Effects of series elasticity and activation conditions on muscle power output and efficiency

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Summary

The activation of a muscle depends on the function that it is performing and on the architectural properties of that muscle; the two are inextricably linked. Activation conditions such as activation timing, duration and amplitude can be varied throughout a cyclical movement (such as locomotion) and the length change of the whole muscle tendon unit (MTU) can also be varied. Architecturally, muscles have a range of fibre lengths, maximum force-producing capabilities and stiffness of the series elastic element (SEE). In the present work we use a model to explore the relationship between power output and efficiency of a muscle across a range of contraction conditions. We have also examined the mechanical and energetic effects of changing muscle architecture within the model. Our results indicate that whilst there are clear optimal conditions for achieving maximum power output and maximum efficiency, the design of the muscle allows high levels of both to be achieved over a range of activation conditions. This range changes with both SEE compliance and the amplitude of the cyclical length change. The results suggest that a compliant SEE allows a muscle to function closer to the maximum of both power output and efficiency. In addition, by varying the amplitude of the activation level, the efficiency can theoretically remain unchanged, whilst the power output can be modulated.

Key words: muscle, model, energetics, elasticity, biomechanics.

Introduction

Muscles generate force under a range of velocity conditions. Muscles can act isometrically (no length change) and perform no net work, or they can shorten or lengthen whilst generating force, which results in performing or absorbing work respectively. The role that an individual muscle performs depends on the activity being performed (Gabaldon et al., 2004; Roberts and Scales, 2002, 2004) and also on the activation conditions of the muscle (Ettema, 1996). For instance during level running the turkey gastrocnemius muscle fibres remain isometric, whilst on an incline the muscle performs net work by shortening during the stance phase. Individual muscles also show architectural adaptations depending on their function. Some have long fibres and can shorten over a large length range and at high velocity. Others have shorter fibres, which means that the length change is less but that the cost of force generation and the mass of muscle tissue required to generate force is also less.

The amount of series elasticity present in a muscle, mostly in the aponeurosis and the tendon, can vary depending on its role. Series elasticity has been identified as an advantage in the antigravity muscles of running animals, because the tendon will elongate under load and store elastic strain energy, which is subsequently returned later in the movement. For instance, in the wallaby gastrocnemius the muscle fibres are almost isometric and do not change length much during stance, but there is considerable elongation in the series elastic element (SEE; Biewener et al., 1998). The wallaby muscles, however, represent one extreme of muscle design, and most muscles consist of longer fibres and less significant series elastic tissue. It has been observed that a large amount of series elasticity will enable energy storage at the cost of accurate length change (Alexander, 2002) and it has been predicted that the SEE will increase the versatility of a muscle since the muscle fibres can contract at a different speed from the overall muscle tendon unit (MTU; Fukunaga et al., 2002; Galantis and Woledge, 2003). It has not been shown how the presence of different amounts of SEE actually influence the economy, power and versatility of muscle under different locomotor conditions, and in particular which activation conditions are optimal.

The relationship between power output and efficiency of a muscle under different contraction conditions has been examined extensively. Experimental comparisons of the optimum activation conditions for power production and efficiency demonstrate that the frequency of oscillation, length

change, duty cycle and phase of activation all affect both the power output and the efficiency of muscle (Barclay, 1994; Curtin and Woledge, 1996; Ettema, 1996). In those experiments, various combinations of phase, duty cycle, length change and frequency of oscillation achieved optimal power output and efficiency. However, the activation patterns used showed a broad optimum and there did not seem to be a direct relationship between power and efficiency. Hence animal muscle has a range of activation patterns and length trajectories in which they can operate at maximal power or maximal efficiency, or perhaps some combination of the two.

We have previously shown that the activation conditions for optimum power output and efficiency can be reproduced using a Hill-type muscle model that estimates the energetic cost of contacting the muscle (Lichtwark and Wilson, 2005). This model was based on experimental data from the white myoseptal muscle of the dogfish and validated using data from the mouse soleus muscle. The inclusion of a series elastic element, which is able to store elastic strain energy for subsequent release, changes the time course of power development from that seen in the muscle fibre bundles themselves. However, muscles that operate with different functions often have a broad range of different elastic tissues (including tendon, aponeurosis, perimyosium and myoseptum) attached both in series and in parallel, and these structures have different levels of compliance. In addition to this, the maximum force-generating capacity of a muscle and the muscle fibre length can vary greatly compared to the compliance of the elastic structures. Therefore the activation conditions and the overall length change of the entire MTU that achieve optimal power output and efficiency should vary greatly between muscles with different architecture and function. It is proposed that the energetic function of a muscle dictates the architecture of the MTU: the length of its muscle fibres, the maximum force-generating capacity and the compliance of the series elastic tissue.

