

Optimal muscle fascicle length and tendon stiffness for maximising gastrocnemius efficiency during human walking and running

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Abstract

Muscles generate force to resist gravitational and inertial forces and/or to undertake work, e.g. on the centre of mass. A trade-off in muscle architecture exists in muscles that do both; the fibres should be as short as possible to minimise activation cost but long enough to maintain an appropriate shortening velocity. Energetic cost is also influenced by tendon compliance which modulates the timecourse of muscle mechanical work. Here we use a Hill-type muscle model of the human *medial gastrocnemius* to determine the muscle fascicle length and Achilles tendon compliance that maximise efficiency during the stance phase of walking (1.2 m/s) and running (3.2 and 3.9 m/s). A broad range of muscle fascicle lengths (ranging from 45 to 70 mm) and tendon stiffness values (150–500 N/mm) can achieve close to optimal efficiency at each speed of locomotion; however, efficient walking requires shorter muscle fascicles and a more compliant tendon than running. The values that maximise efficiency are within the range measured in normal populations. A non-linear toe-region of the tendon force–length properties may further influence the optimal values, requiring a stiffer tendon with slightly longer muscle fascicles; however, it does not alter the main results. We conclude that muscle fibre length and tendon compliance combinations may be tuned to maximise efficiency under a given gait condition. Efficiency is maximised when the required volume of muscle is minimised, which may also help reduce limb inertia and basal metabolic costs.

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1. Introduction

There is a trade-off in muscle architecture between a muscle being energetically economical at resisting force or at performing work during a contraction. The cost of generating force is a direct function of fibre length (and hence the number of activated sarcomeres in series). Force-generating muscles therefore have short fibres. This also acts to increase the cross-sectional area per unit volume and hence force producing capacity of the muscle. Muscles have to generate forces at a range of lengths in a movement. This defines a minimum fibre length, though in many human locomotor muscles much of the length change will occur in series elastic components rather than the muscle fibres. Muscles also need to generate force whilst shortening to

perform mechanical work. Here, due to the force velocity relationship, a longer fibre can achieve the same absolute fibre velocity with a lower sarcomere velocity and a higher fibre force. In addition, maximum power output is achieved at approximately one third of maximum shortening velocity (V_{max}) and efficiency is greatest at velocities of about one-quarter of V_{max} (Alexander, 1997, 2002; Hill, 1950; Hof et al., 2002; Woledge et al., 1985). It is therefore energetically sensible for a muscle fibre to shorten between one-quarter and one-third of V_{max} during movements where a muscle is required to do mechanical work. This favours longer fibres with a length concomitant with the maximum velocity (and force) required of the fibre.

In a muscle which must both generate isometric force and undertake work (e.g. a limb extensor), there is a trade-off where short fibres reduce activation cost but long fibres reduce the sarcomere shortening velocity for any given shortening speed. A third factor is that if a muscle is

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contracting slowly and around optimal length it can have a higher force and hence the muscle can have a smaller activated physiological cross-sectional area (PCSA) and can therefore be smaller and hence lighter, which reduces limb inertia and basal metabolic costs (Rall, 1985). There should therefore be an energetic optimum where the required volume is a minimum.

Series elastic tissue, specifically the tendon and the aponeurosis sheets in the muscle, also aid muscle versatility. Legs appear as springs during running and most of the muscle tendon unit (MTU) length change occurs in series elastic tissues (Biewener et al., 1998; Roberts et al., 1997; Wilson et al., 2003). We have shown in human running that the medial gastrocnemius (MG) fascicles shorten at a velocity concomitant with maximum power (one third of V_{max}) whilst the MTU is shortening three times faster; i.e. at fascicle V_{max} (Lichtwark and Wilson, 2006). In addition, we have used relatively simple models to demonstrate that the Achilles tendon (AT) is of appropriate stiffness to maximise *gastrocnemius* efficiency during locomotion in average, young adults (Lichtwark and Wilson, 2007). This research also showed that increasing or decreasing the stiffness of tendons beyond that of the average stiffness would reduce the efficiency of the muscle. However, AT stiffness varies substantially between individuals (Hof, 1997; Lichtwark and Wilson, 2006; Maganaris and Paul, 2002). Does this imply that some individuals may have substantially less efficient muscle than others? This is unlikely, because individuals may also have different muscle properties that are not accounted for in the previous model. For instance, individuals also have varied muscle fascicle lengths and volumes, which both influence the force producing capacity and efficiency of a muscle.

Fascicle length, muscle volume and tendon stiffness differ between individuals with different sporting histories (Arampatzis et al., 2006; Muraoka et al., 2005; Roy and Edgerton, 1992). It would be logical if these differences reflect an optimum for an athlete's chosen sport but it is not clear whether muscle architecture defines the sport an athlete will be best at or whether the architecture reflects the outcome of long-term training. Here we determine the influence of human *MG* fascicle length and AT stiffness on muscle efficiency for walking and running. We assume that kinematics and kinetics (and hence MTU force and length over time) do not change and vary fascicle length and tendon stiffness of a Hill type muscle model representing the MG. This allows us to determine the active muscle volume required to generate the muscle force for a given fascicle velocity and calculate the metabolic cost incurred by the muscle to undertake the movement. Our hypothesis is that there is an optimum combination of fascicle length and tendon stiffness which maximises efficiency and minimises activated muscle volume for each gait type. Due to the differences in power, force and velocity required from the muscle at each gait and speed, we expect the optimal fascicle length and tendon stiffness combination to be different for each gait.

2. Materials and methods

2.1. Kinematic and kinetic data

Average sagittal plane ankle and knee joint angles and ankle joint moments for walking (1.2 m/s), running (3.2 m/s) and fast running (3.9 m/s) were digitised from Novacheck (1998) and filtered using a zero-phase shift, fourth order, 15 Hz low pass Butterworth filter. Ankle and knee angles were used to estimate the MG MTU strain using the polynomial equations of Grieve and colleagues (1978). The moment arm of the AT at the ankle joint for each angle of dorsi/plantar flexion was estimated using the slope of the muscle length versus ankle joint angle curve (An et al., 1981). AT force was calculated by dividing the ankle joint moment by the moment arm. MG strain and AT force during the stance phase of each gait (Fig. 1) were used as inputs to a muscle model to calculate required activation levels and muscle fascicle shortening velocities for a range of AT compliance levels and muscle fascicle length.

2.2. Modelling the influence of tendon compliance and muscle length

We used a Hill type muscle model to determine the required activation of the MG muscle during walking, running and fast running. The model, described in detail in Lichtwark and Wilson (2007), consists of a contractile element (CE), a series elastic element (SEE) and a parallel elastic element (PEE). The PEE was assumed to act in parallel with the CE only. MTU length at zero strain was assumed to be equal to the average length of the Achilles tendon (237 mm) plus the average length of the MG muscle fascicles (55 mm) in adults (Lichtwark and Wilson, 2006). Many of the calculations performed here are very similar to those documented in Lichtwark and Wilson (2007); however, here we examined the influence of varying L_O , which ultimately influences the maximum force of the muscle (F_{max}), the length of the SEE (L_{SEE}) and also the rate of heat production.

