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Title: The expression of the skeletal muscle force-length relationship in vivo: a simulation study.

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Abstract (298 words): The force-length relationship is one of the most important mechanical characteristics of skeletal muscle in humans and animals. For a physiologically realistic joint range of motion and therefore range of muscle fibre lengths only part of the force-length curve may be used in vivo, i.e. only a section of the force-length curve is expressed. A generalised model of a mono-articular muscle-tendon complex was used to examine the effect of various muscle architecture parameters on the expressed section of the force-length relationship for a 90 degree joint range of motion. The parameters investigated were: the ratio of tendon resting length to muscle fibre optimum length ($L_{TR}:L_{F.OPT}$) (varied from 0.5 to 11.5), the ratio of muscle fibre optimum length to average moment arm ($L_{F.OPT}:r$) (varied from 0.5 to 5), the normalised tendon strain at maximum isometric force (c) (varied from 0 to 0.08), the muscle fibre pennation angle (θ) (varied from 0 to 45 degrees) and the joint angle at which the optimum muscle fibre length occurred (ϕ). The range of values chosen for each parameter was based on values reported in the literature for five human mono-articular muscles with different functional roles. The ratios $L_{TR}:L_{F.OPT}$ and $L_{F.OPT}:r$ were important in determining the amount of variability in the expressed section of the force-length relationship. The modelled muscle operated over only one limb at intermediate values of these two ratios ($L_{TR}:L_{F.OPT}$=5; $L_{F.OPT}:r$=3), whether this was the ascending or descending limb was determined by the precise values of the other parameters. It was concluded that inter-individual variability in the expressed section of the force-length relationship is possible, particularly for muscles with intermediate values of $L_{TR}:L_{F.OPT}$ and $L_{F.OPT}:r$ such as the brachialis and vastus lateralis. Understanding the potential for inter-individual variability in the expressed section is important when using muscle models to simulate movement.

Keywords:

force-length, tendon, model, biomechanics

INTRODUCTION

The force-length relationship of muscle is a fundamental mechanical property of muscle. It is also an important component of most biomechanical models of movement since it determines the maximum isometric force that can be produced at a given joint configuration. The force-length relationship has been shown to consist of three regions at the sarcomere level (Gordon et al., 1966): the ascending limb, the plateau, and the descending limb. However, in vivo different skeletal muscles may operate over all or only some of these regions of the force-length curve, that is over physiological joint ranges of motion only part of the force-length relationship may be expressed (e.g. Herzog and ter Keurs, 1988; Lieber and Friden, 1998). The section of the force-length relationship that a muscle operates over, given the physiological range of motion of the joints crossed by the muscle, will be referred to as the expressed section. Previous work has shown that there is a great deal of variability in the expressed section for the rectus femoris (Herzog and ter Keurs, 1988; Winter, 2004) and the hamstrings (Savelberg and Meijer, 2003). There is apparently not much variability in the expressed section of the gastrocnemius (Herzog et al., 1991a; Winter and Challis, 2008b). The reason for the different amount of variability in the expressed section in different muscles has not been investigated. The section of the force-length relationship that a muscle operates over affects the pattern of force production across the range of motion. The change in muscle force with muscle length must present a substantial challenge to the successful control and co-ordination of movement. It is therefore of considerable interest to investigate which factors determine the expressed section of the force-length relationship in vivo, and to understand why some muscles show more variability in this property than others.

There are several possible sources of the reported variation in the expressed section of the force-length relationship. These are: anatomical differences, for example in the distance of muscle insertion points from joint centres relative to segment length; differences in tissue mechanical properties such as tendon compliance; and differences in muscle architectural features, such as pennation angle. These musculo-skeletal features are reflected in the parameters usually included in muscle models, for example the muscle pennation angle is included in many muscle models (e.g. Otten, 1988). In a previous study gastrocnemius muscles operating over different sections of the force-length curve were modelled in order to assess the ability of an in vivo testing method to accurately reconstruct different sections of the force-length relationship (Winter and Challis, 2008a). In formulating models for muscles operating over different sections of the force-length relationship it was found that certain model parameters affected the expressed section of the force-length relationship more than others.

The purpose of this study was to undertake a more systematic examination of the effect of anatomical, architectural and mechanical muscle-tendon complex parameters on the expression of the force-length curve in vivo using a muscle model. The model was initially formulated as a generalised mono-articular muscle-tendon complex and then each parameter was systematically varied in turn over ranges that reflect the range of parameter values reported in the literature for several mono-articular muscles. It was hypothesised that varying the ratio of resting tendon length to the muscle fibre optimum length ($L_{TR} : L_{F.OPT}$) would have the greatest influence on the section of the force-length relationship that was expressed (Winter and Challis, 2008b).

METHODS

Model Description

The muscle model comprises a contractile component that models the behaviour of the muscle fibres, and a series elastic component (Figure 1). The force produced by the muscle model (F_M) is described by,

$$F_M = q.F_{MAX}.F_L(L_F).F_V(V_F) \qquad [1]$$

where,

q - current active state of muscle model,

F_{MAX} - maximum isometric force possible by the muscle model,

$F_L(L_F)$ - fraction of the maximum isometric force the model can produce given its current fibre length (L_F),

and $F_V(V_F)$ is the fraction of maximum isometric force the model can produce given its current fibre velocity (V_F).

<<Insert Figure 1 around here>>

The current active state of the model (*q*) represents the recruitment as well as the firing rate, or rate coding, of the α-motor neurons. The value of *q* can range from 0 to 1. In the simulations only maximal isometric conditions were examined so the muscle fibres were assumed to have a velocity of zero, making $q=1$ and $F_V(V_F)=1$. The value of F_{MAX} was always set to be 100 arbitrary units of force.

The normalised force-length properties of the muscle were represented by (Gallucci and Challis, 2002),

$$F_L(L_F) = 1 - \left(\frac{L_F - L_{F.OPT}}{w.L_{F.OPT}} \right)^2 \qquad [2]$$

where:

$L_{F.OPT}$ is the optimum length of the muscle fibres, and

w is a parameter specifying the width of the force-length relationship (Figure 1A).

The muscle fibre optimum length is the length at which optimal overlap of actin and myosin occurs and therefore maximum muscle force can be produced. The value for *w* for single fibres in vitro has been reported as 0.56 (Gordon et al., 1966).

In series with the contractile component is an elastic component. Although this component reflects the behaviour of any elastic structure in series with the contractile component, the series elastic component mainly reflects the behaviour of the tendon. The model of this element assumes that the tendon has a linear stress-strain curve (Figure 1B). The force-extension curve of this element is represented by,

$$L_T = L_{TR} + \frac{F_M.c}{F_{MAX}}.L_{TR} \qquad [3]$$

where:

L_T is the current length of the tendon,

L_{TR} is the resting or slack length of the tendon, and

c is the extension of tendon under maximum isometric force as a fraction of tendon resting length.

The length of muscle-tendon complex (L_{MT}) is the length from origin to insertion. For a paralleled fibred muscle it is equal to the length of the muscle fibres plus the length of the tendon (Equation 4),

$$L_{MT} = L_F + L_{TR} \qquad [4]$$

The muscle fibres can be pennate (Figure 1C). In a planar model of pennate muscle it is assumed that the area of the muscle fibres remains constant, this is equivalent to the constant volume assumption for actual muscle (Otten, 1988). Given that the thickness (T) of the muscles must remain constant, the pennation angle (θ) can be computed from,

$$cos(\theta) = \sqrt{1-(T / L_F)^2} \qquad [5]$$

where:

θ is the muscle fibre pennation angle in radians.

If the muscle is pennate then the force in the direction of the tendon is not equal to the force in the muscle fibres (Figure 1C), instead the correction given in Equation 6 has to be applied.

$$F_T = F_M.cos(\theta) \qquad [6]$$

where:

F_T is the force in the direction of the tendon.

The length of the muscle-tendon complex can then be computed from (Figure 1C),

$$L_{MT} = L_F.cos(\theta) + L_T \qquad [7]$$

For input into the model it was necessary to know the length of the muscle-tendon complex (L_{MT}). In many muscle models (e.g. Out et al., 1996) the length of the muscle-tendon complex is computed from the joint angle according to an experimentally determined relationship (e.g. Grieve et al., 1978). The muscle moment arm is then computed by taking the derivative of this muscle-tendon complex length-joint angle relationship with respect to angle (An et al., 1983). However, in order to examine the effect of the ratio $L_{F.OPT} : r$ on the expressed section of the force-length relationship the value of r had to be specified in advance, and the change in the length of the muscle-tendon complex was therefore obtained by integration of the moment arm-joint angle relationship. This ratio is important since it determines the length change that the muscle must go through in order to move through the joint range of motion.