Variation in the elasticity of a muscle has been predicted, using a model, to affect its function by altering its work-generating capacity and its efficiency under various activation conditions (Ettema, 2001). Although similar power outputs and efficiencies can be obtained with a muscle regardless of the SEE stiffness, these maxima have to be achieved with different activation conditions (i.e. different duty cycles and phases). For instance, muscles with a stiff SEE are most efficient when activated during shortening, whereas a compliant SEE would be most efficient when activated during stretch in a stretch–shorten cycle (Ettema, 2001). A stiff SEE is least efficient when activated early in the stretch phase because the contractile element (CE) is forced to absorb work during the stretch phase and then actively generate work at a high energetic cost. However, the amplitude of length change of a muscle will also alter the proportion of length change occurring in the SEE and the CE and this must also be accounted for when determining the influence of SEE stiffness on muscle power output and efficiency. Finally, the level of activation of a muscle may also have an effect on the time course of events

in a cyclic contraction, particularly power output and energetic cost, and therefore its effect on power output and efficiency should also be explored.

By applying an energetic model of muscle contraction (Lichtwark and Wilson, 2005) it is possible to explore and map the relationship between power and efficiency of muscle with varying duty cycle, phase of activation, amplitude of length change and activation level. This type of protocol is difficult to undertake experimentally on muscle tissue due to muscle fatigue and the difficulty in keeping muscles alive for the duration of these lengthy *in vitro* studies. Applying a validated model allows the experimenter to test across a broader range of conditions and also makes it possible to vary the properties of the muscle to explore how this affects muscle power output and efficiency.

We hypothesise that activation conditions (timing and duration of activation) exist that elicit a range of powers with near optimal efficiency and that generation of these from models would match experimental data for locomoting animals. We also hypothesise that the activation conditions required to generate optimum power output and optimum efficiency of a muscle are highly dependent on the stiffness of its series elastic element.

In this paper we test these hypotheses as follows. (1) We vary the timing and duration of activation in a modified Hill-type muscle model (Lichtwark and Wilson, 2005) to determine the optimum conditions to maximise power output and efficiency. We compare the optimum activation conditions for generating maximum power output and efficiency, and explore how a biological system can approach the optima of both simultaneously. (2) We vary the stiffness of the elastic element and the amplitude of the length change that the muscle undergoes to determine their effect on power and efficiency under different activation conditions. (3) We determine how the stiffness of the series elastic elements might influence the behaviour of a muscle and explore some biological examples which highlight this effect. (4) We determine the effect of changing the level of activation on power output and efficiency of muscle under different activation conditions.

Materials and methods

We apply a Hill-type muscle model that has been shown to predict the time course of both force output and energetic output of the *Scyliorhinus canicula* Linnaeus 1758 (dogfish) muscle (Curtin et al., 1998; Lichtwark and Wilson, 2005), so that we can explore how power output and efficiency are affected by the activation conditions, amplitude of length change and series elastic stiffness during sinusoidal length changes. We first explore the interaction of power output and efficiency under validated conditions (Lichtwark and Wilson, 2005) with experimentally determined properties (Curtin et al., 1998), by varying the duty cycle (duration of activation relative to the entire cycle time) and the phase of activation (the time between the start of stimulation and the start of shortening expressed as a percentage of cycle duration). We performed

contractions across a space of duty cycles and stimulus phases to determine the how power and efficiency interact under these conditions. This was done at a frequency of 1.25 Hz, where the constants determining the rise and fall of activation had been optimised to fit experimental data (Lichtwark and Wilson, 2005). A Nelder–Mead simplex (direct search) optimisation technique was also performed in Matlab (Mathworks Inc., Natick, MA, USA) to determine the optimal values of duty cycle and phase of activation maximum power and efficiency.

We then used the same techniques to explore how these results might theoretically vary by changing the series elastic stiffness and also the total length change (amplitude) of the MTU throughout a sinusoidal length change. The original model (Lichtwark and Wilson, 2005) was operated across length changes within the plateau region of the force–length relationship of the muscle. However, in this investigation it was necessary to extend the length change of the MTU such that the muscle fibre length may affect its force and energy output. Therefore a typical force–length relationship of a sarcomere (Gordon et al., 1966) was incorporated to scale the force-generating capacity of the muscle fibre, depending on its length (Fig. 1A). The number of possible crossbridges attached is related to the relative overlap of the actin and myosin filaments, and therefore the maintenance heat rate also needs

to be scaled by the force–length relationship in the same way that activation level scales the maintenance heat rate. Although it has been demonstrated that the force–length properties of a sarcomere do not accurately represent those of whole muscles or muscle fibre bundles (particularly on the descending limb), this model is believed to be satisfactory in this case because the muscle fibre length change should not exceed $L_o \pm 0.25L_o$ (where L_o is optimal muscle fibre length and force P is always greater than 70% of maximum isometric force, P_o).

The muscle model incorporates a SEE stiffness, which is represented in normalised form, relative to P_o and L_o. This represents the amount of force produced (relative to the maximum force) for any given length change (relative to the muscle fibre length). Therefore if the absolute stiffness of the SEE remained constant, but the muscle optimum muscle fibre length doubled, then the relative stiffness would also double.

We used the model to find the optimal activation conditions and length changes for achieving maximum power and efficiency at a stiffness range lower than that measured experimentally, and determined how these optimal conditions change as a result of the lower stiffness. Here, the relative stiffness was reduced from $22{\times}P_o/L_o$ to $4{\times}P_o/L_o$ (with a lower stiffness of $16{\times}$ and $3{\times}P_o/L_o$, respectively, at forces below $0.15P_o$, to account for the toe region of the force–length properties of the SEE; see Lichtwark and Wilson, 2005) and the length change increased from $\pm0.0335L_o$ to $\pm0.2L_o$. With these values of stiffness and amplitude of length change, the power output and efficiency of the muscle were explored across a space of duty cycles and phases of activations. In addition, a Nelder–Mead simplex (direct search) optimisation technique was again used to determine the optimum values of duty cycle, phase of activation and length change to achieve the maximum power and efficiency. The relative stiffness of muscles with similar functions but from a range of species was also determined to compare the findings from the simulations.