The model was subjected to the force and length changes recorded during the stance phase of walking, running and fast running. For each modelled tendon stiffness value, we first calculated the required SEE and CE length change at each time instant of the stance phase. This was achieved with knowledge of the MTU strain and Achilles tendon force (Fig. 1) at each time instant. The length change of the SEE was calculated with knowledge of the Achilles force and the force length relationship of the AT:

$$L_{SEE} = L_{SEE_Slack} + \Delta L_{SEE}, \quad (1)$$

where L_{SEE} is the length of the SEE, L_{SEE_Slack} is the slack length of the SEE, ΔL_{SEE} is length change of the SEE, which is a function of the force in the AT (F_{AT}). For a

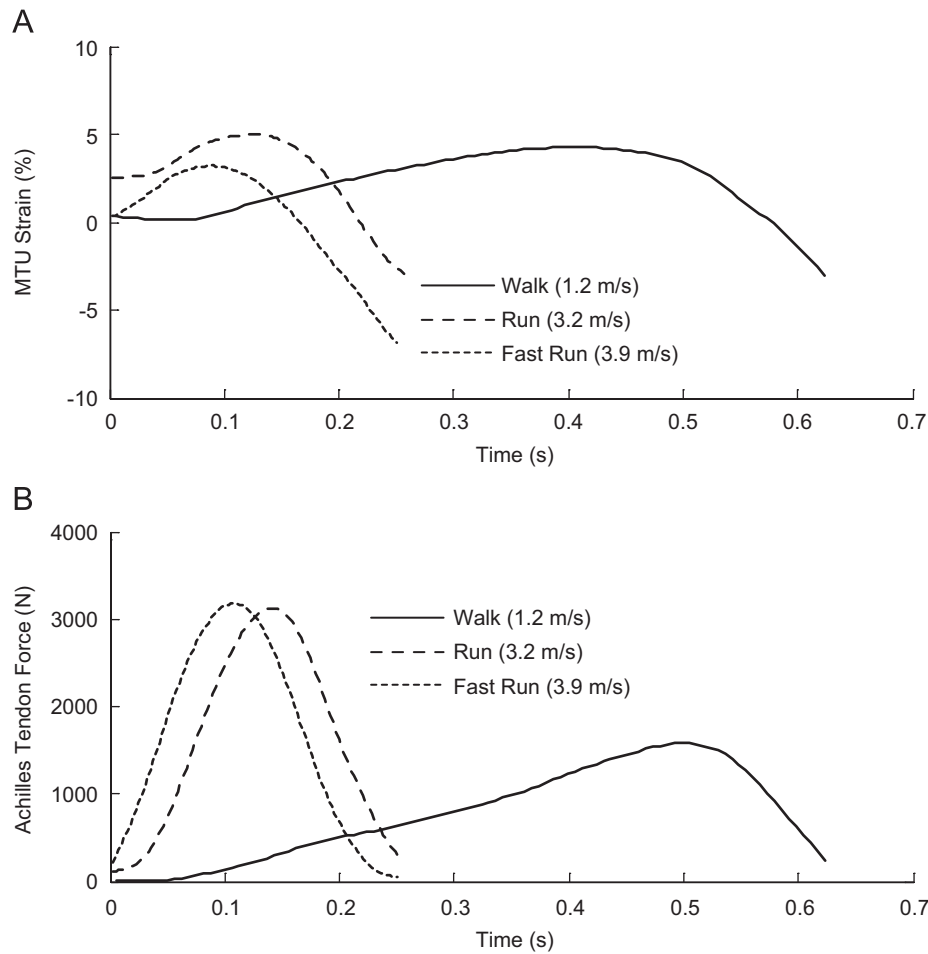


Fig. 1. Muscle tendon unit (MTU) strain and Achilles tendon force during walking, running and fast running calculated from the data of Novacheck (1998). These data were used as an input into the model.

tendon with a linear stiffness:

$$\Delta L_{SEE} = \frac{F_{AT}}{k_L}, \quad (2)$$

where k_L is linear stiffness of the AT.

Unlike in the previous manuscript (Lichtwark and Wilson, 2007), in this study we also examine the influence of having a non-linear force–length relationship at low forces. To achieve this, stiffness was varied as function of the force applied using an exponentially rising function which plateaus at required linear stiffness (Fig. 2A) with the following relationship:

$$k_N = k_L \left(1 + \left(\frac{0.9}{-e^{((Q \times F_{AT})/F_{MAX_TS})}} \right) \right), \quad (3)$$

where k_N is the stiffness at any given force, k_L is the required stiffness in the linear region, Q is a constant that influences the rate of rise of the stiffness relative to the force (here we set this to 20), F_{AT} is the Achilles tendon force, F_{MAX_TS} is the maximum isometric force of the triceps surae muscle group (≈ 5000 N). By changing k_L we can generate different force–length relationships of the AT for force values ranging from 0 to 5000 N. This function allows us to evaluate ΔL_{SEE} for any given AT force. The

non-linear model has a low stiffness at low forces and rises exponentially with increases in force such that the stiffness plateaus to the constant linear stiffness. This effectively creates a ‘toe-region’ in the force length curve compared to the linear stiffness model. A comparison between the linear stiffness solution and the non-linear solution for three different stiffness values is shown in Fig. 2A and B.

For each value of k_L in both the linear and non-linear stiffness models, we determined the length change of the SEE (ΔL_{SEE}) at each time instant throughout the stance phase. From this the length of the CE can also be calculated as follows:

$$L_{CE} = L_{MTU} - L_{SEE}, \quad (4)$$

where L_{CE} is the length of the CE and L_{MTU} is the length of the MTU. Aponeurosis strain in series with the muscle fascicles was accounted for within the SEE, termed the tendon in this study.

