

The influence of tendon compliance on muscle power output and efficiency during cyclic contractions

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SUMMARY

Muscle power output and efficiency during cyclical contractions are influenced by the timing and duration of stimulation of the muscle and the interaction of the muscle with its mechanical environment. It has been suggested that tendon compliance may reduce the energy required for power production from the muscle by reducing the required shortening of the muscle fibres. Theoretically this may allow the muscle to maintain both high power output and efficiency during cyclical contraction; however, this has yet to be demonstrated experimentally. To investigate how tendon compliance might act to increase muscle power output and/or efficiency, we attached artificial tendons of varying compliance to muscle fibre bundles *in vitro* and measured power output and mechanical efficiency during stretch–shorten cycles (2 Hz) with a range of stretch amplitudes and stimulation patterns. The results showed that peak power, average power output and efficiency (none of which can have direct contributions from the compliant tendon) all increased with increasing tendon compliance, presumably due to the tendon acting to minimise muscle energy use by allowing the muscle fibres to shorten at optimal speeds. Matching highly compliant tendons with a sufficiently large amplitude length change and appropriate stimulation pattern significantly increased the net muscle efficiency compared with stiff tendons acting at the same frequency. The maximum efficiency for compliant tendons was also similar to the highest value measured under constant velocity and force conditions, which suggests that tendon compliance can maximise muscle efficiency in the conditions tested here. These results provide experimental evidence that during constrained cyclical contractions, muscle power and efficiency can be enhanced with compliant tendons.

Key words: energetics, elasticity, biomechanics, efficiency.

INTRODUCTION

During animal locomotion, muscles typically contract in a cyclical manner to either generate or absorb mechanical work. The timing and duration of the muscle stimulation influences the interaction of the muscle with its mechanical environment and determines the amount of work generated or absorbed (Josephson, 1985; Josephson, 1993) and the overall mechanical efficiency (Barclay, 1994; Curtin and Woledge, 1991; Curtin and Woledge, 1993a). Experimental studies in which the rate of production of both work and enthalpy (work + heat) have been measured during cyclic contractions have shown that the stimulation conditions required to achieve maximum power output differ from those required to achieve maximum efficiency (Curtin and Woledge, 1996). These experiments were performed on muscle preparations that have very stiff tendons relative to the muscles' force generating capacities and it seems likely that the relative compliance of the tendons (i.e. compliance relative to muscle force generation) can influence the relationships among power output, muscle efficiency, stimulus timing and pattern of length changes. For example, Lichtwark and Wilson used a mathematical model to investigate how series compliance might affect the power output and efficiency of muscles during sinusoidal contractions (Lichtwark and Wilson, 2005). The critical finding of that study was that muscles with compliant tendons could, in theory, achieve close to maximum power and efficiency under the same stimulation conditions.

The ability of tendons to enhance power output and minimise energy expenditure depends on the matching of tendon compliance to the force generating capacity of the attached muscle and the

required task. The timing and duration of muscle stimulation and the amplitude of the change in length of the muscle–tendon unit (MTU) are also likely to affect the capacity of a tendon to increase the power output and efficiency. To directly test the idea that muscle efficiency and power output can be increased as a result of tuning tendon compliance (under the same conditions), a means of varying the series compliance in an isolated muscle preparation is required. We have developed a method using artificial tendons, made of latex, which allows the effects of varying tendon compliance on power output and efficiency to be determined. The aim of the current study was to determine the combinations of tendon compliance (relative to muscle force generating capacity), timing and duration of activation and amplitude of length change that enhance power output and efficiency during sinusoidal contraction cycles.

MATERIALS AND METHODS

Muscle preparation and experimental apparatus

Soleus muscles were dissected from adult, male mice (Swiss strain) that had been rendered unconscious by inhalation of 80% CO₂/20% O₂ gas mixture and then killed by cervical dislocation. All animal-handling procedures were approved by the Griffith University Animal Ethics Committee. Bundles of muscle fibres were dissected from the muscles. The mean (±s.e., N=19) fibre bundle mass and muscle length (excluding tendon) were 2.19±0.13 mg and 9.35±0.17 mm, respectively. Throughout dissection and experiments, preparations were bathed in oxygenated (95% O₂–5% CO₂) Krebs–Henseleit solution of the following composition (mmol l⁻¹): NaCl, 118; KCl, 4.75; KH₂PO₄, 1.18; MgSO₄, 1.18;

NaHCO_3 , 24.8; CaCl_2 , 2.54; glucose, 10. During experiments, solution temperature was maintained at 35°C.

Aluminium foil clips were crimped onto the tendons at each end of the fibre bundles and the bundles were mounted between a force transducer (AE801, SensorOne, CA, USA) and a servo-controlled motor (322B, Aurora Scientific Instruments, Toronto, Canada). The preparations lay along an antimony–bismuth thermopile (Barclay et al., 1995) that was used to measure changes in muscle temperature. Rectangular stimulus pulses (width, 1.5 ms; amplitude 3–5 V) were delivered to the fibres *via* fine platinum wire electrodes. Stimulus amplitude was set to 1.2-times that eliciting maximum twitch force. During experiments, stimulus pulse frequency was 100 Hz, sufficient to produce a fully fused tetanic contraction.