The reference length of the muscle-tendon complex (L_{MTR}) was specified according to,

$$L_{MTR} = L_{F.OPT} + L_{TR} \quad [8]$$

For each simulation there was a reference length of the muscle-tendon complex which was always set to be 50 arbitrary units long. The lengths L_{TR} and $L_{F.OPT}$ were set according to the desired value for the ratio $L_{TR} : L_{F.OPT}$. The angle at which this reference muscle-tendon complex length occurs (ϕ) was specified, this parameter specifies the angle at which the reference length occurs and is therefore important in determining the range of lengths used for a certain joint range of motion. The moment arm length at this reference angle (r_{REF}) was computed according to the desired value for $L_{F.OPT} : r$. The moment arm-joint angle relationship could be constant, increasing, or decreasing according to Equation 9. The range of motion for the joint was always 0 to 90 degrees. A 90 degree range of motion was used since it is a typical range of motion for many joints (Pheasant, 1986).

$$r = r_{REF} + r_{SLOPE}(\phi_{JOINT} - \phi) \qquad [9]$$

where:

r_{SLOPE} is the slope of the moment arm-joint angle relationship, and

ϕ_{JOINT} is the current joint angle in radians.

For a constant moment arm r_{SLOPE} was set to zero.

The length of the muscle-tendon complex at the current joint angle was then computed by integrating the moment arm-joint angle relationship and adding the reference muscle-tendon complex length,

$$L_{MT} = L_{MTR} + r_{REF}(\phi_{JOINT} - \phi) + \frac{1}{2} r_{SLOPE}(\phi_{JOINT} - \phi)^2 \qquad [10]$$

For a given joint angle the moment arm of the muscle was computed and muscle-tendon lengths were computed. Given these muscle-tendon lengths the maximum isometric force the muscle could produce was computed. The length of the fibres was determined by an iterative procedure. First fibre length was estimated by subtracting resting tendon length from the muscle-tendon length at a given joint angle. This value was used to estimate muscle isometric force. The tendon stretch under this force was then computed, and therefore a new muscle fibre length was computed, and a new isometric force computed. This sequence was continued until a consistent value for maximum isometric force was produced, which was always achieved in 20 iterations or less.

Model Parameters

The model parameters under investigation in the present study are: the muscle fibre pennation angle (θ), the compliance of the tendon (c), the ratio of the muscle fibre length to the size of the moment arm ($L_{F.OPT} : r$), the joint position at which the reference muscle-tendon complex length occurs (ϕ), and the ratio of resting tendon length to fibre optimum length ($L_{TR} : L_{F.OPT}$). The model was formulated initially as a generalised mono-articular muscle-tendon complex and then each parameter was systematically varied in turn over ranges that reflect the range of parameter values found in a variety of mono-articular muscles. Five mono-articular muscles were chosen to reflect a variety of anatomical and architectural features. The muscles were: the soleus (SOL), vastus lateralis (VL), the short head of the biceps femoris (SHBF), the brachialis (BR), and the extensor carpi radialis brevis (ECRB). Although the ECRB arises partly from the lateral epicondyle of the humerus it was treated as a mono-articular muscle since it is only a weak elbow flexor (Ettema et al., 1998; Riek et al., 2000).

Table 1 shows the source and range of the values used for each muscle for $L_{F.OPT} : r$, $L_{TR} : L_{F.OPT}$, *c*, and θ parameters. The intention in referring to these parameter values is to ensure that the range of values investigated with the model covers the range of parameter values typically found in vivo.

<<Insert Table 1 around here>>

The maximum normalised tendon strain is specified by *c*. The values for *c* were directly specified for SOL by Magnusson et al. (2001) and for ECRB by Loren and Lieber (1995) (Table 1). No information on either *c* or the tendon cross-sectional area could be found for BR. For the VL and SHBF the values for *c* shown in Table 1 were computed by taking the values for the tendon and muscle cross sectional areas from Pierrynowski and Morrison (1985) and Wickiewicz et al. (1983) and then using the relationship,

$$c = \frac{PCSA \times ST}{TCSA \times E} \qquad [11]$$

Where:

PCSA is the physiological cross sectional area of muscle

ST is the specific tension of muscle (0.3MPa taken from Close, 1972)

TCSA is the tendon cross sectional area, and

E is the Young’s Modulus of tendon (1,500MPa taken from Alexander, 2002).

The reference muscle tendon length is equal to the resting tendon length plus the optimum fibre length. The parameter ϕ, representing the joint angle at which the reference muscle-tendon complex length occurs, was varied in order to shift the optimum length to different points in the joint range of motion. The joint angle at which the optimum length occurs is difficult to determine in vivo since more than one muscle crosses each joint, and for this reason the parameter ϕ was varied through the whole range of motion (0 to 90 degrees). When the muscle is activated at the reference position the muscle fibres will exert force and stretch the tendon, and the muscle fibres will shorten due to tendon stretch. This means that the angle at which the optimum muscle fibre length occurs under full activation will change if a compliant tendon is specified in the model. For this reason a non-compliant tendon was used when examining the effect of changing parameters $L_{TR} : L_{F.OPT}$, ϕ and θ.

RESULTS

It was not feasible to report all possible parameter set combinations, but based on the data presented in Table 1, a representative range has been selected. The combinations of parameter values used are reported in Table 2. The left hand column shows which parameter was varied, the columns to the right show the values of the fixed parameters, and the range of values used for the parameter under investigation. The results are presented in the row order shown in Table 2.

<<Insert Table 2 around here>>

Varying the ratio $L_{F.OPT} : r$ with $L_{TR} : L_{F.OPT}$ held constant affects how much of the force-length relationship is expressed (Figure 2). This was the case regardless of whether the moment arm was held constant over the range of motion or whether the moment arm increased or decreased over the range of motion. Under the model formulation with a constant moment arm the change in the length of the muscle-tendon complex was equal to the length of the moment arm multiplied by the change in joint angle from the reference position in radians. This means that the amount of the force-length relationship used also depends on the joint range of motion relative to the width of the force-length relationship (*w*). Consequently the proportion of the force-length relationship that is used (*p*) can be computed using the inverse of the ratio $L_{F.OPT} : r$ and the joint range of motion (*ROM*),

$$p = \frac{r}{L_{F.OPT}} \cdot \frac{ROM}{2w} \qquad [12]$$

Using Equation 12 it can be shown that the value of $L_{F.OPT} : r$ at which the whole of the force-length relationship is used when there is a constant moment arm, a width parameter of 0.56, and a 90 degree joint range of motion is around 1.4 for an inextensible tendon and slightly more if a compliant tendon is used. In vivo, only values of $L_{F.OPT} : r$ above this will allow some variability in the expression of the force-length relationship.

<<*Insert Figure 2 around here*>>

The effect of varying the value for $L_{TR} : L_{F.OPT}$ depended partly on the size of the moment arm, *r* (Figure 3 and Figure 4). For relatively small moment arms (high ratios of $L_{F.OPT} : r$) and low ratios of $L_{TR} : L_{F.OPT}$ the muscle always operated over the plateau, regardless of the joint angle at which the optimum length was set. The optimum length had to be set at non-physiological joint angles in order to make the muscle operate over one of the limbs (ascending or descending) of the force-length relationship. For large moment arms (low values of $L_{F.OPT} : r$) and high values of $L_{TR} : L_{F.OPT}$ the whole range of the force-length relationship may be used for low values of c and θ if ϕ occurs in the middle of the joint range of motion. The muscle could only operate over just one limb of the force-length relationship when both ratios ($L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$) were at high values, or both were at low values, or both were at intermediate values.

<<*Insert Figures 3 and 4 around here*>>

The effect of varying ϕ throughout the range of motion was to shift the expressed section of the force-length relationship from the descending limb (for ϕ equal to zero degrees), to the plateau (for ϕ equal to 30 to 60 degrees), and then to the ascending limb (for ϕ equal to or greater than 75 degrees) (Figure 5).

<<Insert Figure 5 around here>>

Tendon compliance means that the tendon stretches when the muscle is activated and applies force to it, resulting in a shorter muscle fibre length at a given joint angle with increasing compliance and so shifting the expressed section to shorter muscle fibre lengths. This means that a muscle, with ϕ set to 45 degrees so that the optimum length occurs in the middle of the range of motion, would operate over the plateau region if the tendon were considered inextensible, but would shift to shorter lengths so that it operates over the ascending limb for values of c close to 0.08 (Figure 6). Similarly a muscle with ϕ set to 0 degrees would operate over the descending limb for values of c between zero and 0.05, but the muscle would be shifted to the plateau region for values of c above 0.06 (Figure 7). The effect of changing the parameter c would be smaller for lower values of $L_{TR} : L_{F.OPT}$, since the tendon would be considerably shorter. Note that Figures 3 and 4 show the effect of varying the ratios $L_{TR} : L_{F.OPT}$ and $L_{F.OPT} : r$ while c is set to zero. When c was set at values above 0.01 the expressed section was shifted to shorter lengths, which is consistent with the trend shown in Figures 6 and 7.