Muscle fascicle velocity (V_{CE}) was calculated as the time derivative of muscle fascicle length normalised to its optimum length and is expressed in L_O/s :

$$V_{CE} = \frac{\Delta L_{CE}}{dt}. \quad (5)$$

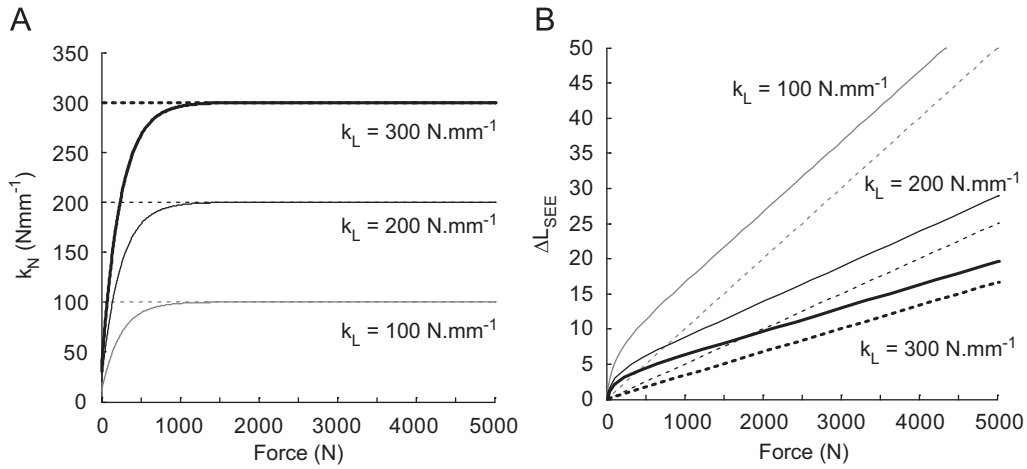


Fig. 2. (A) The relationship between the stiffness of the series elastic element (SEE) relative to the required final linear stiffness and the force applied up to the maximum isometric force of the *triceps surae* muscle group (~ 5000 N). (B) The relationship between the change in SEE length (ΔL_{SEE}) and force for three different stiffness values with both the linear (dashed) and non-linear (solid) relationships.

AT force (F_{AT}) estimations at each time instant in the stance phase were then used to estimate the MG force (F_{MG}). F_{MG} was assumed to contribute to 16% of F_{AT} based on its cross-sectional area relative to the entire *triceps surae* which contribute to AT force (Fukunaga et al., 1992):

$$F_{MG} = 0.16F_{AT}. \quad (6)$$

The passive force produced by the MG PEE (F_{PEE}) was calculated as a function of the CE length, as described by the passive force–length relationship in Fig. 3A. Because the PEE is in parallel with the CE, the active force of the CE (F_{CE}) and the passive force of the PEE (F_{PEE}) must sum to equal that of that entire muscle (F_{MG}). Therefore, F_{CE} can be calculated by subtracting F_{PEE} from F_{MG} :

$$F_{CE} = F_{MG} - F_{PEE}. \quad (7)$$

The required muscle activation at each time instant is equivalent to the proportion of bound cross-bridges within the muscle. This can be calculated by considering the active force–length–velocity relationship of the CE (Fig. 2A and B), which predicts the force capable of being produced by the muscle if the maximum number of cross-bridges are bound. The activation of the muscle can thus be calculated as:

$$\text{Act} = \frac{F_{CE}}{F'}, \quad (8)$$

where Act is the level of activation of the muscle and F' is the maximum force the muscle is capable of producing at a given muscle length and velocity. This assumes a linear scaling of the force–length and force–velocity properties of the muscle with activation (see Section 4). The MG was assumed to have a F_{MAX} of 1290 N (based on PCSA = 43 cm^2 (Fukunaga et al., 1992; Narici et al., 1996), L_O = 55 mm and a maximum isometric stress (σ_{MAX}) of 0.3 MPa; Woledge et al., 1985).

2.3. Energetic model

Muscle energetics were estimated with a phenomenological model based on the Hill type muscle model that predicts heat and work outputs of muscle; such models are prevalent in the literature (Alexander, 1997; Bhargava et al., 2004; Lichtwark and Wilson, 2005b; Umberger et al., 2003). The model we have used has been shown to predict efficiency well in both dogfish and mouse muscle during sinusoidal length changes across a range of different activation and length change conditions (Lichtwark and Wilson, 2005b). The details and equations used in this model, as applied here, are available in the supplementary material of Lichtwark and Wilson (2007). Briefly, this model estimates the rate of heat produced at any given activation level, length and shortening velocity. With increases in both shortening velocity and activation, the rate of heat output also increases in a relatively linear manner (see Fig. 3D for relationship between fascicle velocity, activation and rate of heat production). At each time instant, the approximate rate of heat production is estimated based on the velocity and total fraction of bound cross-bridges (the product of activation level and the maximum force capable of being produced at a given length) and is also scaled based on the maximum isometric force and the optimum muscle fascicle length. The rate of heat production is then integrated over the period of stance phase to estimate the total heat output associated with the power requirement. The efficiency across the stance phase is then calculated as follows:

$$\text{Efficiency} = \frac{\text{Work}}{\text{Heat} + \text{Work}}. \quad (9)$$

It is difficult to determine whether the energy output is accurate without direct energetic measures, which is a limitation of this modelling technique. However, the general principles of how muscles produce heat in response