To investigate the effects of series compliance on muscle energetics, strips of latex (~10 mm long) of different compliance were inserted between the muscle and the motor. The compliance of the latex was varied by using strips of different width or by inserting several strips in parallel. The force–extension properties of each strip were determined before the experiment by measuring the change in force output produced when the length of the strip was varied in a sinusoidal pattern at a frequency of 2 Hz. The force–extension relationships for four strips of different compliance are shown in Fig. 1. All the curves show a region of higher compliance at low forces but the majority of the relationship is linear (i.e. constant compliance). The absolute compliance of the artificial tendons (which will be termed tendons from this point forward) was calculated as the inverse of the slopes in the linear portion of these curves. Relative compliance (expressed as a percentage) was calculated for each muscle–tendon preparation by multiplying the absolute compliance of the tendon by the ratio of maximum isometric force (P_0) to optimum muscle fascicle length for maximising isometric force (L_0).

Calculation of muscle enthalpy output and initial mechanical efficiency

Initial enthalpy output is the sum of the heat and work produced during a brief contraction and is proportional to the extent of ATP breakdown (Homsher, 1987). Work output was calculated as the integral of the active force produced with respect to the change in muscle length. Heat output was calculated as the product of the change in temperature of the muscle and its heat capacity. Temperature records were corrected for heat lost during recording and for heat produced by passage of the stimulus current through the preparation. Rate of heat loss and muscle heat capacity were calculated from the time course of cooling after the muscle had been heated using the Peltier effect (Kretzschmar and Wilkie, 1972). Heat arising from the stimulus current was measured by stimulating muscles ($N=6$) that had been rendered inexcitable by exposure to 30 mmol l⁻¹ procaine. For a typical stimulus amplitude of 5 V, stimulus heat was 0.13 $\mu\text{J pulse}^{-1}$ and corresponded to ~9% of the total heat measured during an isometric tetanus.

The heat recorded in this study excluded basal heat production and had at most only minimal contribution from oxidative recovery processes. The duration of recordings of heat production in this study was sufficiently short (<1 s) that recovery metabolism would have contributed <4% of the measured enthalpy production (Barclay and Weber, 2004). Thus, the enthalpy produced can be considered to have arisen from the net breakdown of phosphocreatine (PCr) due to contraction and is called initial enthalpy output.

Initial mechanical efficiency was defined as the ratio of the power output to the rate of initial enthalpy output. For isovelocity contractions, power and rate of enthalpy output were the average

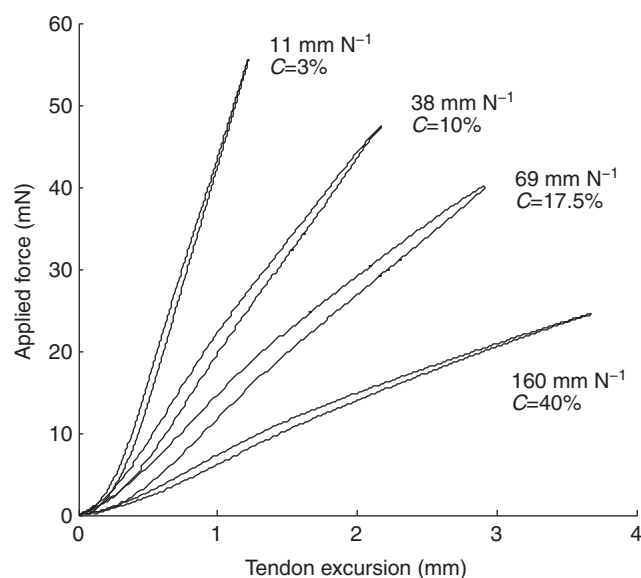


Fig. 1. Examples of force–extension relationships for four artificial tendons during lengthening phase of sinusoidal movement at 2 Hz. Absolute compliance was determined in the linear portion of the curve (at forces >10 mN) for each tendon. The relative compliance (C) was determined by multiplying the absolute compliance by the ratio of average maximum isometric force to average fibre length and is presented as a percentage. A small amount of energy is lost during cyclical contractions (hysteresis), which equates to an average of 6.1% of the input energy.

values during steady shortening. For cyclic contractions, average power output was defined as the product of the net work per cycle and cycle frequency (Barclay, 1994; Josephson, 1985), i.e. average power output is the average rate of net work output. Note that power output calculated in this way excludes any contribution from the tendon because net tendon work is close to zero over a full-length cycle (tendon force is the same at the start and end of the cycle and there is only a very small amount of work lost due to hysteresis – Fig. 1). The average rate of enthalpy output was the initial enthalpy produced during the cycles divided by the duration of the cycles. Instantaneous power output was calculated by multiplying active force by the instantaneous MTU velocity.

Experimental protocols

To characterise steady-state energetic properties during shortening, force output and rate of heat output were determined during isometric and isovelocity contractions as described in detail previously (Barclay et al., 1993). At the start of each experiment, muscle length was adjusted to that at which force output in a brief tetanus was maximal (L_0). Isometric contractions were performed at a range of lengths between 0.8 and 1.1 L_0 . The length change protocol consisted of a shortening step followed by isovelocity shortening (Fig. 2). The length step rapidly unloaded the series elastic element intrinsic to the muscle, allowing the series elastic compliance to be quantified (Barclay and Lichtwark, 2007). Contractions were preceded by a recording of force change in response to the same pattern of length changes delivered without stimulation. The time course of force output in this recording was subtracted from that made with stimulation to provide a record of active force output.