Finally, we explored the effect of activation amplitude on power output and efficiency across the range of duty cycles and phases of activations. The activation amplitude here was defined as a simple arithmetic scaling of the activation properties of the muscle. For instance, an activation amplitude of 0.5 was equivalent to activating 50% of the fibres, thereby scaling the activation maximum level of activation by this amount. This relationship is demonstrated in Fig. 1B. By applying an activation levels at 30%, 50% and 100% we explored how power output and efficiency vary across the space of duty cycles and phases.
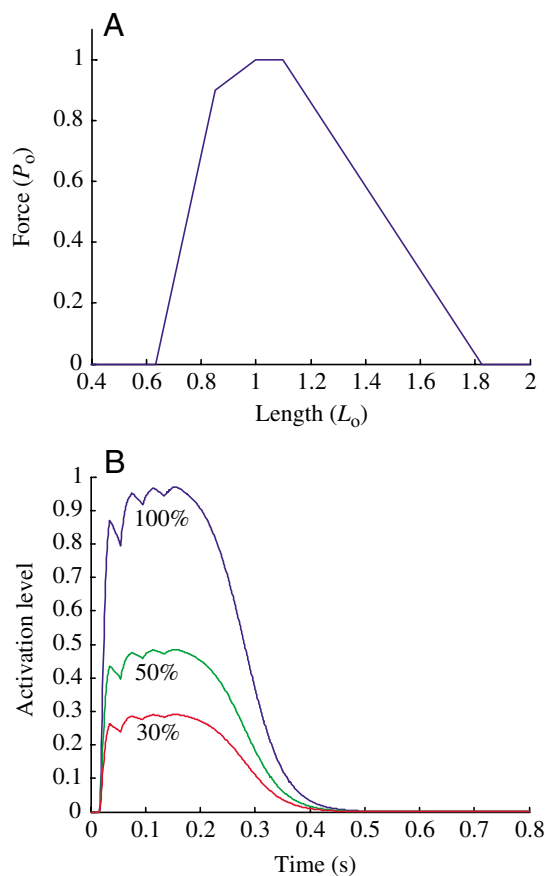
Fig. 1. (A) Force–length relationship used to scale the maximum force output (adapted from Gordon et al., 1966) by scaling the number of possible crossbridges that can attach. (B) Scaling of activation to represent 30%, 50% and 100% of activation levels.

