Analysis and calculations

Mechanical work

Positive work, W_{pos} (the work done by the muscle), and negative work, W_{neg} (the work done on the muscle), were determined for each contraction by integration of force to length over the concentric phase and the stretch phase, respectively.

Energy consumption

Duplicate extractions were made by homogenizing 20 mg of dry tissue powder in 0·75 ml of $1{\cdot}7\,mol\,l^{-1}$ cold perchloric acid. The homogenate was centrifuged at 0 °C

(MSE Mistral 18000 *g*) and the supernatant neutralized with potassium hydroxide and potassium carbonate. After centrifugation (Eppendorf, 10000 rev. min^{-1}) the precipitated potassium perchlorate was removed.

Enzymatic determinations of phosphocreatine (PC), creatine, ATP and lactate were performed on a double-beam spectrophotometer (UV-190, Shimadzu) according to the method of Bergmeyer (1970).

The high-energy phosphate consumption (HEPC) was calculated from the differences in concentrations of ATP, PC and lactate between the experimental and the contralateral GM according to:

$$HEPC = 1{\cdot}5 \times \Delta lactate - \Delta ATP - \Delta PC.$$

The possible influence of some aerobic metabolism due to the presence of oxygen in the muscle can be expected to be very low and was therefore neglected. Moreover, since ΔATP is only 2–4 % of HEPC, the possible utilization of extra high-energy phosphates by hydrolysis of ADP to AMP with subsequent formation of IMP was also neglected. Following de Haan *et al.* (1986), a ratio of wet muscle mass to dry muscle mass of 0·23 was taken for the calculation of the high-energy phosphate utilization for each muscle. An equivalent of 44 kJ mol^{-1} ATP (Kushmerick & Davies, 1969) was used to calculate the energy consumption E in joules.

Positive work efficiency, e_{pos}, was calculated from positive work summed over the 10 contractions and the total energy consumption E. Net efficiency was calculated from the $W_{pos} - W_{neg}$ and E.

Differences in W, E and efficiencies between PI- and PS-contracting muscles were tested for significance using unpaired *t*-statistics ($P < 0{\cdot}05$).

Results

Typical examples of length and force traces of both the PI and PS contractions together with the duration of stimulation and relaxation are shown in Figs 1 and 2. Note the remarkable enhancement of force during stretch in the PS contraction compared with F_1 in the PI contraction. The small decrease in force from the peak force (F_p) to F_1 during the 30 ms isometric plateau in the PS contraction was observed in all six muscles. Average values of the force levels at specific instants indicated in Figs 1 and 2 are presented in Table 1. This table also presents the mean values of the maximal isometric force measured at L_0. F_p values are the maximal values of force observed during the entire contraction. The forces at F_1 and F_3 were used to estimate the amount of stored elastic energy at the onset of the concentric phase and just prior to relaxation of the muscles, respectively (see Discussion). F_2 was the force value halfway through the concentric phase. The ratio between F_1 in the PS contractions and F_1 in the PI contractions was 2·11 and the ratio of the peak forces was 2·43. These ratios are much higher than those observed in comparable experiments with rat extensor digitorum longus (EDL) using the more common stimulation protocol in which the stimulation for PS contraction is started well before the stretch phase (Van Ingen Schenau *et al.*