To determine the influence of series compliance on energetics during cyclic contractions, the muscle and latex strip were subjected to sinusoidal length changes (2 cycles at a frequency of 2 Hz). It

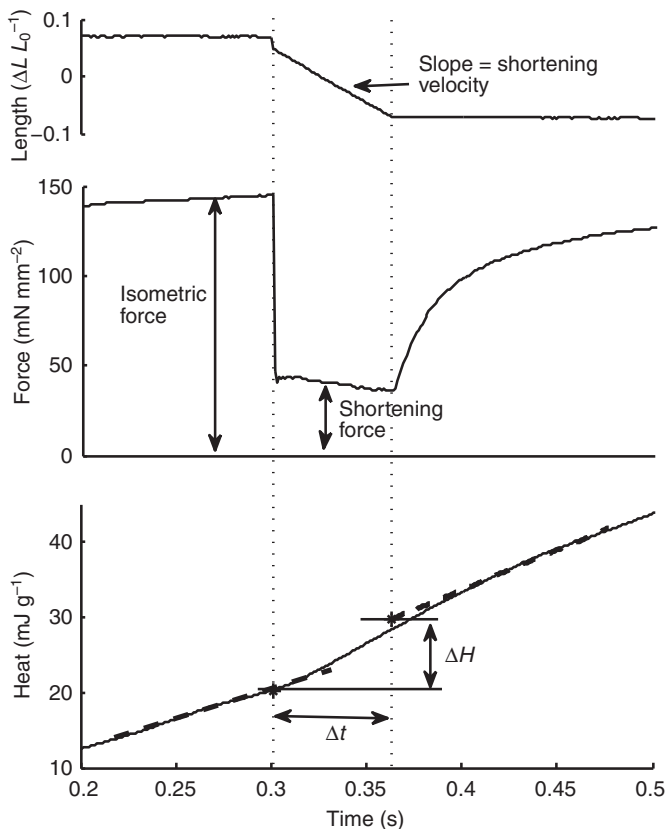


Fig. 2. Example data from a step-ramp experiment to determine steady-state muscle properties. Isometric contractions are followed by a rapid shortening step and constant velocity shortening to maintain a constant shortening force (100 Hz stimulation, 1.5 ms pulse width). Heat (H) rate during shortening is calculated by the ratio of ΔH to t .

was difficult to establish L_0 in the presence of extra series compliance because considerable muscle shortening occurred during fixed-end isometric contractions. Therefore, muscle length was adjusted to that at which passive force was between 0.5 and 1 mN, which corresponded to the typical passive force of these preparations at L_0 . This length was measured using callipers and was used to normalise the length changes of the MTU and muscle fascicles. Stimulus duty cycle and phase were varied to determine how these variables affected average power output and efficiency. Duty cycle was defined as the proportion of the cycle period that the muscle was stimulated and stimulus phase was defined as the time in the cycle at which the first stimulus pulse was delivered relative to the time at which the preparation (i.e. muscle + latex strip) length was longest, and was expressed as a percentage of the duration of the cycle. Three peak-to-peak length amplitudes were chosen to achieve a peak length change of the muscle of approximately 3, 6 and 9% L_0 for each compliance condition; however, this was dependent on the force generating capacity of each muscle bundle and exact compliance of the artificial tendon. The time course of passive force during the cycle was recorded as described earlier and subtracted from the total force record.

Data analysis

Force output was normalised by isometric force produced at L_0 (P_0). Average power output and rates of heat and enthalpy production were normalised by the product $P_0 \cdot L_0$ which reduces variation due

to differences among preparations in the fraction of contracting fibres (Barclay et al., 1995). During the isovelocity shortening experiments with no artificial tendons attached, shortening force output was the average force produced during the constant velocity period (Barclay et al., 1993). Rates of heat output during shortening were calculated as illustrated in Fig. 2. This method excludes transient thermal changes resulting, for example, from changes in series elastic element length that are reversed when shortening concludes and force returns to isometric levels (Homsher, 1987). Power and efficiency were calculated only during the isovelocity shortening period in these experiments.

In the sinusoidal experiments, the length changes of the muscle fibres alone, separate from the extension of the artificial tendons, were also calculated by subtracting the extension of the tendon from the MTU length change. The extension of the tendon was calculated from the instantaneous force and the known force-extension relationship of each tendon.

To accommodate differences in relative compliance among muscle-tendon preparations in the sinusoidal length change experiments, data were grouped according to relative compliance. The ranges for each group were: 2–5% (labelled 3%), 5–12.5% (labelled 10%), 12.5–25% (labelled 17.5%) and 25–60% (labelled 40%). These values simulated an increase in relative compliance from a rat gastrocnemius muscle (~5%) to a wallaby gastrocnemius muscle (~35%) (Lichtwark and Wilson, 2005).