Results

Power and efficiency

Duty cycle and phase of activation

Using the model, it was possible to explore and map the effect of changing duty cycle and phase of activation on the resultant power and efficiency (Fig. 2) and also to determine the optimum activation pattern to achieve these. Activating the muscle for longer and before the muscle begins to shorten
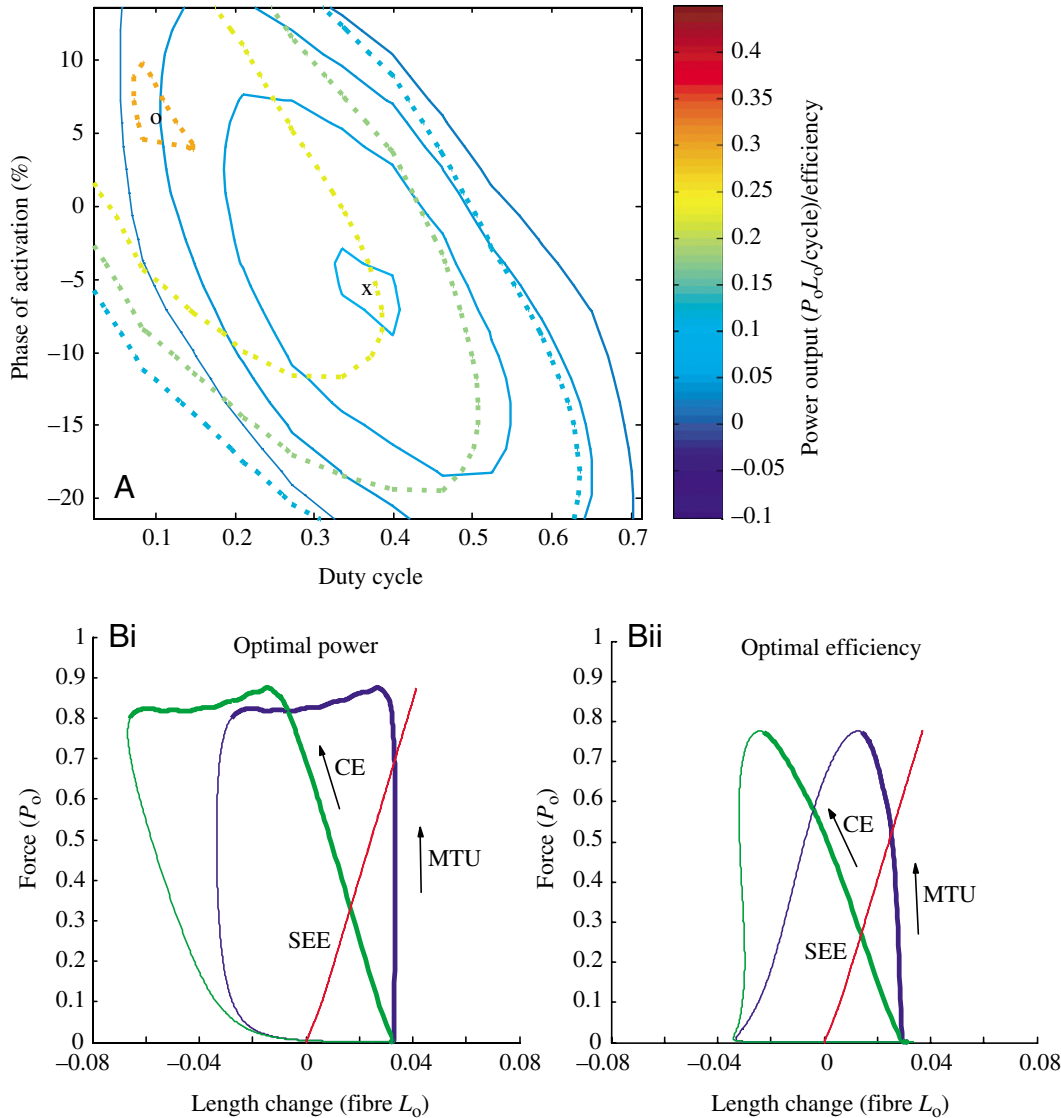
Fig. 2. (A) Contour plot showing the range of duty cycles and phases of activation that can achieve 99%, 80%, 60% and 40% of maximum power output (solid lines) and efficiency (broken lines). The colour bar represents the absolute values for power output (P_oL_o) and efficiency. The values for achieving optimum power (x) and efficiency (o) are also shown. The frequency of oscillation was 1.25 Hz. (B) Work loops (force *vs* length) for optimal power output (Bi) and optimal efficiency (Bii). The work loops of the contractile element (CE, green), the series elastic element (SEE, red) and the muscle tendon unit (MTU, blue) are shown. Positive length changes indicate stretch and the force is the same in the SEE, CE and MTU at any point in time. The duty cycle and phase for optimal power were found to be 0.368 and –5.11, respectively, compared to 0.098 and 5.91 for optimal efficiency. The thick lines indicate the duration of activation.

achieves the greatest power output. It is apparent that there is a distinct optimum for both power and efficiency; however there is a relatively large range of duty cycles and phases that can achieve values close to these optimal values. Fig. 2A demonstrates this by plotting contours at the level of 99%, 80%, 60% and 40% of maximum power and efficiency as well as the position of the optimal values. To achieve an optimal power output, the muscle is activated for a relatively long duty cycle (0.368) and must be activated whilst the muscle is still lengthening (phase=–5.11). In contrast to this, optimal efficiency was achieved with a shorter duty cycle (0.098) and activation was confined to the shortening phase of the muscle length change (phase=5.91). The contours achieving both 80% power and 80% efficiency also overlap for a range of combinations of duty cycle and phase of activation. The range of phases of activation for achieving greater than 80% of both maximum power and efficiency was –15 to 10, while the duty cycle was restricted to between 0.2–0.5.

The work loops of the CE, SEE and the MTU to achieve maximum power output and efficiency at a cycle frequency

of 1.25 Hz and with a length change of $\pm0.035L_o$ are shown in Fig. 2B. To achieve a maximum power output, the MTU has very little length change as the force rises rapidly to a maximum and remains high while the muscle shortens. Once the muscle deactivates (indicated by the thin portion of the line) the force falls quickly, with very little length change in the muscle. This allows the maximum area under the force–length curve to be achieved. The CE, however, shortens (as the SEE is stretched) to produce force and then also lengthens as the force falls (absorbing small amounts of energy). In contrast, during the maximally efficient contraction, the CE has very little length change (and no stretch) as the force falls. As a result the MTU shortens as the force drops. As there is no hysteresis in the model of the SEE, there is no energy lost here and the area under both the CE work loop and the MTU work loop must be the same.

Series elastic stiffness and length change

The relationships between power output and efficiency with

varying series elastic stiffness, amplitude of oscillation and activation parameters (duty cycle and phase of activation) are shown in Fig. 3. When the relative stiffness was reduced, the maximum power output was achieved with a similar duty cycle, but the muscle needed to be activated further into the stretching cycle of the MTU. This is the case for both the small and large amplitude of length change. A similar relationship holds true for maximum efficiency, although smaller duty cycles are required.

A comparison between the activation conditions that produce maximum power and efficiency output shows that at the low amplitude length change, the muscle needs to be activated earlier (during stretch) and for longer to achieve maximum power output. This relationship holds true for both values of relative stiffness. At the higher (since opposite in lower) amplitude, however, the phase can remain very similar to maintain maximum power output and efficiency, and only

the duty cycle has to be greater to achieve optimal power output. The reduction in stiffness requires the muscle to activate earlier to achieve both goals at both amplitudes of length change.