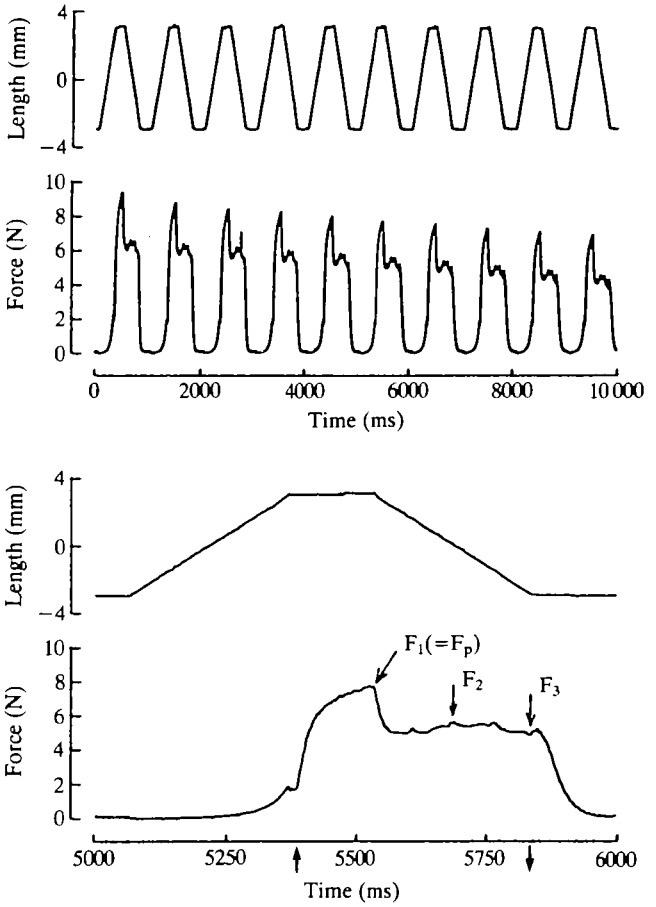

Fig. 1. Typical tracings of muscle length and force during 10 repeated PI contractions (top) and an enlarged example of one complete cycle (bottom). Arrows on the abscissa indicate the onset (↑) and end (↓) of the stimulation. The indicated forces are used to calculate the amount of stored elastic energy. F_p, peak force; F_1–F_3, forces at the beginning, middle and end of concentric contraction.

1988). From those previous expriments a ratio of 1·53 can be deduced for F_1 in PS and PI contractions.

Mean muscle mass, energy consumption, work and efficiency values are presented in Table 2. Muscle mass and energy consumption did not differ significantly between the two groups. The small amount of negative work during the PI contractions (Fig. 1), which is due to the passive properties of the muscle–tendon complexes, can be ignored.

Positive work in PS contractions was 39·4 % higher than in PI contractions. This gain in W_{pos} as a result of the preceding stretch is of the same order as that reported by Cavagna *et al.* (1968) for toad sartorius, frog gastrocnemius and human forearm flexors but much lower than the gains of 256 % and 147 % reported

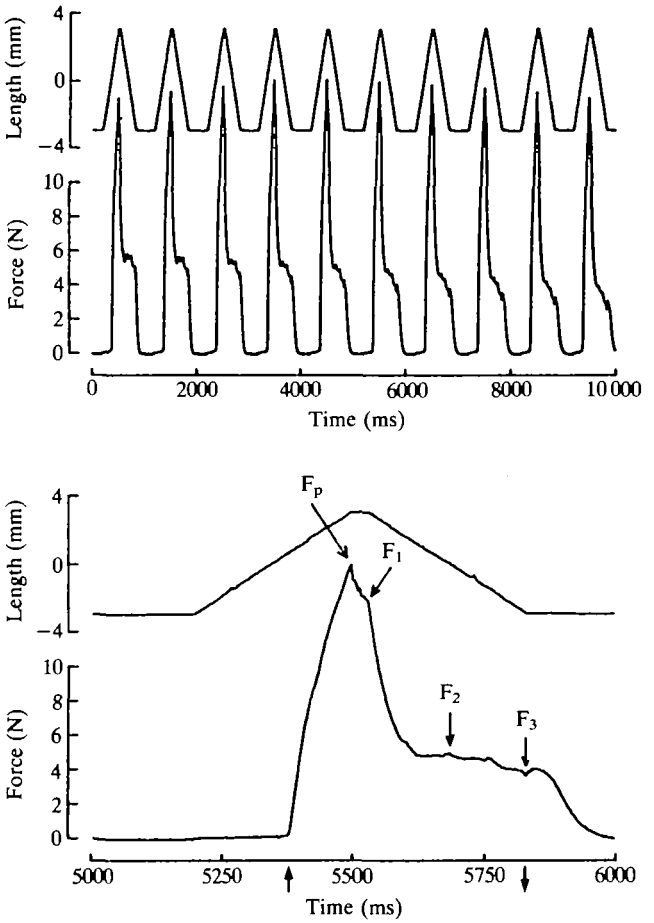

Fig. 2. A typical example of length and force tracings during PS contractions (see legend to Fig. 1 for further details).

by Heglund & Cavagna (1987) for rat EDL and gastrocnemius, respectively. In contrast to the results of Cavagna *et al.* (1968) and Heglund & Cavagna (1987), the positive work in the PS contractions was considerably (51 %) larger than the negative work during the stretch.