RESULTS

Steady-state muscle energetic properties

The relationship between force and rate of enthalpy output during steady-state shortening (without introduced compliance) was first determined using a constant shortening velocity protocol, as illustrated in Fig. 2. In these measurements, force output was reasonably constant during the time that rates of energy output were measured. This is important because it excludes any contribution to power output from the series elastic element (its length depends on the force exerted on it and it can only perform work if its length decreases) so the power and enthalpy outputs and efficiency reflect solely the properties of the muscle contractile apparatus. Mean L_0 was 8.8 ± 0.1 mm and P_0 was 123.1 ± 16.6 mN mm $^{-2}$. Fig. 3 summarises the steady-state, isovelocity energetics of fully activated mouse soleus muscle ($N=6$) during shortening at 35°C. Mean maximum shortening velocity (V_{\max}) was $4.49 \pm 0.04 L_0 s^{-1}$ (Fig. 3A). Peak power output was $0.43 \pm 0.03 P_0 L_0 s^{-1}$ (48.7 ± 5.6 mW g $^{-1}$) and occurred at a mean shortening velocity of $1.4 \pm 0.1 L_0 s^{-1}$, equivalent to $0.31 V_{\max}$ (Fig. 3B). The rate of heat production increased with shortening velocity from 69.1 mW g $^{-1}$ in the isometric contraction (\dot{H}_0) to a maximum value of $\sim 1.8 \dot{H}_0$ at V_{\max} (Fig. 3B). The maximum mechanical efficiency was $33.6 \pm 2.4\%$ and occurred at $1.2 \pm 0.06 L_0 s^{-1}$ ($0.26 V_{\max}$) (Fig. 3C).

Stimulus conditions giving maximum power output

In cyclic contractions, such as used in this study to investigate the effects of tendon compliance on muscle energetics, average power output depends on the amplitude of length changes, the timing of the start of stimulation (i.e. stimulus phase) and the duration of stimulation (Barclay, 1994; Curtin and Woledge, 1996; Curtin and Woledge, 1993a; Josephson, 1985). The combinations of stimulus phase and duration that maximised average power output were established for each of four compliance conditions. In each compliance condition, average power output was maximised with stimulation commencing on average 25 ms before the maximum length was reached (stimulus phase = -5%) and continuing for between 30 and 50% (150 to 250 ms) of the cycle; that is, stimulation

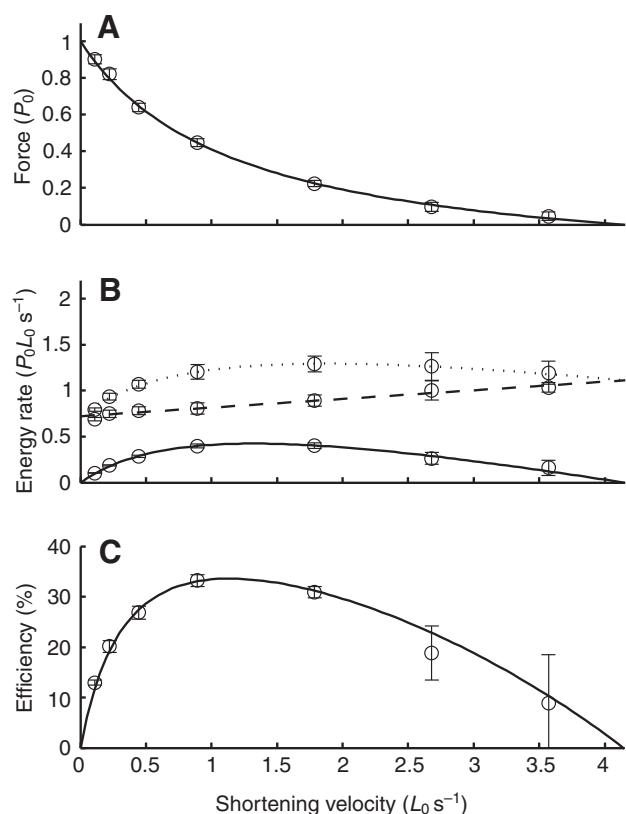


Fig. 3. Steady-state muscle energetic results ($N=6$). (A) Relationship between shortening velocity and force. A least square fit of Hill's hyperbolic equation (Hill, 1964) was used to fit the curve through the force–shortening velocity data (with Hill constants $a/P_0=0.28$ and $b=1.18 L_0 s^{-1}$). (B) Power (solid line), heat rate (dashed line) and enthalpy rate (dotted line) relative to shortening velocity. The power curve is the product of the force–velocity curve and shortening velocity while heat rate is has been fitted with a linear line. Enthalpy is the sum of power and heat rate. (C) Efficiency (ratio of power to enthalpy rate) relative to shortening velocity. Data in all graphs have been binned according to the absolute shortening speed for all muscles with error bars representing the standard error for all muscles in each bin.

continued for the majority of the shortening phase. There were no significant differences between power output, enthalpy output and efficiency for stimulus duty cycles of 30 and 50%. Data for these duty cycles were pooled for subsequent analysis.

The records in Fig. 4A,B summarise the main energetic aspects of the muscle–tendon preparations during cyclic contractions and the effects of tendon compliance. Fig. 4A shows records from a preparation with a low compliance tendon and Fig. 4B shows records from a preparation with a high compliance tendon. In each of these trials, the strain and stimulus timing and duration were such that they maximised average power output for the compliance condition. With a low compliance tendon (Fig. 4A), force output increased upon stimulation to a maximum of $\sim 0.8P_0$ and then declined during shortening, with an increase in the rate of force decline once stimulation ended and the muscle relaxed. MTU work was performed during the shortening phase of each cycle. The muscle fibre length change and muscle fibre work both resembled those of the MTU length. Enthalpy output (proportional to the ATP used) occurred at a relatively high rate during stimulation and a low rate between contractions. At the end of the cycles, work output accounted for approximately 25% of the enthalpy output. When the

high compliance tendon was used (Fig. 4B), a larger amplitude length change was required to maximise average power output and the peak force reached was approximately equal to P_0 . The length change trajectory of the muscle fibres was noticeably different to that of the MTU. The muscle fibres shortened throughout stimulation and subsequent relaxation, while the MTU lengthened to much longer lengths at the beginning of the contraction, prior to shortening. During shortening, force output declined more rapidly than for the less compliant tendon and the work performed was greater. However, there was also a clear decrease in the cumulative work output when stimulation started, indicating work being done on the muscle–tendon preparation. In contrast the muscle fibre work is positive throughout both cycles which was a result of the muscle fibre shortening throughout the cycle while the muscle was active. At the end of the cycles in the example shown, work accounted for approximately 40% of the enthalpy produced.