At the lower amplitude of length change it is apparent that the maximum power output achievable reduced from 0.067 to $0.051 \times P_o L_o$/cycle when the stiffness was changed to the lower stiffness. In contrast, at the high amplitude of length change, the power output was higher for both stiffnesses; however, it is higher for the low stiffness condition (0.175) compared to the experimental stiffness (0.156). A similar effect is found for efficiency, where a reduction in stiffness saw the maximum efficiency change from 0.304 to 0.169 at the small amplitude and 0.416 to 0.399 at the large amplitude. When the muscle model has a small stiffness with a large amplitude length change, the activation conditions that achieve maximum power output and efficiency were closest.
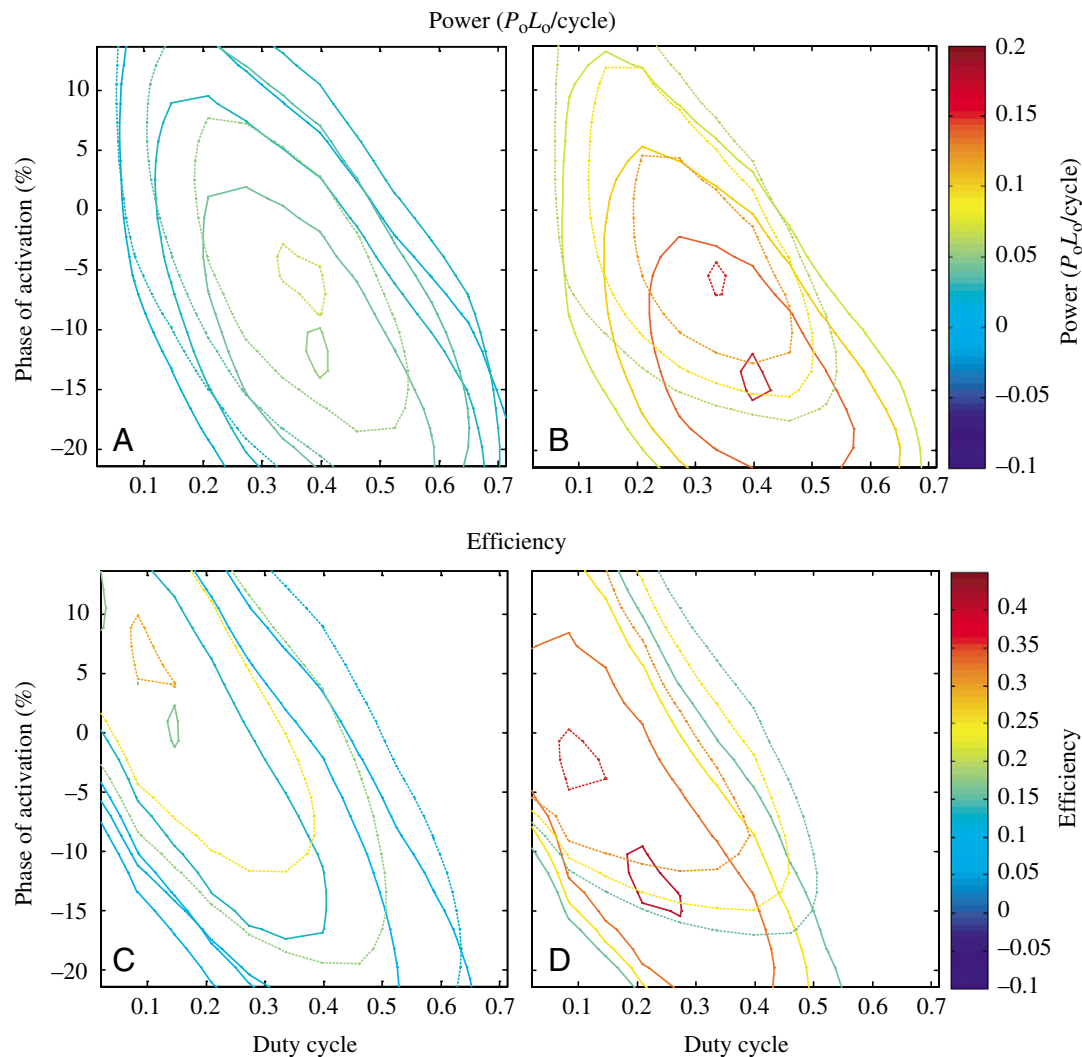

Fig. 3. Contour plot showing the range of duty cycles and phases of activation that can achieve 99%, 80%, 60% and 40% of maximum power output (A,B) and efficiency (C,D) for a compliant relative stiffness (solid lines) and a stiff relative stiffness (broken lines) at two different amplitudes of oscillation ±0.0335L_o (A,C) and ±0.2L_o (B,D). The colour bars represent the absolute values for power (A,B) and efficiency (C,D). Compliant relative stiffness=3–4P_o/L_o; stiff relative stiffness=16–22P_o/L_o (lower stiffness value for forces less than 0.15P_o; see Lichtwark and Wilson, 2005).