The efficiency of positive work in PI contractions was below the 30 % generally assumed to be the maximal value for muscle efficiency. Though e_{pos} for the PS contractions was larger than this theoretical value, it was still far below the values of 40–70 % which have been reported for human running and kangaroo hopping (Margaria, 1968; Cavagna & Kaneko, 1977; Heglund *et al.* 1982).

Discussion

Despite the relatively low contraction velocity used in the present study (1·4 fibre lengths s^{-1}) the efficiency of positive work in the PI contractions is higher

Table 1. *Maximal isometric force F_0 and the forces indicated in Fig. 1 for both groups of muscles*

	F_0	F_1	F_2	F_3	F_p
PI ($N = 6$)					
Mean	11·09	6·59	4·42	3·98	6·59
S.D.	0·89	0·88	0·86	0·64	0·89
PS ($N = 6$)					
Mean	10·84	13·91	4·97	3·76	16·00
S.D.	0·59	0·88	0·59	0·39	0·88
Difference (%)	−2·2	111*	12·4	−3·3	143*

* Significant differences between the groups.

F_0, maximal isometric force at optimal muscle length; F_1, F_2, F_3, forces at the beginning, halfway through and at the end of the concentric phase; F_p, peak force during the contraction.

Table 2. *Mass, energy consumption (E), negative (W_{neg}) and positive work (W_{pos}) and efficiency of positive and net work (e_{pos} and e_{net}) for both types of contraction (PI and PS)*

	Mass (mg)	E (mJ)	W_{neg} (mJ)	W_{pos} (mJ)	e_{pos}	e_{net}
PI ($N = 6$)						
Mean	794	981	21·5	254	26·3	23·9
S.D.	51	251	3·9	49	2·0	1·7
PS ($N = 6$)						
Mean	748	968	234	354	36·8	12·4
S.D.	81	127	13	36	3·5	1·8
Difference (%)	−5·8	−1·3	988*	39·4*	39·9*	−48·1*

* Signficant differences between the PS and PI groups.

than the values of 18·5 % and 15 % reported for rat soleus by Gibbs & Gibson (1972) and Heglund & Cavagna (1987), respectively, and also higher than the values of 14·2 % and 18 % reported for rat EDL by Wendt & Gibbs (1973) and Heglund & Cavagna (1987), respectively. This is probably due to the long phase of active shortening relative to the total stimulation time and the relatively long distance of shortening (6 mm at a mean fibre length of $14·8 \pm 0·8$ mm) in our experiments. From their figures representing the force and length tracings for rat EDL, it can be deduced that Heglund & Cavagna (1987) used distances of active shortening of less than 1 mm for both PI and PS contractions. This small shortening distance can also explain the much larger gains in W_{pos} and e_{pos} as the result of prestretch reported by Heglund & Cavagna (1987) when compared with the present results. For a particular amount of elastic energy stored in the elastic structures of the muscle–tendon complex, the gains in W_{pos} and e_{pos} will be higher

at shorter distances of active shortening owing to an increased relative contribution of elastic energy in the positive work output.

The mean value of approximately 40 % for e_{pos} in PS contractions of rat EDL reported by Heglund & Cavagna (1987) is only slightly higher than the 36·8 % found for rat GM in the present study. Based on the present results, it is not possible to determine the actual efficiency of the contractile machinery in the muscle–tendon complex since the contribution of elastic energy in W_{pos} is unknown. However, the fact that equal energy consumption was found for both types of contractions does not support the suggestion made in a previous study (Van Ingen Schenau, 1984) that the energy consumption might decrease as a result of a short active prestretch. The idea was that, by avoiding a waste of metabolic energy used in taking the (nonconservative) slack of muscle fibres at the onset of a contraction, the enhancement of work output induced by an active stretch might be accompanied by a decrease of metabolic power input. This should have led to a higher efficiency of the contractile element in PS contractions compared with PI contractions.