The relationship between the amplitude of the length change in each condition and average power and efficiency is shown in Fig. 5. For each of these measures there was a significant effect of the amplitude of length change ($P<0.001$). Average power output and efficiency were both independent of the amplitude of length change for the two largest amplitudes tested. Therefore data from these two conditions were pooled for subsequent analysis of the effects of compliance.

The greatest average power output measured using cyclic contractions ($0.20 \pm 0.01 P_0 L_0 s^{-1}$) was only half that achieved during isovelocity shortening in fully activated muscle. Average power output for relative tendon compliance values of 40% and 17.5% was significantly greater than that for less compliant tendons (<10% and 3%) (Fig. 6A). Net enthalpy output was independent of the amplitude of length change ($P=0.48$) but depended significantly on compliance, being significantly higher at a compliance of 40% ($\dot{H}=0.58 \pm 0.02 P_0 L_0 s^{-1}$) than at other values. Net efficiency was greater with more compliant tendons. Net efficiency was significantly greater with compliance values of 40% and 17.5% compared with values of 10% and 3%. The maximum net efficiency was $34.5 \pm 1.3\%$ at 40% compliance. The 95% confidence interval (CI: 31.4–37.6%) for cyclic efficiency with compliant tendons overlaps that for maximum efficiency during steady-state shortening (27.5–39.7%) and therefore the two are not significantly different at the 95% level.

The contour plots in Fig. 7 demonstrate the influence of stimulus phase and duty cycle on average power output and efficiency with low and high compliance tendons (for the longest amplitude of length change tested in each condition). While average power and efficiency increased with increasing tendon compliance, the stimulation conditions under which both were maximised were also different between compliance conditions. With the most compliant tendon, maximum average power and efficiency could be attained with a shorter stimulation period (reduced duty cycle) and power and efficiency were both maximal with similar stimulation timing and duration.

Over a full contraction cycle, there was no net work output from elastic elements; force at the start and end of the cycles was the same and, therefore, the length of any series elastic elements was the same. However, in relation to locomotion it is not just the amount of work stored in the tendon but also the rate at which the stored work is released that is important. Peak power output during shortening depended on tendon compliance and was greatest with the two most compliant tendons used (Fig. 5A). The greatest peak power output values were almost $2 P_0 L_0 s^{-1}$, over 4-times greater than the peak power output of muscle alone.