Maximum power output and efficiency

Effects of series elastic stiffness

Fig. 4 demonstrates the effect that the relative stiffness of MTU has on maximum power output and efficiency (with optimised activation conditions) at different amplitudes of length change. This shows that a MTU with a higher relative stiffness of the SEE will achieve its optimum power output at a lower amplitude of length change compared to that of its optimum efficiency. However, the simulation with the lower relative stiffness achieved its maximum for both power and efficiency at a similar amplitude of length change. The absolute value of maximum power output and efficiency varied very little with the change in stiffness.
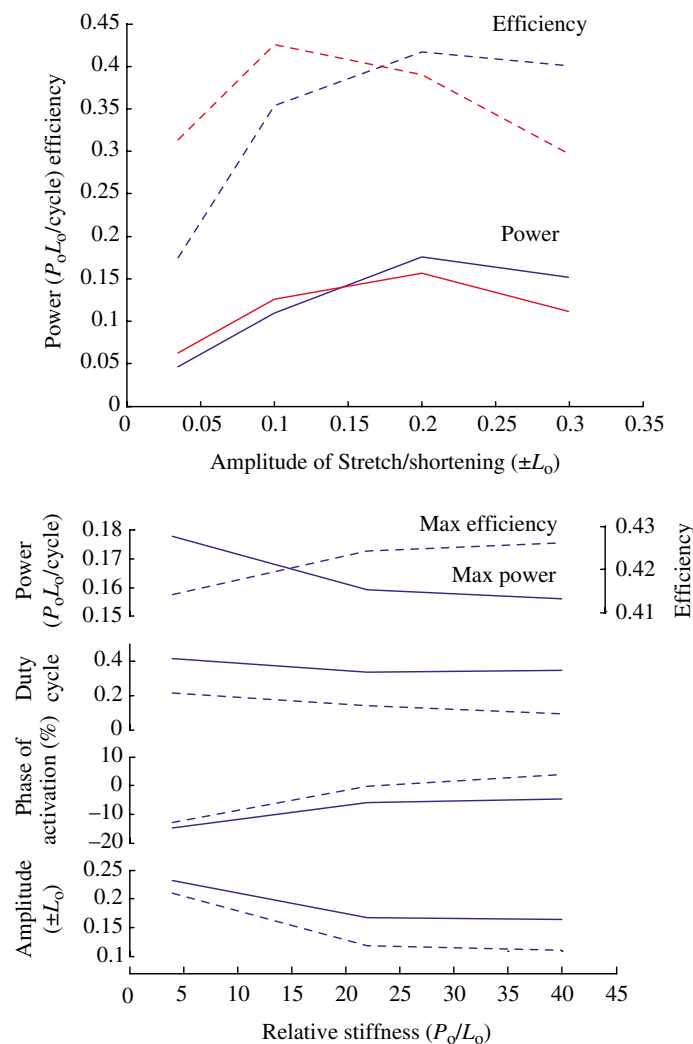

Fig. 4. (A) Maximum power output (solid lines) and efficiency (broken lines) with changes in the amplitude of stretch/shortening at a low stiffness (blue) and high stiffness (red). (B) Maximum power output and efficiency and the duty cycle, phase of activation and amplitude of stretch/shortening that achieve that power output with varying relative stiffness. Solid lines represent the values obtained for maximum power output and broken lines those obtained for maximum efficiency.

Optimisation of both activation conditions and the amplitude of length change at different relative stiffnesses demonstrated that under the optimal conditions, the maximum values of power output and efficiency do not vary greatly with relative stiffness (Fig. 4B). However it is apparent that there is a trend of reduced maximum efficiency and increased maximum power with a reduction in stiffness. The conditions that produce these maxima are also plotted in Fig. 4B. A higher duty cycle is required for optimal power output, compared to efficiency; however, this changes very little with relative stiffness. With increases in stiffness, the onset of activation must be later (i.e. phase of activation must be higher; closer to the beginning of the shortening phase, 0) and this effect is more apparent to achieve optimal efficiency. The opposite is true for the amplitude of length change, where the optimal length change of the MTU reduces with increasing stiffness and must be smaller to achieve maximum efficiency.

Table 1 lists a number of anti-gravity muscles from animal species ranging from a hopping mouse to a horse and the relative stiffness of each. From this table it is apparent that, relative to the length of the fibre and the maximum force-generating capacity, the compliance of the tendon tends to increase (decreasing stiffness) with the size of the animal. The stiffness of the horse SEE is almost an order of magnitude smaller than that of the hopping mouse.

Power and efficiency

Effects of amplitude of activation

By varying the amplitude of the activation, which may be thought of as reducing the number of active fibres in a whole muscle or bundle of fibres, it is possible to map the change in power output and efficiency with varying activation conditions. Fig. 5 shows the variation in power output and efficiency as the result of varying the maximum activation level to be 30%, 50% and 100% (amplitude of length change=0.0335). It is apparent the optimal activation conditions to achieve maximum power output and maximum efficiency and the actual level of efficiency are very similar, regardless of activation level. However, the magnitude of the power output is dependent on activation level.