<<Insert Figures 6 and 7 around here>>

The effect of varying the pennation angle of the muscle fibres (θ) was to shift the expressed section to longer lengths, i.e. towards the descending limb (Figure 8). This is because the fibre length at a given joint angle is inversely proportional to the cosine of the pennation angle. As the pennation angle increases, the cosine of the angle decreases and the fibre length at the specified joint angle increases. However, the shift in the operating range was not sufficient to change the expressed section from one limb to the other, i.e. from the ascending limb to the descending limb. The maximum force in the direction of the tendon decreased with increasing pennation angle, this would be expected as the force in the direction of the tendon is only the cosine of the pennation angle times the force in the muscle fibres. The cosine of 45 degrees is 0.707, so the force in the direction of the tendon is only around two thirds of that in the muscle fibre with such a high pennation angle. The value specified for θ represents the pennation angle at rest; the pennation angle increases with decreasing muscle length.

<<Insert Figure 8 around here>>

DISCUSSION

The model parameters that were most critical in allowing variability in the expressed section of the force-length relationship were the ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$. For high $L_{TR} : L_{F.OPT}$ ratios, representing a long tendon and short muscle fibres, the whole of the force-length relationship was used due to the shortness of the muscle fibres. For very low ratios of $L_{TR} : L_{F.OPT}$ the expressed section was always the plateau unless the optimum length was set at a joint angle that was very far outside a physiologically realistic range of motion. The effect of changing the value of $L_{TR} : L_{F.OPT}$, however, was modified by the value of $L_{F.OPT} : r$. This is because for a fixed range of motion and a given value for the width of the force-length relationship, the inverse of $L_{F.OPT} : r$ was proportional to the fraction of the force-length relationship that was used (Equation 12). For the range of motion and the width of the force-length curve used here only values of $L_{F.OPT} : r$ above 1.5 resulted in only one limb of the force-length relationship being expressed. For intermediate values of $L_{TR} : L_{F.OPT}$ and $L_{F.OPT} : r$ the effect of increasing tendon compliance was to shift the expressed section to increasingly shorter lengths and the effect of increasing the pennation angle was to shift the expressed section to increasingly longer lengths.

The width parameter used in the simulations was 0.56 (Gordon et al., 1966), but due to variability in the number of sarcomeres per muscle fibre (Meijer et al., 1998) it is likely that the width of the force-length relationship is broader in vivo in whole muscle than it is in an isolated fibre preparation (Challis, 2000). However, the effect of a higher value for a width parameter can be explored using Equation 12. For example, with $L_{F.OPT} : r$ equal to 2, ROM equal to 90 degrees or ${}^{\pi}\!/_{2}$ radians and w equal to 0.56 the length change required would be 0.7 times the range of the force-length relationship. Changing the width parameter to 0.7 reduces the proportion of the force-length relationship used to 0.561.

While some muscles have constant moment arms throughout their joint range of motion, others have a variable moment arm – joint angle relationship. For variable moment arm muscles, the proportion of the force length relationship used can still be calculated if the mean moment arm over the joint range of motion is calculated and then substituted into Equation 12. Equation 12 can also be used to adjust results for joints with restricted ranges of motion, either due to joint anatomy or due to pathologies such as osteoarthritis, though such pathologies would doubtless affect the value of other parameters in the model.

When only one limb of the force-length relationship is used, whether an individual operates over the ascending or descending limb will depend on the joint angle at which the optimum length occurs. In the model, varying the joint angle at which the optimum length occurs (ϕ) caused a change in the length of the muscle tendon complex at a given joint angle of around 10%. This inter-individual variability in muscle-tendon complex lengths at a given joint angle could be caused in vivo by inter-individual differences in attachment sites, and therefore differences in the distance between origin and insertion sites. Such inter-individual differences in attachment sites have been reported, for example Duda et al. (1996) found that the coefficient of variation for the centroid of the attachment site of various muscles arising from and inserting onto the femur was 80%. Inter-individual variability in the limb of the force-length curve used for a given muscle could also arise in vivo due to small variations in $L_{TR} : L_{F.OPT}$. Variability in $L_{TR} : L_{F.OPT}$ would mean that muscle-tendon complex lengths at a given joint angle may be similar between individuals but that differences in the expressed section could occur due to inter-individual differences in the tendon length or in the muscle fibre length at a given joint position. Different muscle fibre lengths at a given joint angle could occur in different subjects as a result of the addition or removal of sarcomeres. Evidence from animal studies (Lynn et al., 1998) and human studies (Brockett et al., 2001) show such changes in sarcomere numbers are possible.

Most models used in biomechanical analyses are of the phenomenological ‘lumped single sarcomere’ type used here. The intention of this study was to discover the broad principles concerning the expression of the force-length relationship when considering the behaviour of the muscle-tendon complex as a whole. However, a complex three dimensional muscle architecture may be seen in vivo (Huijing, 1998) that may introduce subtleties that cannot be represented by the more simple model used here. For example, variability in the curvature and length of individual fascicles can cause fascicle strains that are not uniform throughout the muscle (Blemker et al., 2005). Nevertheless, very few biomechanical models have attempted to include such detail and indeed it may be that the amount of inter-individual variation in muscle architecture when considered at this level prevents the drawing of general conclusions about muscle-tendon complex behaviour in vivo.

A second consideration is that the model parameters are inter-related and this means that changes in one parameter can affect the value of other parameters. For example, when an elastic tendon is assumed (*c* equal to or greater than

0.01) then the absolute length change at maximum isometric force will depend on the value of $L_{TR} : L_{F.OPT}$ since a long tendon extending by say 6% will extend more than a short tendon extending by 6%. For this reason an inextensible tendon was sometimes assumed when varying the other model parameters in order to make clearer the effect of the parameter under investigation.

Some aspects of the generalised muscle model used here have been simplified in order to allow a more straightforward examination of the parameters considered. For example, non-linearity in the tendon length-extension relationship was not modelled, similarly the model did not include a parallel elastic component. Under maximal activation for most of the results the forces are likely to be high enough for the non-linear toe region of the tendon length-extension relationship not to have an effect. Some simulations do show expressed sections that encompass the limits of the force-length relationship where the forces would be low and the toe region may be expected to apply. However, these results are included to illustrate the proportion of the force-length relationship used. It may be anticipated that in vivo the expressed section is actually shifted so that the limits of the force-length relationship would not be reached for physiological joint ranges of motion. A parallel elastic component could affect the load placed on the tendon, and therefore tendon stretch, and may also affect the muscle fibre excursion. Both of these effects would be joint angle dependent. Future work will address the influence of additional more complex architectural features on the expression of the force-length relationship.

The findings from this study allow some predictions to be made about the amount of variability that may be expected in vivo for the five muscles considered as sources for the range of parameter values considered. The short head of the biceps femoris has a high value of 4.39 for $L_{F.OPT} : r$ and a low value of 0.52 for $L_{TR} : L_{F.OPT}$ (Table 1), meaning that this muscle is likely to operate entirely over the plateau region or one of the limbs of the force-length relationship (Figure 9).

The value of $L_{TR} : L_{F.OPT}$ for SOL is high, and the value of $L_{F.OPT} : r$ is low, which would indicate that most of the force-length relationship would be used. However, there is a fairly high amount of variability in the values reported for $L_{F.OPT} : r$ by Maganaris et al. (2006). For subjects at the lower end of the range with a value of 0.5 for $L_{F.OPT} : r$ the maximum joint range of motion that would be allowed by the force-length relationship assuming the width of the force-length relationship is 0.56 would be 0.56 radians or 32 degrees according to Equation 12. At the other end of the range, a subject with a value of 1.5 for $L_{F.OPT} : r$, assuming an ankle joint range of motion of 60 degrees, would use only 62% of the force-length relationship (these values are used for the soleus in Figure 9). One of the problems with modelling the soleus is that pennate muscle fibres have a long aponeurosis. The length of this aponeurosis is included in the estimate of the tendon resting length given by Hoy et al. (1990), yet the fact that the muscle belly extends along the series elastic component instead of sitting on top reduces the effective value of $L_{TR} : L_{F.OPT}$. This would mean that SOL would be likely to operate over only part of the force-length relationship for most of the values of $L_{F.OPT} : r$ quoted by Maganaris et al. (2006) (Figure 9). Whether the muscle operates over the ascending or descending limb would be affected by the values of θ and c. Magnusson et al. (2001) report values of 0.044 - 0.056 for c. Increasing tendon compliance would shift the expressed section of the force-length relationship to shorter lengths as is shown in Figure 9. Given the long Achilles tendon and its relatively high strain value it would be expected that the majority of individuals would operate over the ascending limb. Nevertheless, Figures 6 and 7 demonstrate that it is possible that individuals with long SOL muscle bellies, and therefore lower effective values of $L_{TR} : L_{F.OPT}$, and tendons at the stiffer end of the range could still use the descending limb.