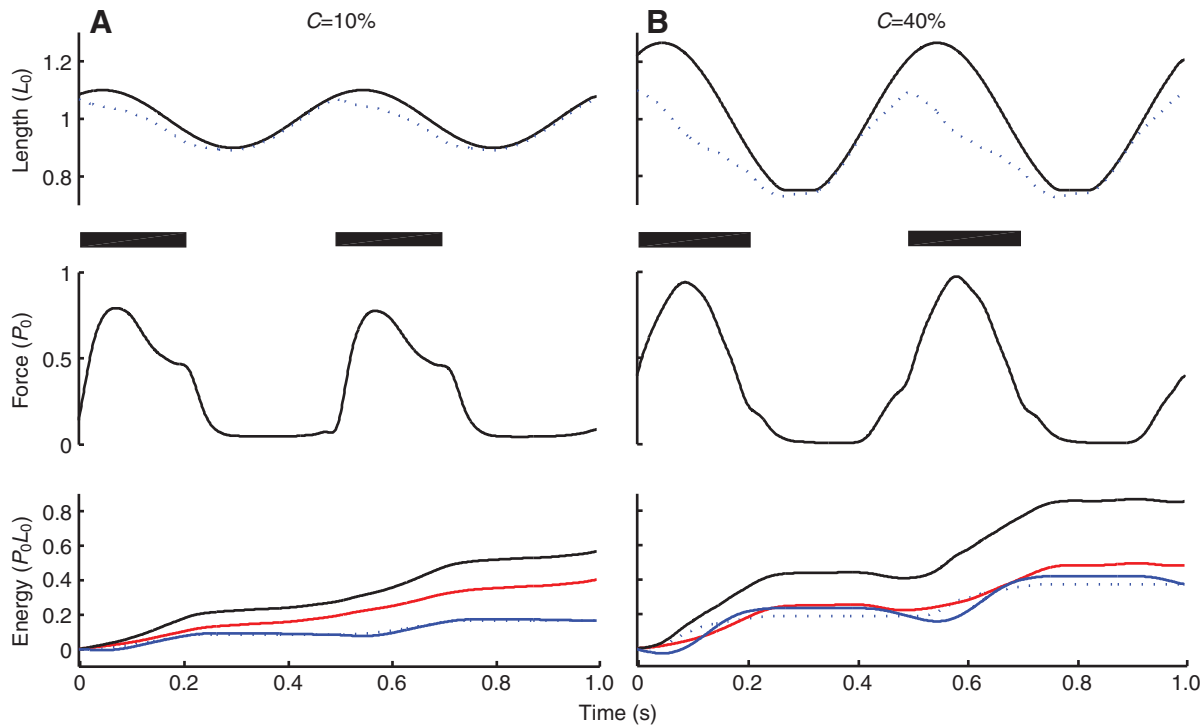


Fig. 4. Example data showing the relationship between muscle length, force and energy for stiff (A) and compliant tendon (B) under similar activation conditions relative to time across two complete cycles. Top panels: MTU length (solid) and fibre length (dotted) represented relative to the optimum muscle fibre length for maximising isometric force (L_0). Middle panels: force represented relative to the maximum isometric force (P_0). Bottom panels: energy divided into MTU work (blue solid), fibre work (blue dotted), heat (red solid) and enthalpy (black solid). Stimulation time is indicated by the black bars below the length panel. (Note: the muscle is held at a constant length for a short period in the shortening phase of the cycle in the compliant tendon due to the limits of the motor; however, the muscle is relaxed at this time and therefore this will not influence the results.)

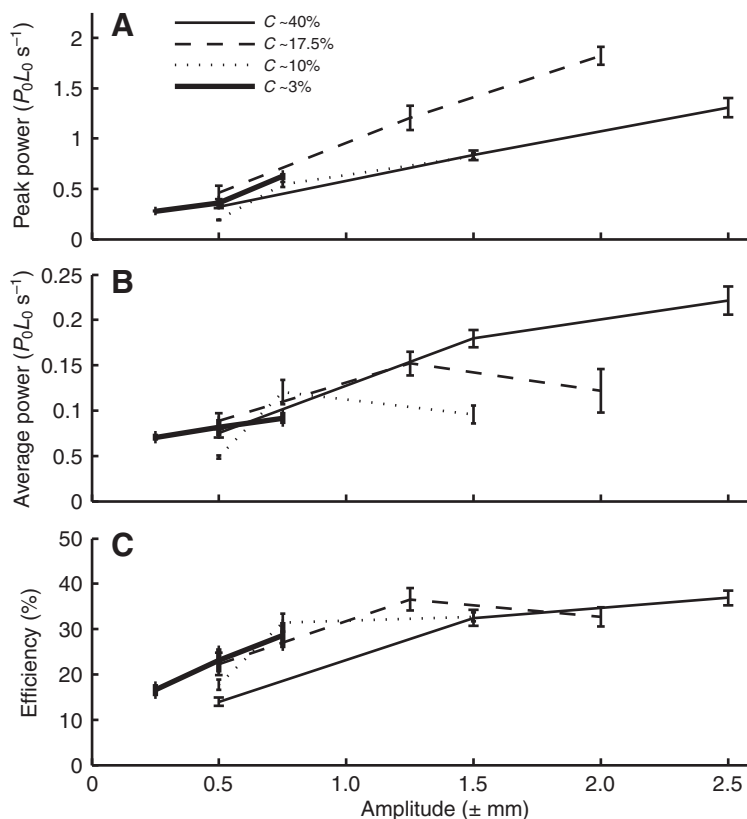


Fig. 5. Relationship between the (A) peak instantaneous power, (B) average power and (C) efficiency and amplitude of length change of the muscle-tendon unit for conditions where average power is maximised (phase of activation=5%, duty cycle=30–50%). The range of length change was adjusted to achieve approximately 3, 6 and 9% strain of the muscle fibres for each tendon compliance condition.

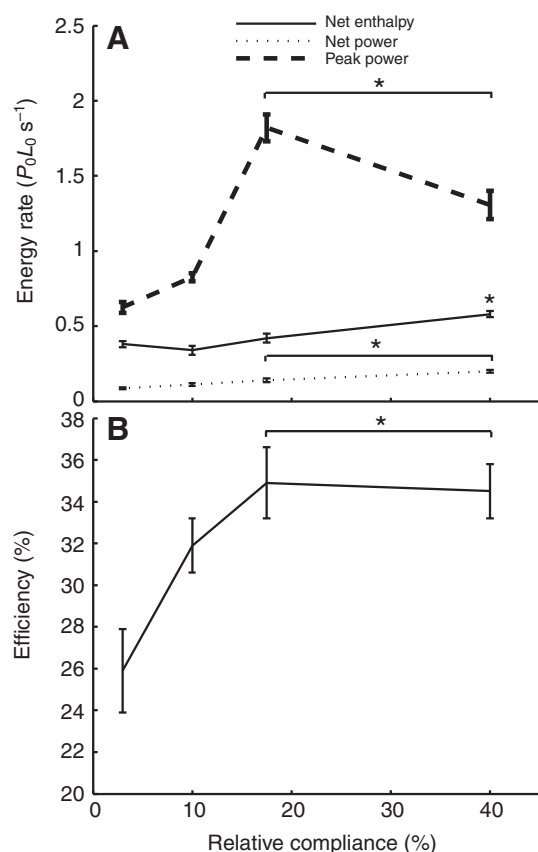


Fig. 6. Relationship between tendon compliance and (A) energy rate (average power, dotted line; net enthalpy rate, solid line; peak power, dashed line), and (B) efficiency. Data have been pooled by phase of activation (-5%) and duty cycle ($30\text{--}50\%$) and amplitudes of length change (the two longest length change conditions for each different tendon compliance were pooled for all values except peak power, where only the longest length change amplitude was used). *Significant difference from the low compliance condition (3%).