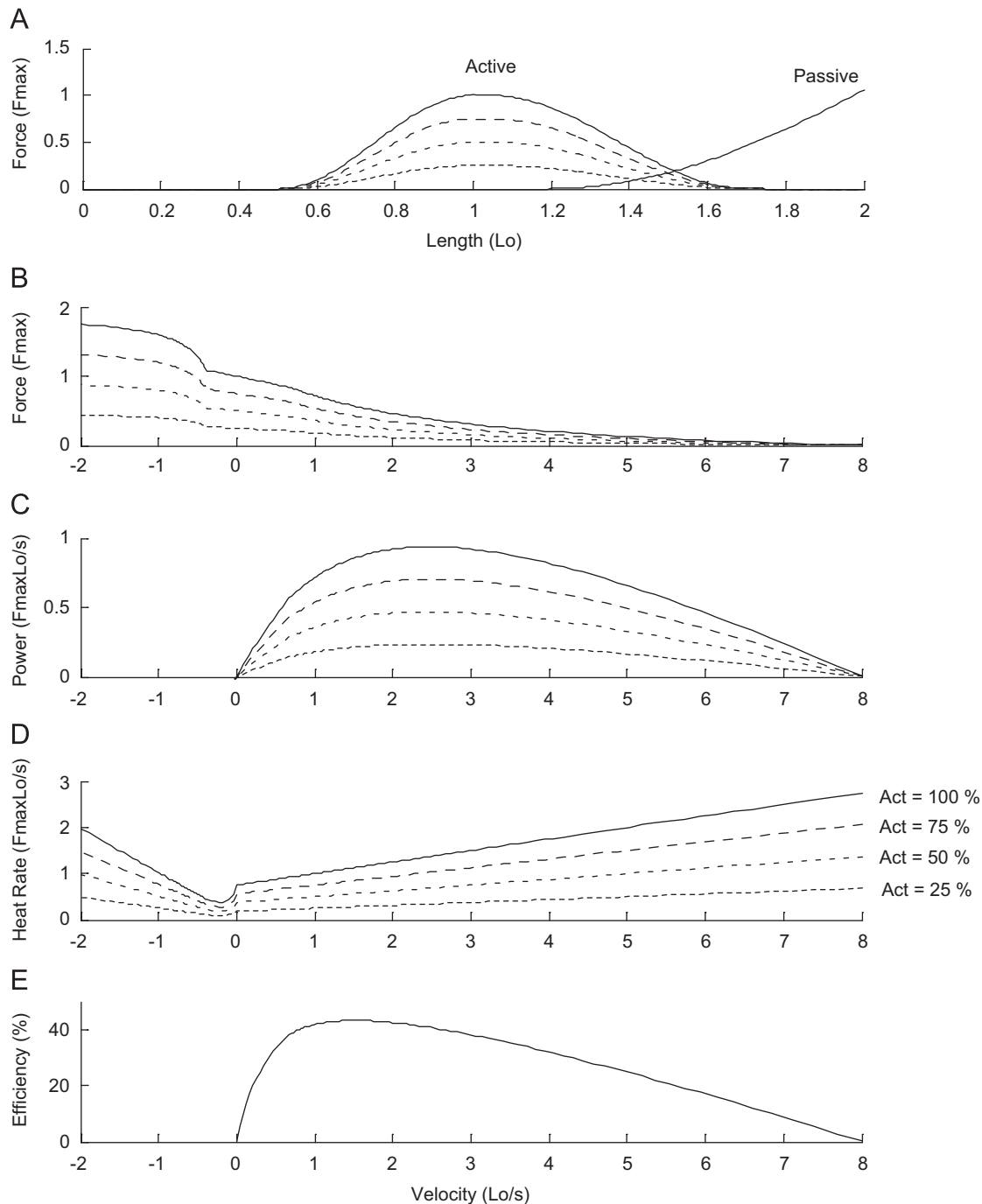


Fig. 3. (A) The active and passive force–length relationship used in the model. Length is expressed relative to the optimum length ($L_0 \sim 55$ mm) and the active curve is scaled linearly with activation level. (B–E) The relationship between muscle fascicle velocity and (B) force, (C) power, (D) heat rate and (E) efficiency for a muscle (assuming optimum fascicle length) with a maximum muscle fascicle velocity of 8 L_0/s . This relationship is also scaled linearly with activation and activation levels (Act) of 100%, 75%, 50% and 25% are shown. (Reprinted from Journal of Biomechanics, 40, Lichtwark & Wilson, Is achilles tendon compliance optimised for maximum muscle efficiency during locomotion?, 1768–1775, with permission from Elsevier.)

to producing force and shortening have been found to be consistent across different species (Woledge et al., 1985). The model ignores fibre type distribution and assumes that muscle fascicle have a constant force–length and force–velocity properties; however, this could be included in the model to determine its influence (Bhargava et al., 2004; Umberger et al., 2003). This simplified model of muscle

energetics resembles that proposed by Alexander (1997), which relates heat and work rates to CE velocity. Here we also take into consideration the number of bound cross-bridges, by scaling these relationships for activation level and CE length. Basal metabolic rates, which increase with increasing muscle volume (Rall, 1985), were ignored for this analysis.

2.4. Model implementation

A range of k_L and L_O values were modelled to determine their influence on energetic cost and efficiency: k_L was varied between 18 and 900 N/mm and L_O was varied between 5.5 and 110 mm. The MTU length at zero strain was constant (292 mm); therefore, changes in L_O changed the SEE slack length but not the stiffness. The maximum isometric force capacity of the muscle was determined based on the following relationship between L_O and maximum isometric force:

$$F_{MAX} = \sigma_{MAX} \left(\frac{\text{Vol}}{L_O} \right), \quad (10)$$

where σ_{MAX} is the maximum isometric stress of the muscle (~ 0.3 MPa, [Woledge et al., 1985](#)), Vol is the volume of the GM muscle. Here we used a muscle volume of 220 cm³ which corresponds to an F_{max} of 1200 N and $L_O = 55$ mm. We calculated the maximum activated volume (MAV) of muscle required with each muscle fascicle length/tendon stiffness combination by multiplying the maximum activation in the stance phase by the volume. Trials that required a MAV over 260 cm³ were disregarded because they would require an activation level greater than 120% at the prescribed muscle volume which is a conservative estimate of MAV that accounts for possible increases in force output due to variation in model parameters. The influence of increasing the muscle volume is discussed further in the discussion.

The SEE was modelled as having a linear stiffness which we varied between 18 and 900 N/mm. The average Achilles tendon stiffness is approximately 180 N/mm, but this can vary substantially across a population ([Hof, 1997](#); [Lichtwark and Wilson, 2005a](#); [Maganaris and Paul, 2002](#)). We also examined the influence of including a non-linear toe-region in the SEE force–length relationship by varying stiffness relative to force.

Both the force–velocity and force–length relationships of the muscle fascicles were chosen to resemble the data of [Hof et al. \(2002\)](#) for the same muscle. These data suggests a V_{max} of approximately 8 L_O/s (~ 0.45 m/s). The data from Hof et al. also demonstrate that the PEE force is low across most of the length range of the muscle fascicle and PEE increases with length for CE lengths greater than $1.2L_O$.

3. Results

[Fig. 4A](#) shows how efficiency is influenced by fascicle length and linear AT stiffness. With increase in speed, it is apparent that a longer muscle fascicle with a stiffer tendon will maximise fascicle efficiency. The model predicts that with optimum architecture efficiency is slightly higher in both running and fast running (40.2% and 40.1%, respectively) than in walking (37.5%). However, a relatively broad range of muscle fascicle lengths and tendon stiffness values can achieve high efficiency ($>25\%$) at all speeds. The influence of having a non-linear stiffness at low

forces (a toe-region) is shown in [Fig. 4B](#). A non-linear stiffness increases the required fibre length and tendon stiffness required to maximise efficiency and also to produce the required power output for each activity.

The relationship between fascicle length, linear AT stiffness (for the linear stiffness model only) and the required muscle volume is shown in [Fig. 5](#). It is apparent that the optimum combination of architectural parameters is similar to that which maximises efficiency (see [Table 1](#)). A greater volume of muscle is required for fast running compared to walking and running for all architectural combinations. Values of L_O and k_L less than 46 mm and 160 N/mm are unable to produce the required power output during fast running without exceeding 120% activation. The range of fascicle length and stiffness values that minimise MAV in each condition is relatively small during running where large volumes of muscle are required with long muscle fascicles (>65 mm) and stiffer tendons (>300 N/mm).

[Fig. 6A](#) and [B](#) presents MTU interaction and the time course of total muscle fascicle energetic output (work + heat) of the MG muscle during walking and fast running with different combinations of muscle fascicle length and tendon stiffness. Supramaximal activations may be required during fast running if the tendon is too compliant (e.g. $k_L = 150$ n/mm) and requires shortening velocities beyond that capable of the muscle; or if the muscle fascicles are too short ($L_O = 40$ mm) and require shortening beyond the range of the force–length characteristics.