The muscles ECRB, BR, and VL have intermediate values for $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$, low tendon compliance and low to intermediate pennation angles making it likely that these muscles operate over one limb or only the plateau region of the force-length relationship. Lieber & Friden (1998) measured ECRB sarcomere lengths using laser diffraction and muscle fibre lengths at different joint angles, and calculated from results averaged across 12 subjects that, in agreement with the present findings, the ECRB operated over only one limb of the force-length relationship: the descending limb.

There are several implications of the finding that some muscles may operate over different limbs of the force-length relationship in different subjects, but that other muscles may not demonstrate variability. When using muscle models in forward dynamics simulations of movement, researchers often use parameter values taken from the literature. These may result in the modelled muscle operating over one or other of the limbs of the force-length relationship. However, in some muscles such as the brachialis the muscle could theoretically operate over either limb or the plateau depending on the subject specific anatomical features of the muscle-tendon complex. This implies that when using Hill-type muscle models it would be sensible to consider whether the muscles could potentially operate over different limbs since this may change the optimal solution.

A second implication arises from the finding that some muscles may exhibit sport-specific or functional specialisations, for example Herzog et al. (1991b) and Savelberg and Meijer (2003). These studies showed that the expressed section of the force-length relationship was different for runners and cyclists, such that cyclists tended to be stronger at short rectus femoris lengths (i.e., they exhibited a negative gradient to the force-length curve indicating that they operated over the descending limb), whereas the runners were stronger at longer rectus femoris lengths (i.e., they exhibited a positive gradient to the force-length curve indicating that they operated over the ascending limb). It is not known whether this specialisation arises from genetically controlled factors such as tendon length, which would affect the ratio of tendon slack length to fibre optimum length, or whether it arises from training induced adaptations such as the addition or removal of sarcomeres to change the muscle fibre optimum length or changes in tendon stiffness. Nevertheless, it would seem that for muscles such as the soleus where the values of the $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ and *c* found for this muscle in vivo, that the scope for such specialisation is limited. Conversely, for a muscle such as brachialis, with its typically more moderate values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ and *c*, there would be more scope for specialisation in which limb of the force-length relationship is used.

Finally, the expression of the force-length relationship has implications for the motor control of movement. For example, the equilibrium point hypothesis (e.g. Feldman and Latash, 2005) relies on the assumption that muscle force increases with muscle length, i.e. that all muscles work on the ascending limb of the force-length relationship. However, the present results suggest some muscles use the whole of the force-length relationship whereas others use only the plateau region. Inter-subject differences in the expression of the force-length relationship should also be considered when training or rehabilitating muscle (Savelberg and Meijer, 2003), and when identifying candidates for surgical procedures (Orendurff et al., 2002).

In conclusion, the values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ seem important in determining the likely inter-individual variability in the expressed section of the force-length relationship. High values of $L_{F.OPT} : r$ and low values of $L_{TR} : L_{F.OPT}$

result in a muscle that operates over the plateau section. Low values of $L_{F.OPT} : r$ and high values of $L_{TR} : L_{F.OPT}$ result in a muscle that uses the whole of the force-length relationship. Intermediate values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ allow a muscle to operate over one or other limb of the force-length relationship. Whether this is likely to be the ascending limb or the descending limb is then determined by the exact values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ and the values of the remaining parameters: ϕ, θ and c. It appears on the basis of values reported for these parameters in the literature that there is scope for inter-individual variation in the values of these parameters for different human muscles, and that some inter-individual variability in the expressed section of the force-length relationship is possible, particularly for muscles with intermediate values of $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$.

FIGURES

Figure 1: The essential elements of the muscle model, including the A) series elastic component, B) force-length properties, and C) overall model structure. Where F_M – force produced by the muscle fibres, q - current active state of muscle ($0 \leq q \leq 1$), F_{MAX} - maximum isometric force possible by muscle, $F_L(L_F)$ - fraction of maximum isometric force muscle can produce at current length (L_F), L_T - the current length of the tendon, L_{TR} - the resting length of the tendon, c - extension of tendon at F_{MAX} expressed as fraction of tendon resting length, $L_{F.OPT}$ - optimum length of muscle fibre, w - parameter indicating width of force-length curve, T – thickness of muscle, L_{MT} – length of muscle-tendon complex, θ – pennation angle, and F_T is the force in the tendon.

Figure 2: The effect of varying ratio of optimum fibre length to moment arm length ($L_{F.OPT} : r$) for a moment arm that is constant through the range of motion.

Figure 3: The effect of varying the ratio $L_{TR} : L_{F.OPT}$ with ϕ equal to 75 degrees and $L_{F.OPT} : r$ equal to a) three, and b) five.

Figure 4: The effect of varying the ratio $L_{TR} : L_{F.OPT}$ with ϕ equal to 15 degrees and $L_{F.OPT} : r$ equal to a) three, and b) five.

Figure 5: The effect of varying the ϕ parameter throughout the range of motion. The ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ were set to 3, c and θ were set to zero.

Figure 6: The effect of varying tendon extension at maximum isometric force (c) from 0 to 0.08 for a muscle with ϕ set to 45 degrees. The ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ were set to 3, and θ was set to zero.

Figure 7: The effect of varying tendon extension at maximum isometric force (c) from 0 to 0.08 for a muscle with ϕ set to 0 degrees. The ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ were set to 3, and θ was set to zero.

Figure 8: The effect of muscle fibre pennation angle (θ) with the ratios $L_{F.OPT} : r$ and $L_{TR} : L_{F.OPT}$ set at 3, c set at 0 and ϕ set at a) 75 degrees, and b) 15 degrees.

Figure 9: The values from Table 1 for soleus and short head (SH) of biceps femoris have been used to plot the predicted expressed section of the force-length relationship. A range of motion of 60 degrees has been used for the soleus and 120 degrees for the short head of biceps femoris. The ϕ parameter for both muscles has been set at the mid-point of the range of motion, but the expressed section is shifted for the soleus due to its longer, more compliant tendon.

TABLES

Table 1: Model parameter values for the soleus (SOL), vastus lateralis (VL), short head of the biceps femoris (SH BF), brachialis (BR) and extensor carpi radialis brevis (ECRB).

Table 2: Values of fixed parameters and range of values used for the parameter under investigation for each simulation reported.