The equality of energy consumption suggests, however, that, at least under the conditions and protocol used in this study, the difference in positive work efficiency has to be explained by other phenomena such as storage and release of elastic energy and by what is mostly referred to as 'potentiation' of the contractile machinery (Cavagna *et al.* 1968, 1985; Hill, 1970; Alexander & Goldspink, 1977).

Based on data concerning compliance of mammalian muscles described in the literature and in the light of the new stimulation protocol used in the present study, the present results allow the highlighting of aspects which may shed some new light on these well-known phenomena.

Enhancement of force and of positive work

The majority of previous studies on the effects of a stretch were performed with amphibian muscles. As discussed previously (Van Ingen Schenau *et al.* 1988), a major problem in studying eccentric contractions in mammalian muscles concerns the high risk of damaging the muscle, particularly when using the long active stretch distances necessary to achieve the maximal gain in positive power during the concentric phase as reported for amphibian muscles (Cavagna *et al.* 1968; Edman *et al.* 1978). The present study, however, shows that with the applied stimulation protocol a strong enhancement of force and positive power can be achieved without such damage. Although in both PI and PS contractions an effect of fatigue is observed during the course of repetitive contractions (see top of Figs 1 and 2), the experiments performed in the pilot study (with an intact blood supply) showed that muscles attained the original force levels after rest.

When maximal force during stretch (achieved at L_0+3 mm) is compared with F_1 during the PI contractions (at the same length) the difference is striking. The ratios between these forces are much higher than that previously observed in rat EDL (Van Ingen Schenau *et al.* 1988) or in amphibian muscle (e.g. the values in Cavagna *et al.* 1968) but comparable to the results reported for dog muscles

(Stainsby, 1976). This means that the stimulation protocol used in the present study leads to a strong enhancement of force despite the relatively short distance of active stretch (2·4 mm). This stretch distance will be distributed over the contractile structures as well as the tendinous structures of the muscle–tendon complex. Moreover, the majority of the crossbridges will not attach directly at the onset of the stimulation since it takes time for the active state to develop fully. So, one might argue that the stretch distance of many crossbridges is short enough (see next paragraph) to allow a large number of crossbridges which attach during the stretching phase to remain attached until the concentric phase.

The enhancement of positive work due to this stretch shows that it is not necessary to apply long stretch distances and large amounts of negative work to achieve this enhancement. The enhanced force and positive work output as well as the relatively low amount of negative work compare well with *in vivo* movements. In the majority of these movements where muscles show a stretch–shortening cycle (as in running, jumping and overarm throwing), the amount of negative work is less than the amount of positive work and, as also stated by Tidball & Daniel (1986), the onset of activation seems mostly to take place in the last phase of the stretch.

The role of elastic energy

For a deeper understanding of the physiological significance of the efficiencies e_{pos} and e_{net} for the PS contractions one needs to know which part of W_{pos} is due to the release of elastic energy. Based on previous experiments with the rat EDL (Van Ingen Schenau *et al.* 1988) and on data concerning the compliances of other mammalian muscle–tendon complexes, an estimation can be made of this role of storage and release of elastic energy. To calculate the stored and released amounts of elastic energy one needs to know the force–extension characteristics of the series elastic elements of the muscle–tendon complexes. Since these characteristics were not measured, a rough estimate is made based on the mean values of force and muscle length of the muscles in the present study. The mean muscle length of the twelve muscles was $L_0 = 43{\cdot}8 \pm 0{\cdot}9$ mm (length of total muscle–tendon complex; the mean fibre length was $14{\cdot}8 \pm 0{\cdot}8$ mm). Though many different mathematical functions for the force–extension component (SEC) have been proposed in the literature (Hof *et al.* 1983; Hatze, 1978; Proske & Morgan, 1987), it has been shown that these functions can be fairly well approximated by a simple quadratic relationship, $F = k\Delta L^2$, where F is the force, k is a constant and ΔL is the extension of the SEC due to F (Van Ingen Schenau, 1984). To determine this function one needs to know ΔL at one particular force. Data in the literature give extensions at maximal isometric force in the range of 2–5 % of total muscle length (Walmsley & Proske, 1981; Morgan *et al.* 1978; Morgan, 1977). Using quick-release experiments, the force–extension characteristic of rat EDL was calculated by Van Ingen Schenau *et al.* (1988). The extension at F_0 appeared to be 3·2 % of L_0. Since the rat GM has shorter tendons relative to its total muscle length than the rat EDL, it seems likely that the SEC of the GM will be slightly stiffer