4. Discussion

The efficiency of a muscle working in series with a tendon is task specific. We demonstrate that different muscle fascicle lengths and tendon compliance combinations are required to maximise efficiency under different gait conditions and speeds. To maximise efficiency during walking requires shorter muscle fascicles and more compliant tendons than for running. A broad range of muscle fascicle lengths (ranging from 45 to 70 mm) and tendon stiffness values (150–500 N/mm) can, however, achieve close to optimal efficiency at each speed of locomotion. We have also found that minimising the MAV (which is equivalent to minimising the required activation level) also has the effect of simultaneously maximising efficiency. This is because it is effectively selecting for conditions where muscle velocity is low (hence fibre stress is high) and muscle efficiency is highest at relatively low contraction velocities. In addition, the costs of activating muscle are likely to dominate the total energetic costs when the muscle fascicle length and tendon compliance are close to optimal. This suggests that minimising MAV by optimising tendon stiffness and muscle fascicle length may be important in muscle development and design because this also reduces the required volume of muscle which has the added benefits of reducing both limb inertia and basal metabolic costs.

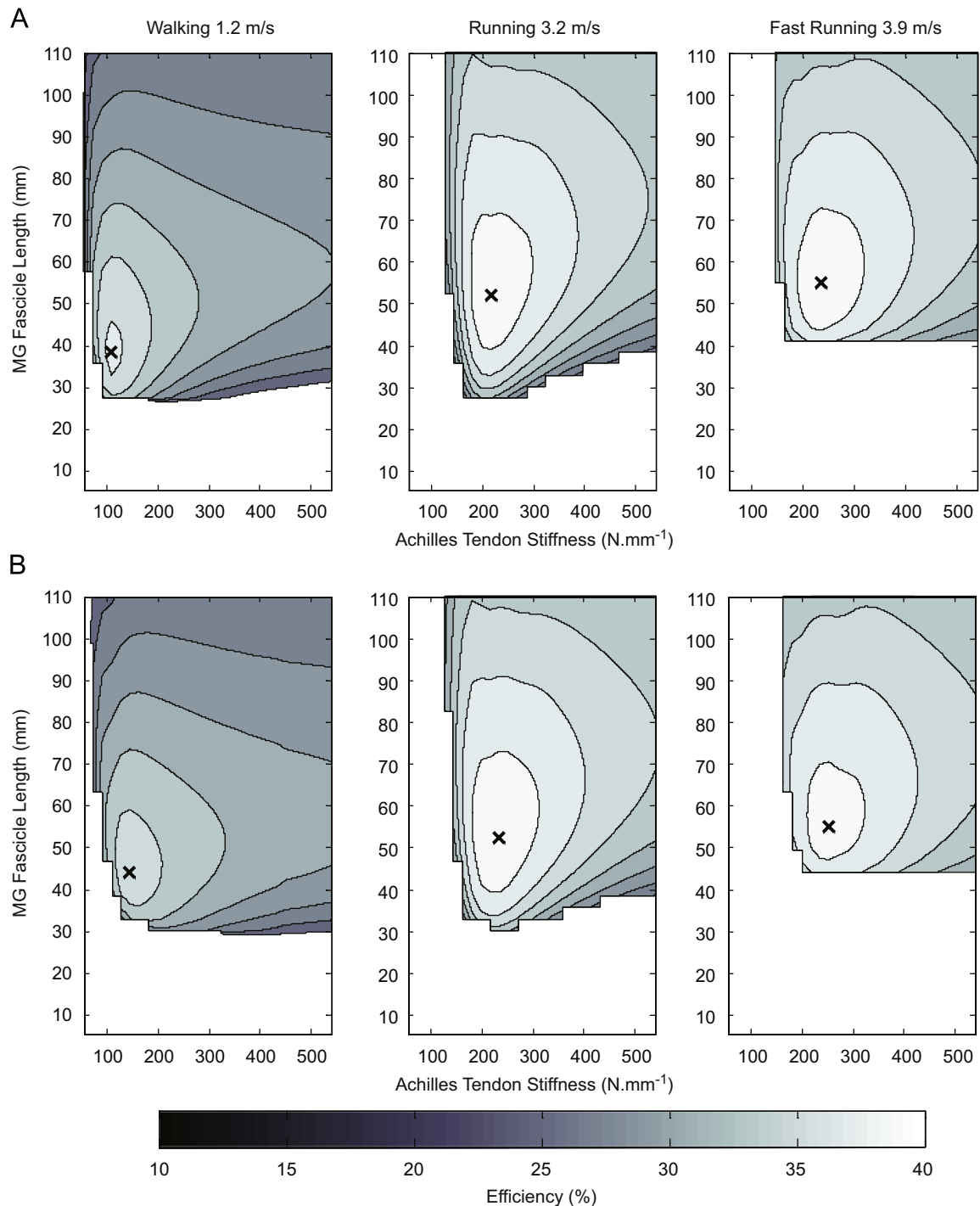


Fig. 4. Contour plots of the relationship between AT stiffness, MG fascicle length and MG muscle fascicle efficiency for different gait conditions assuming: (A) linear tendon stiffness and (B) non-linear tendon stiffness (toe-region). Optimal values for maximising efficiency are indicated by with a cross (x). White regions of the contour plots indicate combinations of fascicle length and tendon stiffness where the required muscle fascicle power could not be achieved with the muscle without supramaximal activation (>120%) (contour interval = 2%, maximum efficiency values reported in Table 1).

In our previous study (Lichtwark and Wilson, 2007) we only examined the influence of tendon compliance on the efficiency of muscle. Although being beneficial to our understanding of the influence of this parameter on muscle energetics, the previous study ignored the possibility that a different muscle fascicle length will compensate for a more stiff or compliant tendon to maintain high efficiency. Here

we have demonstrated for walking, where the required power output from the MTU is low, that efficiency could be high with a compliant tendon provided that the muscle fascicles are also much shorter. However, if this were the case then it may prove difficult for the muscle to generate the required power output during running or fast running without a greater muscle volume. Increasing the muscle