Discussion

The use of a validated model of muscle mechanics and energetics has allowed us to explore the relationships between activation conditions and power output and efficiency, and also to determine the effect of changing properties of the muscles architecture (SEE stiffness) and function (amplitude of length change). The major difference in the activation conditions for optimal power as opposed to efficiency (under the experimentally measured conditions of the dogfish white muscle) are that the duty cycle is greater and the phase of activation is earlier for maximising power output. Increasing the relative compliance of the SEE allows a muscle to activate earlier in the stretch–shortening cycle and allows for higher power outputs and efficiencies to be achieved than with a stiff

Table 1. *A range of muscles with similar roles from animals of different size and their properties*

Muscle type	P_o (N)	L_o (mm)	Stiffness (N mm^{-1})	Relative stiffness (P_oL_o)
Hopping mouse gastrocnemius*	3.6	7.3	7.7	15.61
Rat gastrocnemius*	11.3	13.8	15.9	19.41
Human gastrocnemius[†]	875	65	150	11.14
Wallaby gastrocnemius*	135	18.7	21	2.91
Horse superficial digital flexor[‡]	716	7.5	118	1.23

The calculated relative stiffness is normalised to muscle fibre length and maximum isometric muscle force.

*Data from Ettema (1996); [†]data from Maganaris and Paul (2002); [‡]data from Swanstrom et al. (2005) and Brown et al. (2004).

muscle. The optimum activation conditions for both maximum power output and maximum efficiency are also closer together for relatively compliant tendons acting with larger amplitude length changes. Therefore we have demonstrated that the SEE has an important effect on activation conditions for power and efficiency.
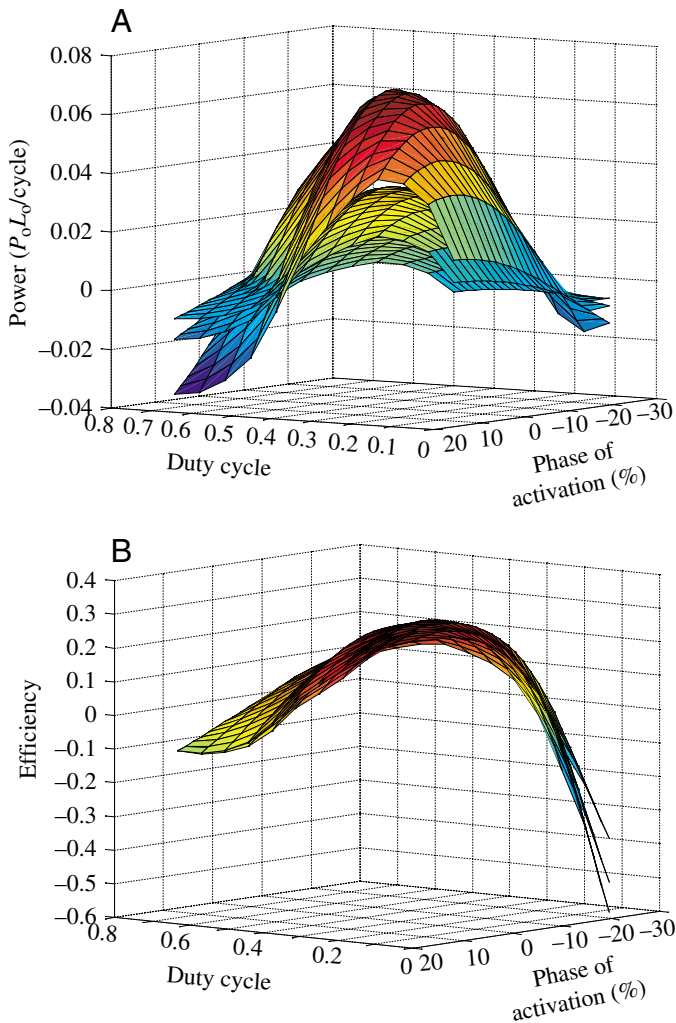

Fig. 5. Surface plot of variation in power output (A) and efficiency (B) with duty cycle and phase of activation at three different amplitudes of activation levels. Activation levels were scaled to 30%, 50% and 100% of activation.

It was assumed that during animal locomotion a muscle's power output is constrained by the movement that it wants to perform. If the conditions of locomotion change, for instance if an animal accelerates or runs uphill, some muscles will need to increase their power output to produce the required work on the centre of mass in a limited of period of time (Gabaldon et al., 2004; Roberts and Scales, 2002). To achieve the required power output the activation pattern can be varied in numerous ways, not only by changing the duty cycle and phase, but also the activation level and frequency of stimulation. Therefore there are obviously large, but finite, combinations of activation patterns that can achieve the required power output. It is likely that these activations may also be constrained by pressure towards efficiency. The results of this modelling study suggested that there are indeed activation patterns (at least for the two activation variables altered in this simulation) that achieved a combination of both. For instance, if the animal needed to produce 90% of its maximal power, it is conceivable that it would use a smaller duty cycle and activate at the beginning of shortening of the muscle to achieve the highest efficiency available for that power output (Fig. 2).

An examination of the work loops arising from activating the muscle for optimal power and efficiency helps demonstrate the importance of the SEE in determining the conditions for optimum power output and efficiency. In maximum power conditions, the work performed by the MTU (area underneath the force–length trace) is maximised for the conditions, and is almost square in shape. For this to occur the contractile component shortens whilst at high force (and activation), and then lengthens during deactivation. This is not the case for achieving maximum efficiency, and in fact the CE only lengthens whilst fully deactivated. This is necessary for high efficiencies because work is not then absorbed by the CE, and less time shortening at high activation reduces the heat output during the contraction. Therefore there are distinct differences in how the muscle must be activated to achieve either maximum power or maximum efficiency.