DISCUSSION

These results, for isolated mouse soleus muscle performing cyclic contractions at 2 Hz, demonstrate that greater average power output and efficiency can be achieved with a compliant tendon than with a stiff tendon connected in series with a muscle. This was only achieved if sufficient amounts of stretch were applied to the active muscle tendon unit before shortening occurred in the high compliance conditions. Increasing the tendon compliance increased both the average power produced by the muscle and its efficiency across the stretch–shorten cycle. This implies that the muscle fibres were able to operate at more favourable lengths and velocities whilst actively generating tension. In contrast, stiff tendons required the muscle fibres to contribute to a greater proportion of the required length change, which limited the power generating capacity and efficiency. The ability to increase the amplitude of length change with compliant tendons also increased the peak power output of the MTU, which was up to 3-times greater than the maximum achievable power output for stiff tendons at the same operating frequency. The experimental evidence also supports previous modelling work (Lichtwark and Wilson, 2005) which suggested that tendon compliance can allow muscles to operate with high power output and efficiency across a range of stimulation conditions.

It is important to understand the mechanisms behind the increases in average power output and efficiency of muscles with compliant tendons. Increases in average power output must come from the muscle itself, since the amount of energy released from the tendon must be equal to or slightly less than the energy stored in the tendon. During sinusoidal strain protocols, shortening velocity alters continuously. In the stiff tendon conditions, the length change trajectory of the muscle fibres mirrored that of the MTU because the tendon had little scope for length change (Fig. 4A). In contrast, the muscle fibres in the compliant conditions followed a different trajectory to that of the MTU (Fig. 4B). The muscle fibres initially shortened while the MTU and tendon were stretched to long lengths. The fibres continued to shorten when the MTU began shortening, but at a much slower speed. It is apparent that the addition of a suitably compliant tendon altered the range of velocities experienced by the muscle fibres so that they were closer to a velocity that maximises power and efficiency ($\sim 0.25\text{--}0.3V_{\max}$; Fig. 3). Calculation of the mean shortening velocity of the muscle fibres during contraction indicated that the muscle contractile apparatus for the most compliant tendon ($1.33 \pm 0.05 L_0 s^{-1} = 0.29V_{\max}$) was closer to the optimal velocity for maximising power output and efficiency than that for the least compliant tendon ($0.54 \pm 0.02 L_0 s^{-1} = 0.12V_{\max}$). In addition, the increase in MTU excursion imposed during contractions with the compliant tendons meant that the muscle fibres could continue to shorten at favourable speeds for generating power (even during relaxation) whilst the MTU shortened greater distances than in the stiff tendon conditions. This allowed the muscle fibres to perform more work throughout each cycle with little increase in heat output. These results are consistent with the idea that appropriate tuning of muscle function and tendon compliance can allow muscle fibres to act at more favourable speeds to maximise power output and efficiency.

Efficiency during cyclic contractions with compliant tendons (34.5%) was very similar to the peak efficiency in steady-state conditions (33.6%). This supports previous modelling work that predicted that under the correct stimulation and cyclical length change conditions, the efficiency of muscles in series with more compliant tendons can be greater than that with less compliant tendons and close to the maximum steady-state efficiency (Lichtwark and Wilson, 2005). Therefore it seems that modelling the energetics of muscle contraction from the steady-state energetic properties can adequately predict energetics during cyclical contractions; however, a precise comparison of the data is difficult due to variations that occur under different stimulation conditions. Cyclical contractions in muscles with stiff tendons have previously been shown to increase muscle efficiency above that found in isovelocity experiments (Barclay, 1994; Curtin and Woledge, 1993a; Curtin and Woledge, 1993b). The increase could be due to history dependent effects, such as enhanced force output caused by stretch (Edman et al., 1976; Herzog and Leonard, 2000). However, in the conditions tested here, average power was maximised by stimulating the muscle only just prior to shortening in all tendon compliance conditions, and therefore the muscles experienced only a small amount of active stretch which would limit such effects. In addition, in the compliant conditions tested here, there was little active lengthening of the muscle fibres themselves (lengthening was primarily achieved in the tendon – Fig. 4). Therefore stretch induced force enhancement is unlikely to play a large role in enhancing muscle power output and efficiency.

Increasing tendon compliance not only influenced the maximum power and efficiency but also affected the optimum activation conditions for achieving such outcomes (Fig. 7). With more compliant