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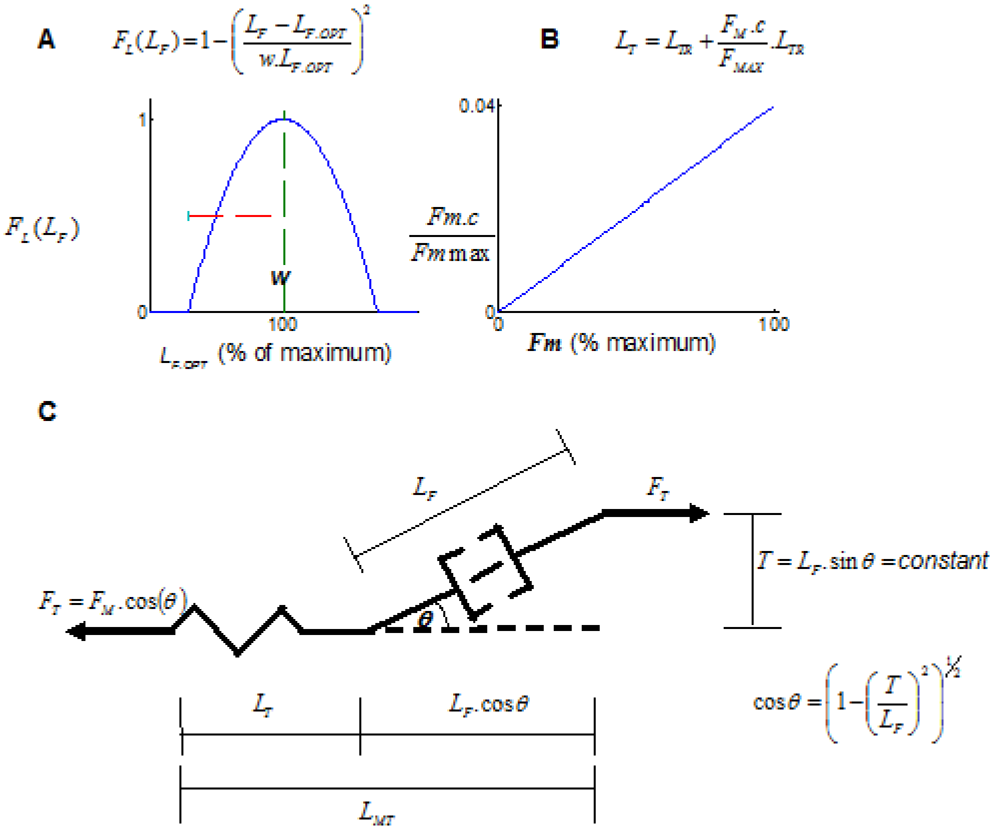
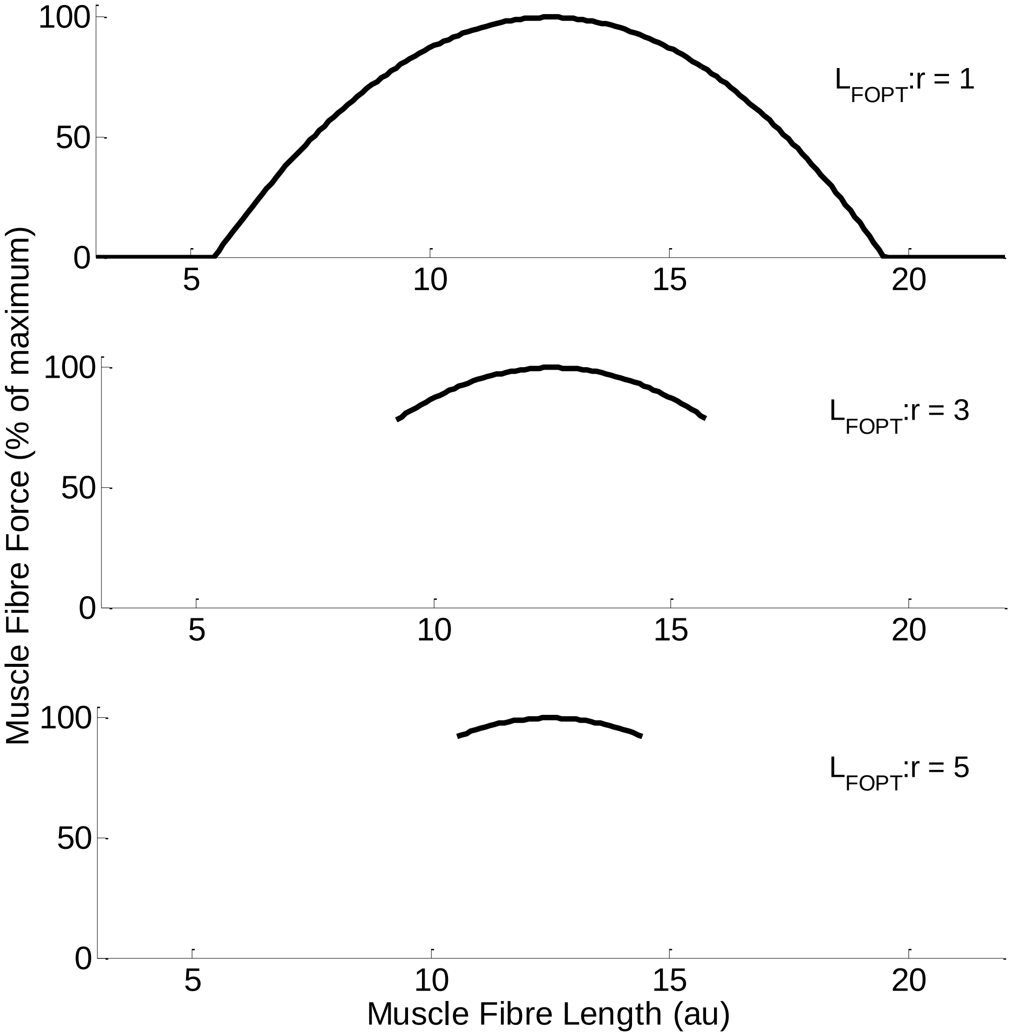
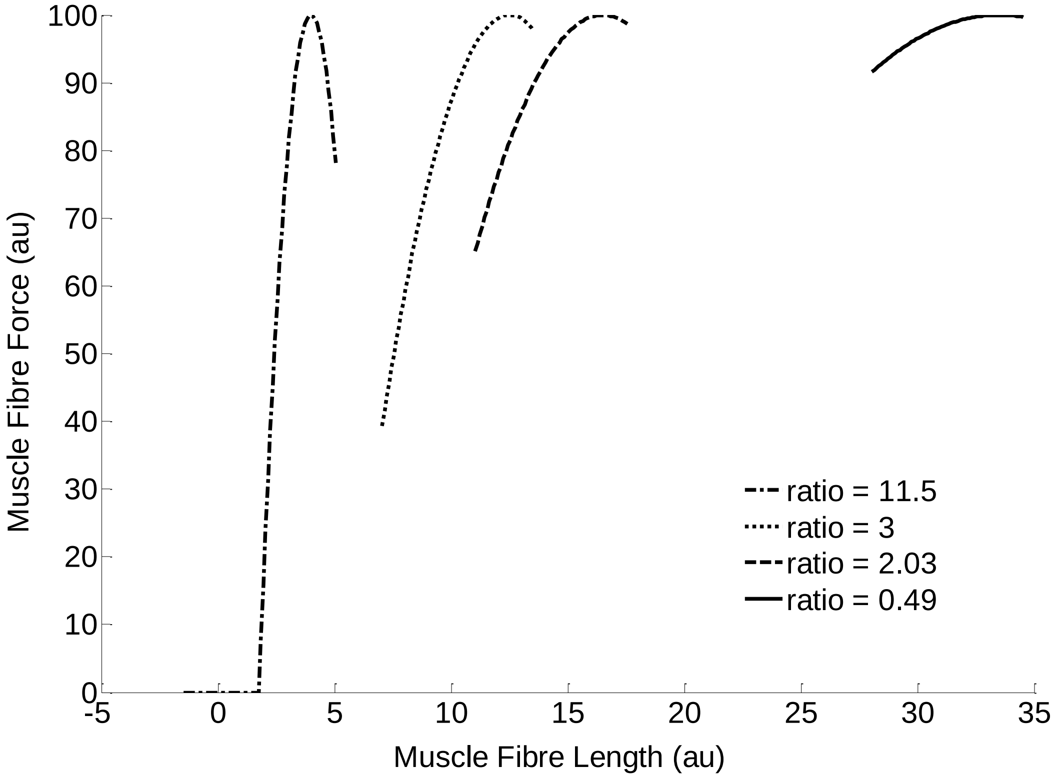

A
$F_L(L_F) = 1 - \left(\frac{L_F - L_{F.OPT}}{w.L_{F.OPT}}\right)^2$
$F_L(L_F)$
1
0
W
100
$L_{F.OPT}$ (% of maximum)
B
$L_T = L_{TR} + \frac{F_M.c}{F_{MAX}}.L_{TR}$
0.04
$\frac{Fm.c}{Fm\max}$
0
0
100
Fm (% maximum)
C
L_F
F_T
$T = L_F.\sin\theta = constant$
$F_T = F_M.\cos(\theta)$
θ
L_T
$L_F.\cos\theta$
$\cos\theta = \left(1 - \left(\frac{T}{L_F}\right)^2\right)^{1/2}$
L_{MT}

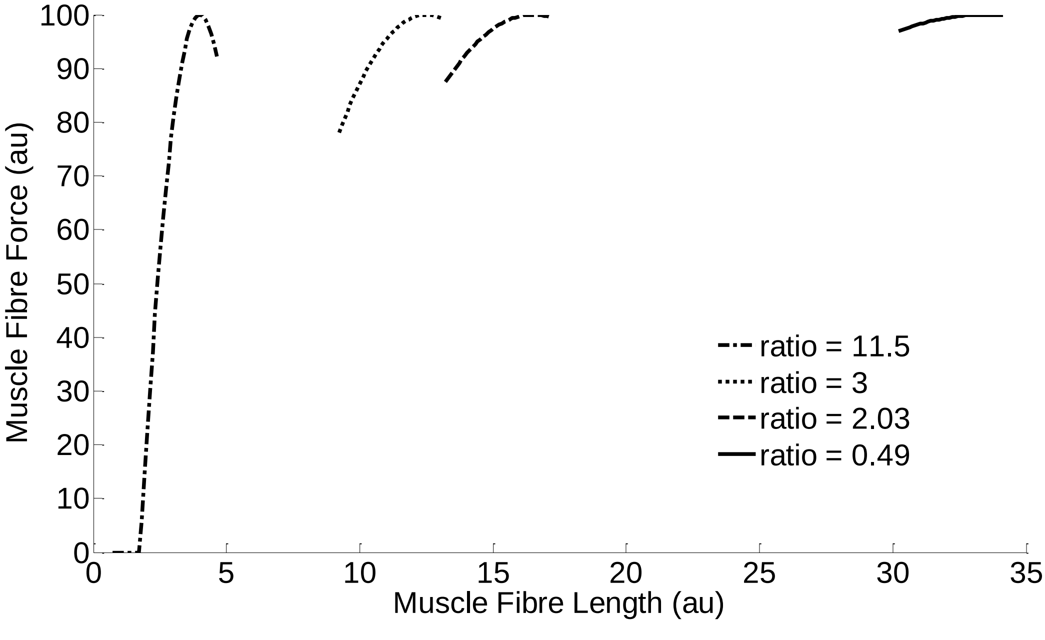

100
50
0
5
10
15
20
L_{FOPT}:r = 1
100
50
0
5
10
15
20
L_{FOPT}:r = 3
100
50
0
5
10
15
20
L_{FOPT}:r = 5
Muscle Fibre Force (% of maximum)
Muscle Fibre Length (au)

a)