Table 3. *Positive work of the CE (W'_{pos}) calculated from W_{pos} and the contribution of elastic energy in both types of contraction (PS and PI) and relative contributions of elastic energy and muscle potentiation in W_{pos}*

SEC extension at F_0					
ΔL (mm)	$\Delta L/L_0 \times 100\,\%$	$W'_{pos}(PS)$ (mJ)	$W'_{pos}(PI)$ (mJ)	Elastic energy (%)	Potentiation (%)
1·3	3 %	295	264	19	10
0·9	2 %	315	261	13	15
1·7	4 %	275	267	26	2
2·2	5 %	256	271	32	−4

The data are calculated for different assumptions for the compliance of the series elastic component.

than that of the EDL. For this first approximation an extension of 3·0 % is assumed to occur at the mean isometric force, $F_0 = 10{\cdot}97$ N, of the twelve muscles. With these data the constant k is $6{\cdot}4 \times 10^6$ N m^{-2}. The amount of elastic energy stored in the SEC can then be calculated according to $W_{el} = F^{3/2}/3\sqrt{k}$. With this equation the positive work done by the contractile element CE is estimated for both types of contraction. For PI contraction, the small W_{neg} is neglected. Positive work done by CE (W'_{pos}) is then equal to W_{pos} plus the elastic energy which is still stored in the SEC at the end of the concentric contraction [$W_{el}(F_3)$]. Then $W'_{pos} = W_{pos} + W_{el}(F_3)$. For PS contractions it is assumed that all elastic energy which is stored at the onset of the concentric contraction [$W_{el}(F_1)$] originates from external sources, stored in the SEC during the active stretch phase. It is further assumed that no elastic energy is converted into heat during the concentric contraction. The positive work output of CE can then be calculated according to $W'_{pos} = W_{pos} + W_{el}(F_3) - W_{el}(F_1)$. The results of these estimations are presented in Table 3. Calculations are also carried out using other compliances of the SEC to demonstrate the influence of our choice on the results. The last two columns show the relative contribution of elastic energy to the uncorrected W_{pos} and the contribution to extra work which is assumed to originate from a nonelastic mechanism. This last contribution is assumed to be caused by some potentiation effect of the crossbridges caused by the active stretch (Cavagna *et al.* 1985). It was suggested that the crossbridges are charged to a level of (nonelastic) potential energy which cannot be attained in a contraction without prestretch (Cavagna *et al.* 1985).

Given the compliance, which is judged as the most reliable estimate (yielding 3 % extension), these calculations show that two-thirds of the extra positive work which can be gained by a preceding stretch originates from release of elastic energy and one-third from this potentiating effect.

However, these fractions appear to be strongly dependent on the estimation of the SEC compliance. SEC extensions larger than 4 % seem not to be realistic, since the major part of the stretch is then taken up by the stretch of the SEC. In this

case it is difficult to explain why only 43 % of the negative work reappears as extra work. For the remaining part, which will be converted into heat, one needs a non-conservative force working over a certain stretch distance (as is the case in an eccentric contraction of the CE).

Muscle efficiency and efficiency of running

Since the high efficiency of positive work of almost 37 % can be explained by the elastic and nonelastic mechanisms described above, this study does not provide evidence that the efficiency of the contractile machinery after a prestretch is larger than the 30 % mentioned in the Introduction. Even if the estimated contribution of elastic energy is subtracted from W_{pos}, an efficiency for the positive work of the CE of not more than 29 % can be calculated.