Varying the compliance of the SEE will have the effect of altering the timing of the rise and fall of force and also the length change of the CE, therefore this will have a large influence on the relationship between conditions for optimal power or efficiency. This is confirmed by the results shown in Fig. 3, which demonstrates that with a significant decrease in

the stiffness of the SEE, the phase of activation required to maximise the power and efficiency is earlier than for the high stiffness. Duty cycle for these conditions changes little, except during large length change (±0.2L_o), where the maximum efficiency can be achieved with a significantly longer duty cycle of 0.22 (compared to approximately 0.1), closer to that of the maximum power. This suggests that relatively compliant tendons may enable a muscle to activate with both high power output and also high efficiency.

The amplitude of the length change of the muscle relative to its stiffness was also shown to be important in influencing the relationship between power output and efficiency. Although similar optimum values for power output and efficiency can be achieved with muscles, regardless of compliance, the length change of the muscle during the cyclical length change heavily influences the magnitude of the maximum values achievable (under optimal activation conditions). Fig. 4 demonstrates that longer relative length changes (about 0.2L_o) can achieve the highest power output and efficiency of muscle with compliant SEE, whereas the stiffer SEE would require small amplitude length changes for optimal efficiency and larger length changes for optimal power output.

Whilst considering the design of a muscle, one must also examine the primary function of a particular muscle. It is interesting to note that the optimal duty factors and phases of activation are well within those recorded biologically during repetitive activation in a range of species that employ oscillatory movements. Consistently, investigators of animal locomotion have found that muscles that undergo cyclical length changes will activate before shortening begins (negative phase) and deactivate when the muscle is still shortening (Askew and Marsh, 2002; Biewener et al., 1998; Griffiths, 1991; Tobalske et al., 2003). This is in agreement with our findings, which suggest that to have a high efficiency at any given power output, the muscle should be activated just before or after shortening begins, and the muscle should only continue to be activated whilst the muscle is still shortening (smaller duty cycles).

The stiffness of the SEE relative to the CE length places the results of the simulations into context. It was interesting to find such a large change in the relative stiffness with an increase in animal size. Fig. 4 would suggest that this range of stiffness differences would not have a great effect on the maximum power output or efficiency of the muscle; however, the conditions under which this can be achieved would vary greatly. For instance, MTU values with low relative SEE stiffness are likely to have undergone larger amplitude length changes relative to the CE length and activated early during the stretch of the muscle to obtain optimal power output and maximum efficiency. This is certainly the case for many large animals which, according to Table 1, have low relative SEE stiffness. These muscles often have long tendons and short muscle fibres, which is the architecture required for low relative stiffness. Whilst these muscles are not required to achieve high positional control, it is important that they are efficient and powerful.

The timing, amplitude and duration of muscle activation are indeed important for power production and also efficient movement. During cyclical movements such as locomotion, the theoretical power output of many muscles is actually low, but under varying conditions such as acceleration and changes in grade, muscle can be required to produce (or absorb) power (Gabaldon et al., 2004). The present results provide evidence that a muscle can activate with near maximum power output and also near maximum efficiency. However, to vary power output, experimental results suggest that muscles generally change the amplitude of muscle activation (measured from EMG) more so than the timing and duration (Hof et al., 2002). Our simulations, which vary the activation amplitude, suggest that the same conditions of muscle contraction can produce maximum power output and efficiency at different levels of activation (Fig. 5). However, in changing the activation level the power output invariably drops and the efficiency of the muscle remains consistent. Therefore reducing the activation level and maintaining similar timing and duration of activation is perhaps the best method for modulation of power output in an efficient manner. This finding is supported by the results of Hof (2003) and Hof et al. (2002), who examined the human triceps surae. The effect of the relationship between activation level and fibre type recruitment is of interest but beyond the scope of this paper.

There are certainly confounding issues in extrapolating these data outside the muscle types for which the model has been validated. For instance, each muscle has different properties, including the maximum shortening velocity, the curvature of the force–velocity curve, the rate of activation/deactivation and basic metabolic costs. Indeed each of these factors will either increase or decrease a muscle's power-producing capabilities and efficiency. However, the relationships between power output, efficiency, optimal conditions of activation, SEE stiffness and amplitude of length change presented here provide an insight into why muscles (including the CE and the SEE) with specific architecture and function activate the way they do.

In summary, here we present a model that can be used to explore the parameter space of activation conditions that can achieve optimal power output and efficiency of muscle, and also a framework for determining the effect of SEE stiffness and length change on these optimal conditions. The results of this study show that a more compliant SEE allows the activation conditions for achieving maximum efficiency closer to that for achieving maximum power output. This is, however, length change dependent, with a compliant SEE requiring greater length change amplitude. This has implications in the design of muscle for its specific function, muscles with short muscle fibres (in comparison to the length change of the SEE) being more powerful and efficient with proportionately long amplitude length changes. In choosing the activation timing, amplitude and duration, simulations also suggest that biological systems would obtain greatest benefit by using conditions of optimal efficiency and varying the amplitude of activation to achieve the required power output.

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