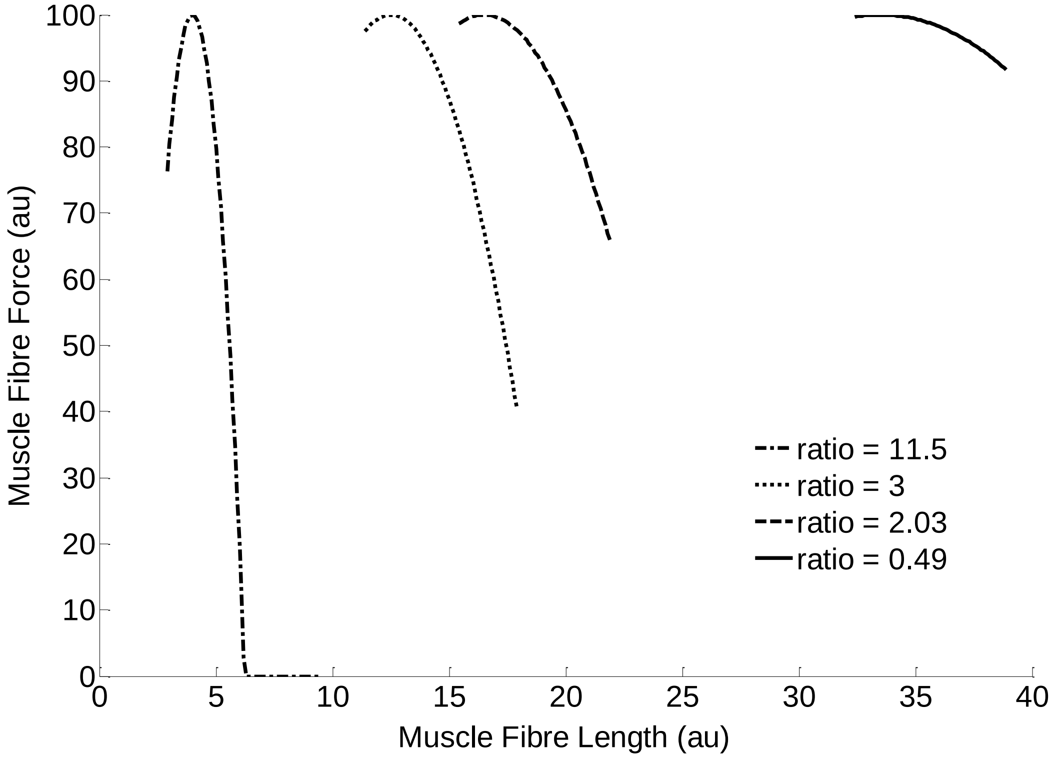
Muscle Fibre Force (au)
0
10
20
30
40
50
60
70
80
90
100
-5
0
5
10
15
20
25
30
35
Muscle Fibre Length (au)
ratio = 11.5
ratio = 3
ratio = 2.03
ratio = 0.49

b)



Muscle Fibre Force (au)
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25
30
35
Muscle Fibre Length (au)
ratio = 11.5
ratio = 3
ratio = 2.03
ratio = 0.49

a)