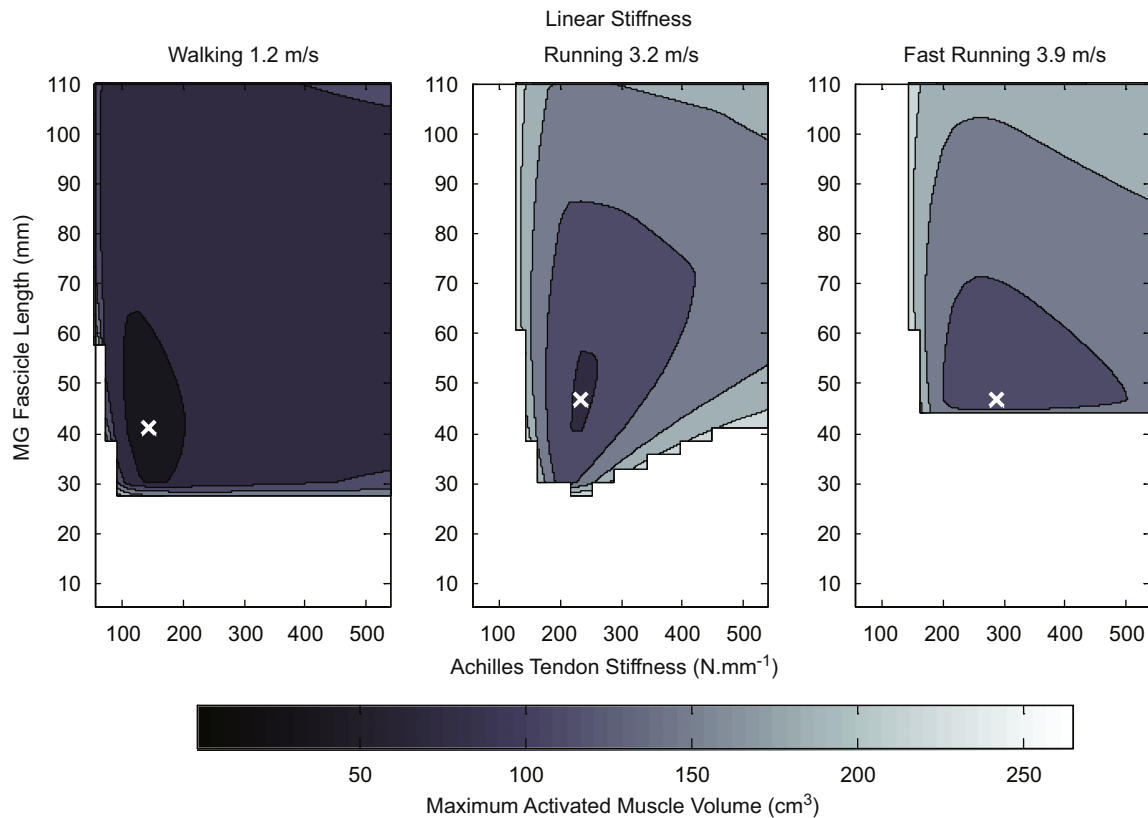


Fig. 5. Contour plots of the relationship between linear AT stiffness (k_L), MG fascicle length and MG maximum activated volume (MAV) for different gait conditions assuming linear tendon stiffness. Optimal values for minimising MAV are indicated by with a cross (\times). White regions of the contour plots indicate combinations of fascicle length and tendon stiffness where the required muscle fascicle power could not be achieved with the muscle without supramaximal activation ($> 120\%$) (contour interval = $40,000 \text{ cm}^3$, minimum MAV values reported in Table 1).

Table 1

Optimum values of fascicle length (L_O) and tendon stiffness (k_L) and resulting energy output, muscle efficiency and maximum activated muscle volume (MAV) for each gait condition when (A) minimising MAV using a linear tendon stiffness model (B) maximising the efficiency with a linear tendon stiffness model and (C) maximising the efficiency with a non-linear tendon stiffness model

Condition	Optimum fascicle length (mm)	Tendon stiffness (N/mm)	Total energy output (J)	Efficiency (%)	Maximum activated volume (cm^3)
(A) Minimise MAV					
Walk (1.2 m/s)	41.2	144	7.6	36.5	83.9
Run (3.2 m/s)	46.8	234	10.5	39.9	121.9
Fast run (3.9 m/s)	46.8	288	10.6	38.9	145.2
(B) Maximise efficiency—linear					
Walk (1.2 m/s)	38.5	108	7.4	37.4	91.1
Run (3.2 m/s)	52.2	216	10.4	40.1	134.6
Fast run (3.9 m/s)	55.0	234	10.2	40.2	155.5
(C) Maximise efficiency—non-linear					
Walk (1.2 m/s)	44.0	144	7.7	36.1	110.2
Run (3.2 m/s)	52.3	234	10.4	40.3	128.8
Fast run (3.9 m/s)	55	252	10.2	39.8	172.4

volume has the effect of increasing the maximum isometric force capable of being produced by the muscle (see Eq. (9)) and hence smaller activation levels are required to attain a specific force output. This would therefore expand the combinations of fascicle length and tendon compliance that

could achieve a given output, but would have little effect on the optimum values for maximising stiffness or minimising MAV.

The average muscle MG fascicle length in healthy young subjects is approximately 63 (S.D. ± 9 mm) (Mademli and