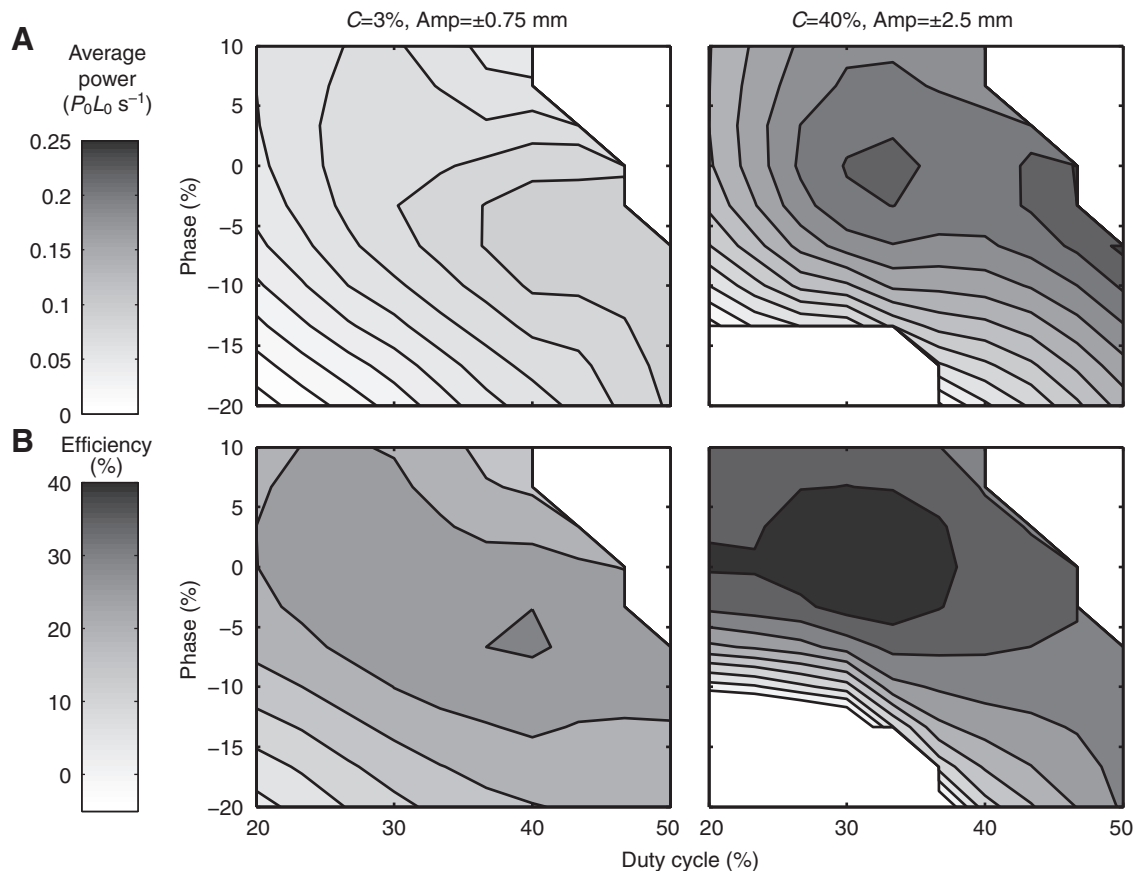


Fig. 7. Contour plots of (A) average power and (B) efficiency relative to duty cycle and phase for a stiff ($C=4\%$) and compliant ($C=40\%$) tendon at the maximum amplitude tested for each condition. White areas represent areas where no power was generated or phases and duty cycles that were not tested in this study.

tendons, high power outputs were achieved with shorter duration contractions compared with those required for stiff tendons (for length change amplitudes that maximised average power output). A shorter duration contraction reduces the total energy cost and, because the average power was still higher, this may have contributed to the higher efficiency measured with more compliant tendons. This effectively allows muscles with compliant tendons to operate with both high power and efficiency under the same stimulus conditions (phase and duty cycle), which does not seem possible with muscle alone (Barclay, 1994; Curtin and Woledge, 1996) or muscles with stiff tendons. This is very similar to previous results from theoretical modelling studies based on the isovelocity properties of muscle (Lichtwark and Wilson, 2005), which showed that tendon compliance could allow muscles to operate with very high power and efficiency across a wide range of stimulation conditions.

Our results apply to contractions with sinusoidal length changes. With this protocol, achievable average power output was restricted by the frequency of oscillation of the sine wave and the amplitude of the length change, both of which limit the length and velocity range of the muscle fibres themselves (particularly in the very stiff tendon conditions). It is conceivable that different, non-sinusoidal length change trajectories could result in greater power output in both the stiff and compliant tendon conditions. For instance, if we applied the length change trajectory of the muscle fibres in the compliant condition in Fig. 4 to muscle fibres alone, then we would expect that the muscle would produce more power than in the sinusoidal condition. Therefore, the precise gait pattern of an

animal and the amount of energy that can be applied to the muscle from the outside environment are obviously important factors in determining whether benefit can be attained from compliant tendons compared with stiff tendons.

One major advantage of utilising tendon compliance during cyclical contractions is that it not only increases the average power but also increases the ability to create high instantaneous power (Fig. 6). Our results show that under optimal conditions in sinusoidal contractions, tendons can increase the instantaneous power output by up to 4-times that of the peak muscle power output in steady-state conditions. These high power outputs during shortening reflect the contribution to power output of the tendon that had been stretched when force developed. It is possible that higher peak power outputs may be achievable using this protocol, as this is largely dictated by the amplitude of stretch of the MTU and the energy stored in the tendon. However, there will be a limit on the ability to stretch the muscle fibres without causing muscle damage, particularly prior to stimulation.

Direct measures of muscle fibre length in different species support the idea that elastic tendons can increase the positive muscle power during animal movement, particularly when short muscle fibres relative to the length of the MTU are required to generate power over long distances, for instance when travelling up hill (Biewener et al., 2004; Lichtwark and Wilson, 2006; Roberts et al., 1997). Such studies have shown that fibres act almost isometrically while the MTU is stretched prior to shortening. However, during steady-state animal locomotion, many animals produce only a small amount of net work

from active muscle, despite possibly producing large amounts of positive work (Cavagna et al., 1977; Heglund et al., 1982). Therefore the results of this study, which explicitly examined situations where the power output was maximised during constrained movements, may not apply directly to animal locomotion as they are primarily focused on efficient generation of power.

LIST OF ABBREVIATIONS

\dot{H}_0	rate of heat production during isometric contraction
L_0	optimum muscle length for maximum isometric force
MTU	muscle tendon unit
P_0	maximum isometric force
SE	standard error
V_{\max}	maximum shortening velocity

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