Muscle Fibre Force (au)
100
90
80
70
60
50
40
30
20
10
0
0
5
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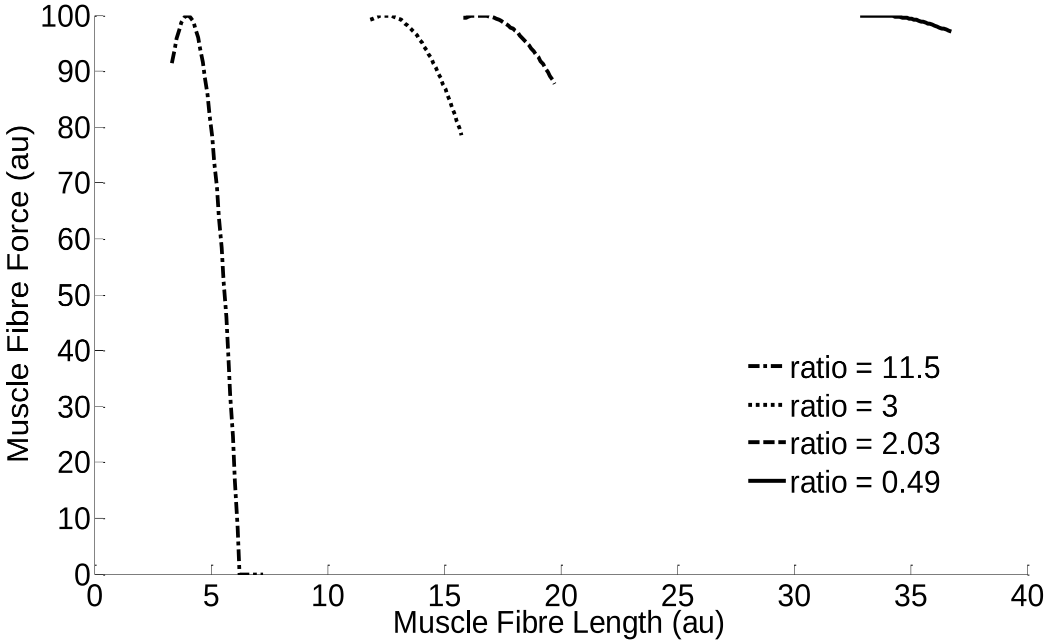
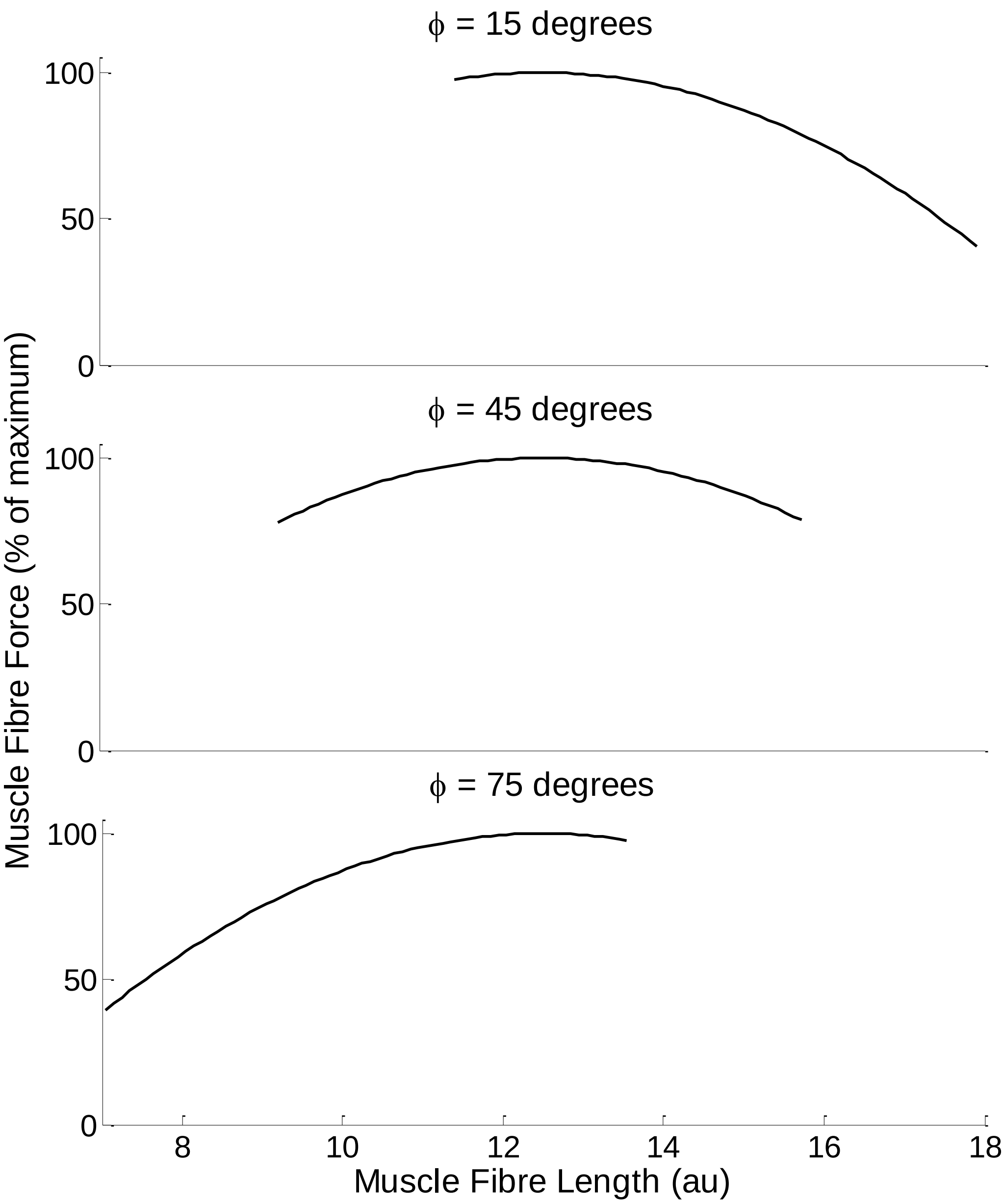
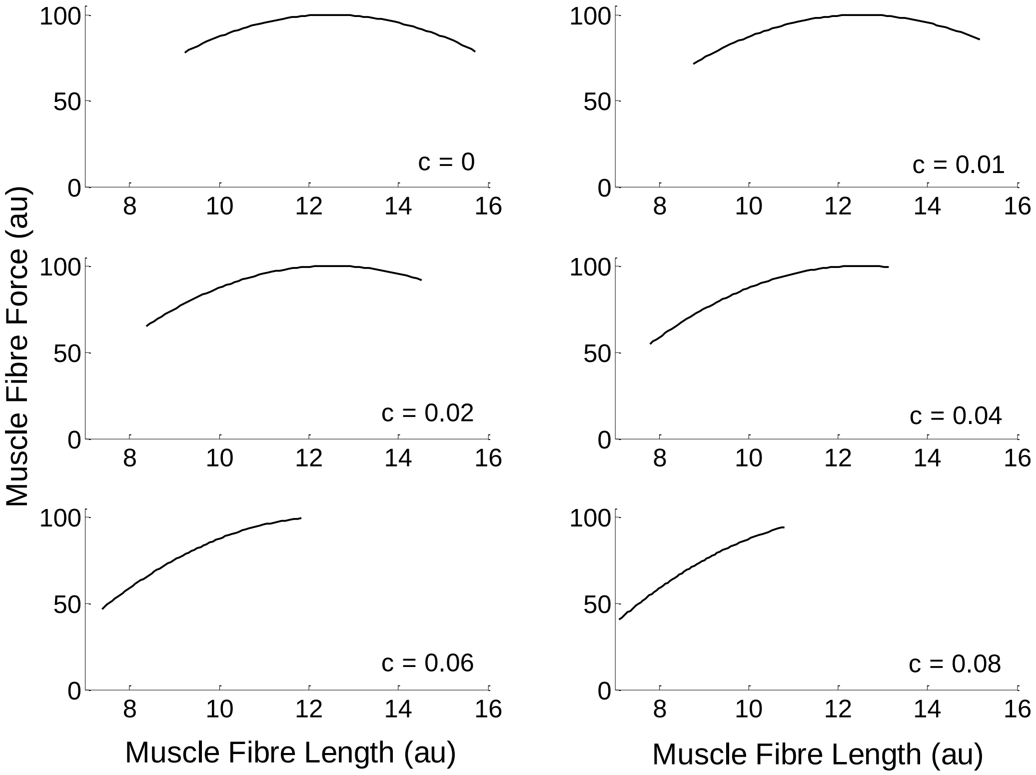
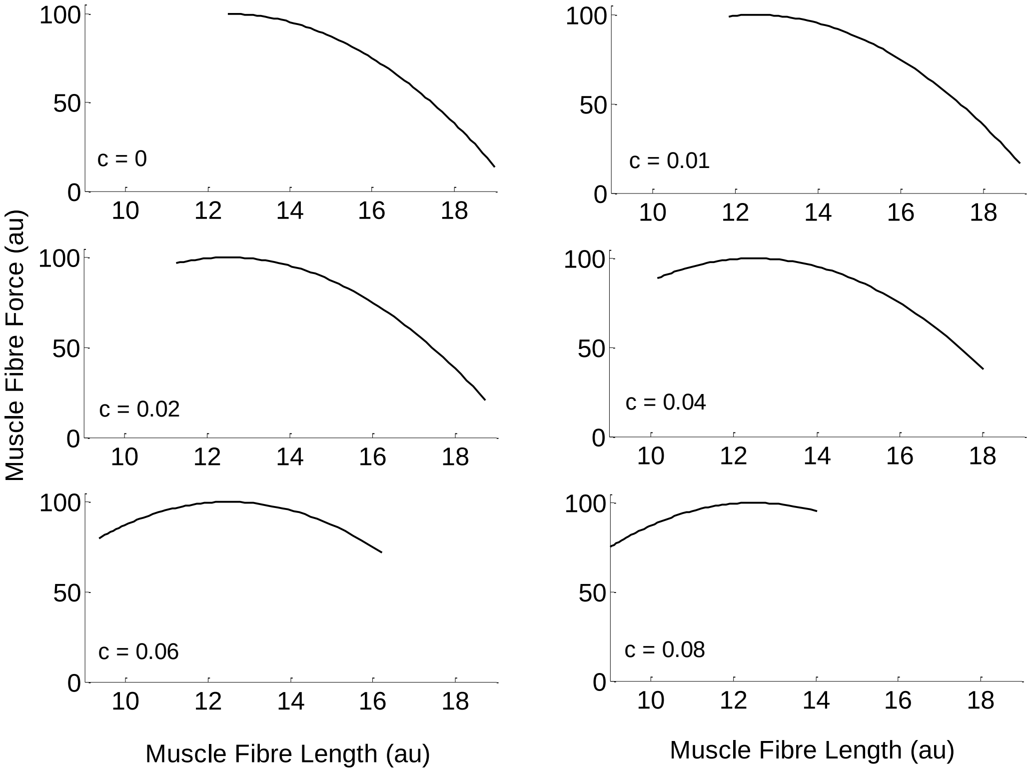
25
30
35
40
Muscle Fibre Length (au)
ratio = 11.5
ratio = 3
ratio = 2.03
ratio = 0.49

b)

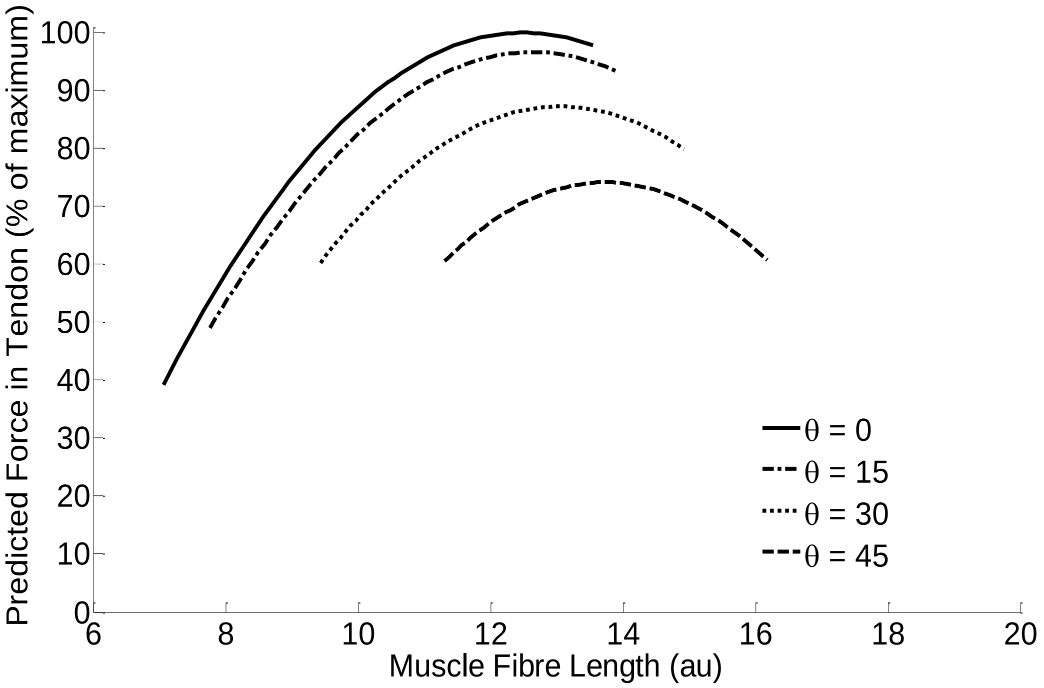

Muscle Fibre Force (au)
100
90
80
70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
35
40
Muscle Fibre Length (au)
ratio = 11.5
ratio = 3
ratio = 2.03
ratio = 0.49