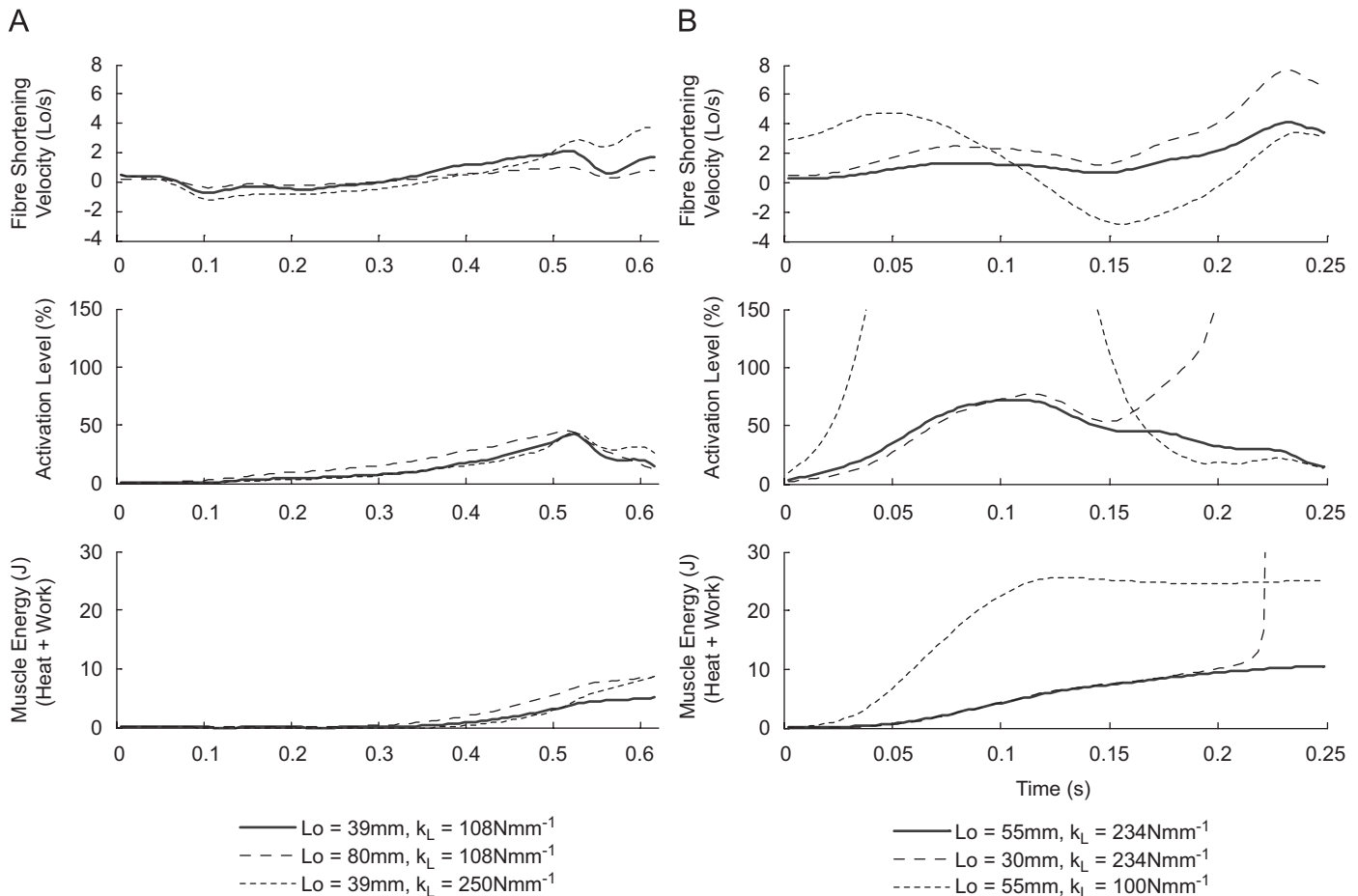


Fig. 6. Predicted MG muscle fascicle shortening velocity, MG muscle activation level and total MG energy output (heat + work) during (A) a walking stride and (B) a fast running stride with three different combinations of muscle fascicle length (L_o) and AT stiffness (k). The optimum combination for maximising efficiency (red) and two other combinations containing either the optimal stiffness (black solid) or optimal fascicle length (black dashed) are shown. The volume of the muscle is 220 cm^3 . Supramaximal activations (> 1) are required during fast running if the muscle has to produce force at high shortening velocities (e.g. $k = 150\text{ N/mm}$) or if the short muscle fascicles are required to shorten beyond the range of the force-length properties (e.g. $L_o = 30\text{ mm}$).

Arampatzis, 2006) and the average AT stiffness is $174\text{ N}\cdot\text{mm}^{-1}$ (S.D. ± 38) (Lichtwark and Wilson, 2005a; Maganaris and Paul, 2002). These average values are between the optimal values for maximising efficiency (and minimising MAV) for walking and running. Increases in the power requirement of our muscles (e.g. with speed) require a stiffer tendon to produce optimal efficiency and also to produce the required power with the given muscle volume. This supports the findings that sprint athletes have greater Achilles tendon stiffnesses than endurance athletes (Arampatzis et al., 2006). At small muscle fascicle lengths ($< 45\text{ mm}$) and low stiffness ($< 130\text{ N/mm}$), the required power output cannot be produced without substantial increases in muscle size. This is due to the smaller fascicle length range and the higher shortening velocities required in these circumstances (Fig. 6). It would be interesting to determine the optimum fascicle length and tendon stiffness for other sporting activities and compare them to data from specialists in those sports.

In our previous analysis (Lichtwark and Wilson, 2007), we used changes in Achilles tendon length to estimate the force produced during walking and running at one speed (Lichtwark and Wilson, 2006), rather than joint moments. Although this method gives a reasonable estimate of tendon force, particularly early in the stance phase where co-contraction exists, it is limited by the small speed range and subject numbers for such an analysis. Instead, here we have used ankle joint moment to estimate Achilles tendon force. Joint moment measurements are unable to account for muscle force which results from co-contraction; when the force produce by antagonist muscles oppose each other. Therefore, the estimates of muscle efficiency made here do not account for co-contraction and estimates of efficiency are higher as a result. This should have little influence on the optimal values of muscle fascicle length and tendon stiffness for achieving maximum efficiency, however, because the period and amplitude of co-contraction is not likely to be influenced greatly by either variable.

One of the limitations in this study is that it relies on the reliability of the data from Novacheck's review article (1998). The maximum ankle joint moment recorded in this review paper for fast running was approximately 2 Nm/kg. For a 75 kg subject, this is approximately equal to a maximum joint moment of 150 Nm. At a comparable speed, Hof et al. (2002) reports an average maximum ankle joint moment of 197 Nm ($N = 4$, average subject mass 73.5 kg). There is obviously some discrepancies between these values, with Hof's ankle joint moments over 20% larger than those of Novacheck's data. To assess the influence this might have on these results, we have increased the ankle joint moment data used in the model by 20% for each condition. The results of this analysis reveal that the L_O for maximising efficiency at all three speeds would remain unchanged from the original analysis. In contrast, the required k_L for optimising efficiency would actually increase to 126, 270 and 288 N/mm for walk, run and fast run respectively (this corresponds to an increase in and k_L of between 16% and 23%). This also has the effect of reducing the possible combinations of L_O and k_L that can produce the required power, which has increased. The values of optimal k_L for the 20% increase in joint moment during fast running are quite a bit larger than that measured experimentally for humans; however, variations may exist in the joint kinematics that are associated with increased joint moment.

Here, we assumed that ankle and knee kinematics and kinetics would not change with tendon compliance. Hof et al. (2002) demonstrated that although tendon stiffness of subjects could vary substantially, the ankle kinematics of participants were remarkably similar. Hof (2003) also suggests that the time course of force production may also be influenced by the stiffness of the tendon; however, this effect also depends on the effective mass being supported by the tendon. In Hof's analysis a simple linear model was used to describe how the time course of force is influenced by a muscle's active state and the elastic properties of the tendon. After some elegant derivation, Hof concludes with the following equation that predicts the time course of force production:

$$F(t) = F_W + e^{-t/2\tau_M}[(F(0) - F_W) \cos(w_0 t) + (2\beta F_0 + v(0)\sqrt{k_1 m}) \sin(w_0 t)], \quad (11)$$

where F is the force, F_W is the weight (~ 76 kg), t is the time, τ_M is a time constant (~ 0.372 s), k_1 is the linearised series elastic stiffness, m is the effective inertial mass in series with the tendon (~ 483 kg; greater than body mass due to relative moments of GRF and AT at ankle), w_0 is the resonant frequency of what? ($\sqrt{k_1 m} \sim 19.7$ rad/s), β is a damping factor (~ 0.07) and F_0 is the active state (activation level?) of the muscle, $F(0)$ is the initial force (~ 0 N) and $v(0)$ is the initial velocity (~ 0.07 m/s) (all values are estimates for running taken from Hof (2003)).