The value of 37 % is far too low to explain the 40–70 % efficiency estimated for positive work done during human and animal running (Margaria, 1986; Cavagna & Kaneko, 1970; Heglund *et al.* 1982). However, the methodology to calculate mechanical work used by Margaria and many others is open to discussion (Cavagna & Kaneko, 1977; Williams & Cavanagh, 1983; Williams, 1985; Aleshinsky, 1986). Williams & Cavanagh (1983) give estimates for various variables. If they take into account transfer of energy within and between segments, the metabolic cost of positive and negative work and the contribution of elastic energy, they still appear to need an efficiency of positive work at the contractile machinery of 44 % to explain mechanical work in human running (Williams & Cavanagh, 1983). This is far in excess of the 29 % for rat GM muscle mentioned above. Although one might argue that their estimate of the metabolic cost of negative work (one-third of the cost of positive work) is too high compared with the experimental results obtained by Curtin & Davies (1975) and Stainsby (1976), a large discrepancy remains between muscle efficiency as reported in the present study and the gross efficiency of running, even if it is assumed that eccentric work does not require any metabolic cost. Part of this discrepancy, however, may be due to an effect related to the body dimensions of the rat compared to that of humans and other large animals for which the efficiency of running was measured. It is known that the efficiency of running increases with body size (Taylor, 1980; Heglund *et al.* 1982). This will in part be due to the differences in architecture of the muscle–tendon complexes. Since the compliance of the series elastic elements of a muscle–tendon complex is mainly located in the tendinous tissues and to a much lesser extent in the muscle fibres (Morgan *et al.* 1978; Bressler & Clinch, 1975), it seems likely that muscles which have relatively long tendons compared to their mean fibre length may be more suitable for storage and release of elastic energy than muscles with relatively short tendons. When the calf muscles of rat are compared to those of man (Huijing, 1985; Bobbert *et al.* 1986) and the camel (Alexander *et al.* 1982), it is clear that the relative tendon length is strongly dependent on the size of the animal. The tendon of the GM of the camel represents 89 % of the total length of the muscle–tendon complex, whereas it is 85 % for human GM and 66 % for the rat GM used in the present

study. It is therefore possible that the relative contribution of elastic energy to positive work is larger in larger animals. This will lead to a larger value of e_{pos}.

It has also been suggested that calf muscles in large animals are mainly used as force generators, allowing their tendons to store and release elastic energy (Taylor, 1980). As discussed above, e_{pos} will be larger the shorter the concentric range of the contractile elements. In such contractions, however, it will be difficult to achieve a net work output larger than zero. Moreover, one might question how these muscles can contribute to work done on the environment when running uphill or against an opposing wind. As argued previously (Van Ingen Schenau, 1986), a large part of the physiological length range of the relatively short fibres of the human GM will be necessary to stretch the series elastic component of the GM if compliances are assumed for the human GM which correspond to an extension ΔL of the series elastic element at F_0 of more than 4–5 % of L_0. It has been shown that in such a case it would not be possible to explain how GM can contribute to external work in, for example, a vertical jump. In the light of such arguments, it is not surprising that even for kangaroo GM an extension ΔL at F_0 of only 4 % has been reported (Morgan *et al.* 1978). With such limited extensions, the role of storage and release of elastic energy is also smaller than if the compliances were larger. This means that in larger animals W_{pos} has to be much larger than W_{neg}. So a large part of W_{pos} will have to be delivered by the contractile elements of the muscle–tendon complexes in a contraction comparable to the PS contractions used in the present study. Such contractions could explain the relatively high values for maximal oxygen uptake found in human running compared to those reported for cycling (Astrand & Rodahl, 1977). Such contractions would be difficult in running, where it is assumed that the calf muscles are mainly used as generators of isometric force. Moreover, this type of contraction correlates with the onset of (increased) muscle activation in a late phase of the stretch, as observed *in vivo* (Tidball & Daniel, 1986).

It should be noted, however, that other structures, such as the arch of the foot or even the elastic properties of the shoes, can contribute to storage and reutilization of elastic energy during running (Alexander, 1988) and consequently to a high efficiency of positive work.

From the above it is clear that for a more complete understanding of the energetics of running, much more study is necessary of, for example: the role of elastic energy in muscle–tendon complexes (actual compliances) and other structures (the arch of the foot, the spine; Alexander, 1988); the enhancement of W_{pos} and the metabolic costs in contractions with different prestretch histories (stretch velocity, stretch distance), different timing of the onset of the stimulation and different velocities of concentric contractions.

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