ϕ = 15 degrees
ϕ = 45 degrees
ϕ = 75 degrees
Muscle Fibre Force (% of maximum)
100
50
0
8
10
12
14
16
18
Muscle Fibre Length (au)

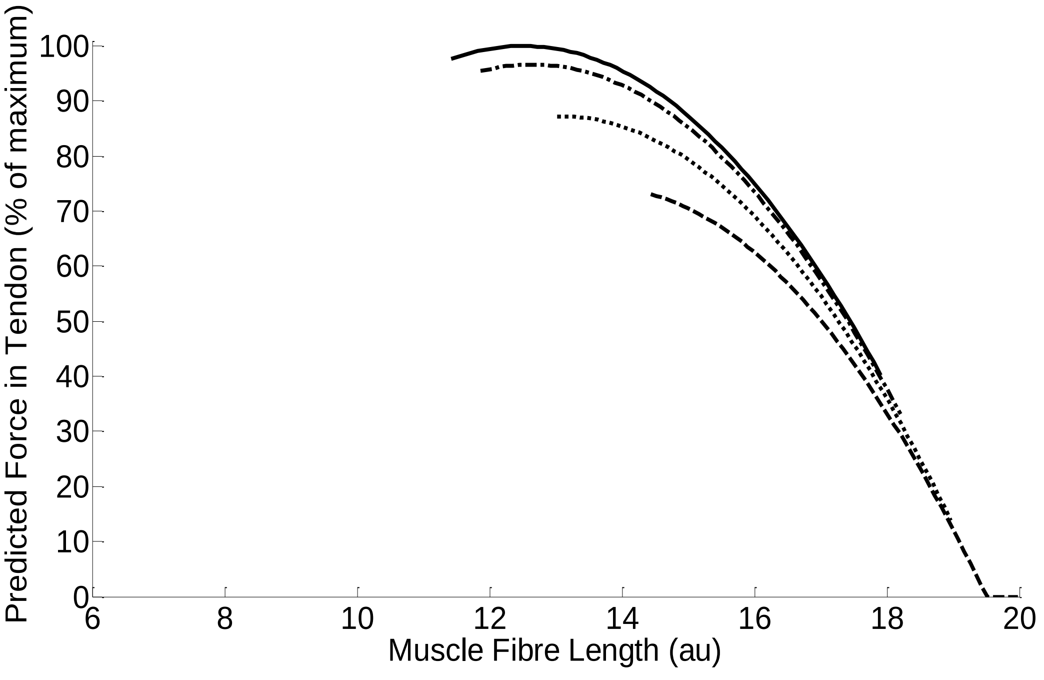

Muscle Fibre Force (au)
100
50
0
8
10
12
14
16
c = 0
c = 0.01
c = 0.02
c = 0.04
c = 0.06
c = 0.08
Muscle Fibre Length (au)
Muscle Fibre Length (au)


Muscle Fibre Force (au)
c = 0
c = 0.01
c = 0.02
c = 0.04
c = 0.06
c = 0.08
100
50
0
10
12
14
16
18
Muscle Fibre Length (au)
Muscle Fibre Length (au)

a)


Predicted Force in Tendon (% of maximum)
0
10
20
30
40
50
60
70
80
90
100
6
8
10
12
14
16
18
20
Muscle Fibre Length (au)
θ = 0
θ = 15
θ = 30
θ = 45

b)


Predicted Force in Tendon (% of maximum)
0
10
20
30
40
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60
70
80
90
100
6
8
10
12
14
16
18
20
Muscle Fibre Length (au)

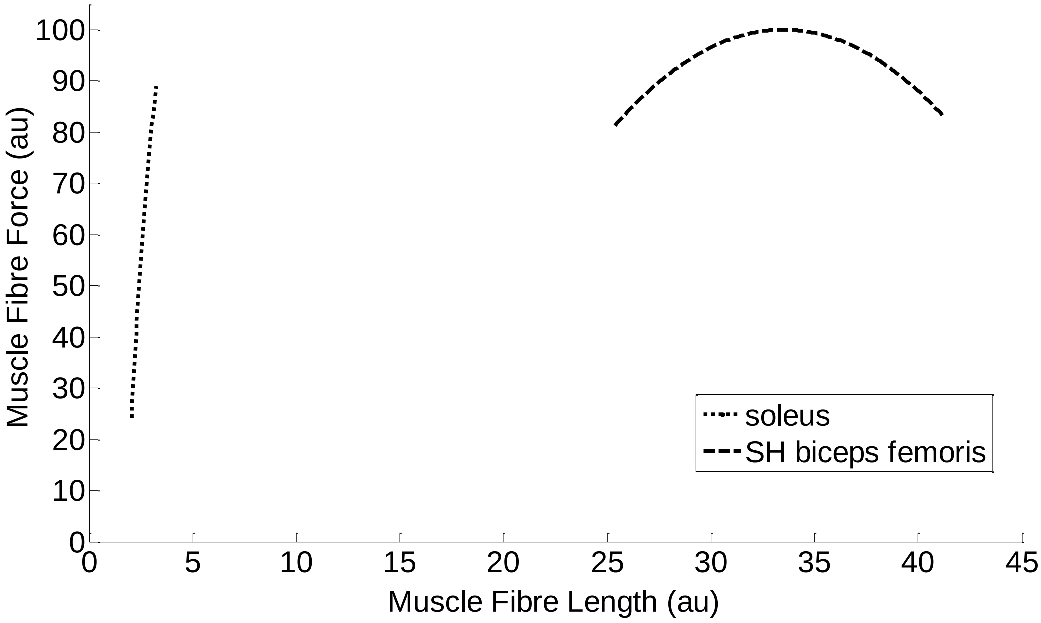
Muscle Fibre Force (au)
100
90
80
70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
35
40
45
Muscle Fibre Length (au)
soleus
SH biceps femoris

Table 1: Model parameter values for the soleus (SOL), vastus lateralis (VL), short head of the biceps femoris (SH BF), brachialis (BR) and extensor carpi radialis brevis (ECRB).

Parameter	Muscle	Range of parameter values used	Sources from which range of parameter values were taken
θ (degrees)	SOL	9-35	Morse et al. (2005)
	VL	7-33	Kawakami et al. (2006)
	SH BF	0 - 25	Alexander and Vernon (1975) & Wickiewicz et al. (1983)
	BR	6.5-12.9	Herbert and Gandevia (1995)
	ECRB	5-13	Lieber et al. (1990)
c	SOL	0.044 – 0.056	Magnusson et al. (2001)
	VL	0.01	Wickiewicz et al. (1983) & Pierrynowski & Morrison (1985)
	SH BF	0.01 – 0.02	Wickiewicz et al. (1983) & Pierrynowski & Morrison (1985)
	ECRB	0.0199	Loren & Lieber (1995)
$L_{TR} / L_{F.OPT}$	SOL	11.25	Hoy et al. (1990)
	VL	2.68	Hoy et al. (1990)
	SH BF	0.52	Hoy et al (1990)
	BR	3.0 5.87	Winters and Stark (1988) Garner and Pandy (2003)
	ECRB	2.89	Loren et al. (1996)
$L_{F.OPT} / r$	SOL	0.5-1.5	Maganaris et al. (2006)
	VL	1.5-2.4	Maganaris et al. (2006)
	SH BF	4.39	Hoy et al. (1990)
	BR	1.6-7.56	Ettema et al. (1998) & Garner & Pandy (2003)
	ECRB	3.62	Loren et al. (1996)

Table 2: Values of fixed parameters and range of values used for the parameter under investigation for each simulation reported.

Parameter varied	Relevant figures	Values used				
		$L_{F.OPT} : r$	$L_{TR} : L_{F.OPT}$	ϕ (degrees)	c	θ (degrees)
$L_{F.OPT} : r$	Figure 2	Varied from 0.5 to 5	3.0	45	0.04	0
$L_{TR} : L_{F.OPT}$	Figures 3 and 4	3 and 5	Varied from 0.49 to 11.5	15	0	0
ϕ	Figure 5	2	3	0 to 90 in steps of 15 degrees	0	0
c	Figures 6 and 7	3	3	45 and 0	Varied from 0 to 0.08	0
θ	Figure 8	3	3	15 and 75	0	0 to 45 degrees