Applying this equation with tendon stiffness values across the range measured experimentally in Lichtwark

and Wilson (2005a) (100–240 kN/mm), we find that the predicted peak force changes from 2480 to 2730 N, only a 9% change in maximum force. Therefore, the change in stiffness across the biological range will not have a large influence on peak tendon and muscle force. Changes in tendon stiffness may however be linked with changes in body mass and hence the effective mass on the tendon. This will lead to further increases in maximum force during walking and running according to the above equation, which may account for the large variation in data reported by Hof et al. (2002) and Novacheck's (1998) data. Further studies are required to examine the relationship between muscle tendon properties and resultant kinematics and kinetics.

The present model is relatively simple and does not take into account distributions of fibre type or basal energetic costs. Fibre type will influence the achievable power output of the muscle (due to the change in V_{max}). Faster fibre types can also achieve maximum efficiency at higher muscle shortening velocities. Increases in fast fibre proportion may therefore allow shorter muscle fibres to be more efficient. Increases in muscle volume increase the power output and may also influence time to fatigue (since a lower proportion of muscle volume is used in any one contraction), but it also influences the basal metabolic cost for that muscle. This will have only a minor effect on the efficiency of the muscle during the duration of a single stride; however it will have a greater influence across the period of a whole day. Therefore, it is likely if high power outputs are not required of a muscle that it will not maintain large muscle volumes due to the increased basal metabolic cost and inertial load. There are both specialist tasks and everyday tasks that do require higher power outputs (like acceleration movements, jumping, standing, etc.) and as such it is likely that there is a trade-off between the design of a muscle to operate with optimal efficiency and to be powerful enough to perform these tasks.

The model does not provide a distinct representation of the influence of muscle fibre stiffness (due to elastic nature of cross-bridges) and connective tissue stiffness, like aponeurosis, to the force production and energy consumption. Instead, these values are lumped into the SEE so that the optimal stiffness of the SEE (tendon) is the combination of all elastic structures in series with each other. However, it is likely that the length change that these elastic structures experience is much smaller than that of the tendon, because the length of the tendon is so much greater. This was the same conclusion found by Alexander and Bennet-Clark (1977) who found that the energy stored in the Achilles tendon should be much greater than that stored in the muscle fibres. Here the SEE stiffness includes all elastic structures in series with the CE, and therefore the optimal stiffness determined is likely to be lower than that of the tendon alone.

While Hill-type muscle models are good at characterising the force output of MTUs, they have been shown to have a number of limitations. Muscle activation has been shown

to be influenced by both length and velocity of the muscle fibres; e.g. stretch induced force enhancement or shortening deactivation (Askew and Marsh, 1998; Herzog and Leonard, 2000; Rassier and Herzog, 2002, 2004; Sandercock and Heckman, 1997). Therefore, in the current model it is likely that at high velocities (either lengthening or shortening) or large excursions from the optimum length, the activation levels predicted may have some error associated with them. This is unlikely to influence the optimum values greatly, because the optimum values are also associated with minimising the maximum shortening velocity or length change (which maximises efficiency). However, combinations that require large fascicle excursions are likely to either over estimate activation (during stretch) or underestimate activation (during shortening), which will have a small effect on the overall efficiency of the muscle as activation level affects the rate of heat production.

In an thorough examination of the effectiveness of Hill-type models in predicting force output, Sandercock and Heckman (1997) found that although the inclusion of a non-linear, toe-region in the tendon force length relationship has little influence on the predicted force output, it does influence the predicted fibre trajectory. This error will have an influence on predicted energetics. Here we have shown that this toe-region has the most influence on our predictions of optimum fascicle length and tendon stiffness during walking, where forces are lower and the tendon is likely to operate for a greater amount of time in that toe-region. Specifically, this reduces the maximum achievable efficiency and requires a longer muscle fascicle and stiffer tendon to optimise efficiency. This is to be expected, because whilst operating in the toe region the muscle fascicles will experience greater length changes at lower forces, particularly for compliant tendons. However, co-contraction early during foot contact may influence these results, as the Achilles tendon may be preloaded beyond the toe-region which is supported by EMG data which shows that the *Tibialis Anterior* co-contracts during heel contact. It is also interesting to note that inclusion of the toe-region requires tendons that are stiffer than 180 N/mm (the average AT stiffness measured experimentally) to produce the required power output. The optimum for fast running is between 240 and 260 N/mm, which is much higher than average stiffness. However, the pre-stretch of the tendon with co-contraction and also load sharing differences between the soleus and the gastrocnemius muscles (as discussed below) may make it possible to achieve the required power output during fast running with k_L values below 180 N/mm.

The current model relies on the assumption that force sharing between the muscles of the *triceps surae* is constant throughout the stance phase for all gait types. It is not likely that this is the case due to the slightly different roles the muscles play due to the number of joints each muscle crosses. Such variable recruitment of muscles has been shown to occur in numerous small quadrupeds (Kaya

et al., 2003) and humans (Arndt et al., 1998) and it is likely that the force produced by each of the muscles is not uniform during any specific movement. We hypothesise that during fast running, the soleus is likely to contribute more to ankle joint extension moment, so as to reduce the knee flexion moment produced at the knee by the gastrocnemius muscles. This should reduce the required tendon stiffness for maximising efficiency of the MG; however, such a hypothesis has yet to be tested.

The force estimated to be produced by the muscle fascicles is further complicated by the influence of fascia of connected muscle groups which allows force to be transferred from one muscle to its neighbour (Maas et al., 2001, 2003). Each of these parameters may influence the precise optimal values predicted to maximise efficiency or minimise MAV at each gait speed and may alter the gradient of the contour plot in Fig. 4A; similar to the influence of including a non-linear tendon stiffness (Fig. 4B). However, inclusion of these parameters in this model is beyond the scope of this investigation and will not change the final conclusions; that the optimal fascicle length and tendon compliance combination for maximising efficiency is different for walking compared to running at different speeds, but that high efficiency may be achieved over a large and physiological range of these combinations for all gaits. This leaves scope for the muscle to adapt to specific tasks while maintaining high efficiency for locomotion.

In conclusion, we have implemented a modelling technique that shows how fascicle length and tendon stiffness interact to achieve a maximum muscle efficiency during walking and running at different speeds. The optimum properties identified by the model are similar to those observed in adult humans. The results show that minimising MAV (or activation level) or maximising efficiency yield a similar optimum anatomy which is a consequence of searching for solutions with a low fibre velocity and hence high efficiency and high fibre force. We have shown that optimum muscle fascicle lengths and tendon stiffness values are key to providing the required power output from a muscle and that muscles with short fascicle lengths or low tendon stiffness cannot provide adequate power for fast running unless very large muscle volumes are present. However, this analysis has been performed with a relatively simplistic model that neglects some of the state dependent properties of muscle and the more complex interactions of connective tissues. Further examination of how muscles adapt with training is required to support whether muscle fascicle length and tendon compliance can be tuned to maximise muscle efficiency for a particular activity.

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