A phenomenological model and validation of shortening-induced force depression during muscle contractions

Craig P. McGowan [a,*], Richard R. Neptune [a], Walter Herzog [b]

[a] Department of Mechanical Engineering, The University of Texas at Austin, Austin, TX 78712, USA
[b] Faculty of Kinesiology, University of Calgary, Calgary, Alberta, Canada T2N 1N4

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ABSTRACT

History-dependent effects on muscle force development following active changes in length have been measured in a number of experimental studies. However, few muscle models have included these properties or examined their impact on force and power output in dynamic cyclic movements. The goal of this study was to develop and validate a modified Hill-type muscle model that includes shortening-induced force depression and assess its influence on locomotor performance. The magnitude of force depression was defined by empirical relationships based on muscle mechanical work. To validate the model, simulations incorporating force depression were developed to emulate single muscle *in situ* and whole muscle group leg extension experiments. There was excellent agreement between simulation and experimental values, with *in situ* force patterns closely matching the experimental data (average RMS error $< 1.5\,N$) and force depression in the simulated leg extension exercise being similar in magnitude to experimental values (6.0% vs. 6.5%, respectively). To examine the influence of force depression on locomotor performance, simulations of maximum power pedaling with and without force depression were generated. Force depression decreased maximum crank power by 20–40%, depending on the relationship between force depression and muscle work used. These results indicate that force depression has the potential to substantially influence muscle power output in dynamic cyclic movements. However, to fully understand the impact of this phenomenon on human movement, more research is needed to characterize the relationship between force depression and mechanical work in large muscles with different morphologies.

1. Introduction

History-dependent effects on muscle force development following active changes in length have long been known to exist in skeletal muscles. For example, the isometric force produced by a muscle following active shortening has been shown to be depressed relative to isometric force without previous shortening (e.g., Abbott and Aubert, 1952; Herzog et al., 2000; Marechal and Plaghki, 1979; Meijer et al., 1998). Following an active muscle stretch, the isometric force produced has been shown to be elevated relative to a corresponding isometric contraction without a previous stretch (e.g., Abbott and Aubert, 1952; Cavagna and Citterio, 1974; Edman et al., 1982; Herzog and Leonard, 2002; Hisey et al., 2009). Both force depression and enhancement are long lasting and have been identified in isolated muscles and muscle fibers (e.g., Abbott and Aubert, 1952; Edman et al., 1978; Edman and Tsuchiya, 1996), whole muscles *in situ* (Herzog and Leonard, 2002; Marechal and Plaghki,

1979), whole muscles *in vivo* (e.g., De Ruiter et al., 1998) and whole muscle groups *in vivo* (e.g., Chapman et al., 1985; Lee et al., 1999).

Several studies have shown that shortening-induced force depression has a linear relationship with the magnitude of length change when shortening at constant velocity (e.g., Edman, 1975; Marechal and Plaghki, 1979), and an exponential relationship with velocity when shortening over a fixed distance (e.g., Marechal and Plaghki, 1979; Meijer et al., 1998). However, others have shown that force depression is independent of velocity if the magnitude of force remains constant during shortening (Herzog et al., 2000). These relationships have been the basis for previous modified Hill-type muscle models incorporating history-dependent muscle properties (Ettema and Meijer, 2000; Meijer et al., 1998). Other studies have shown that force depression is significantly related to muscle work, with variation in muscle work accounting for over 85% of the variation in force depression (Herzog et al., 2000). This relationship has been supported in a recent analysis of mouse muscles (Kosterina et al., 2008).

However, the experimental protocols required to identify history-dependent effects do not readily permit the evaluation of how they influence muscle force and power output during

* Corresponding author. Tel.: +1 512 471 0848.
  E-mail address: cpmcgowan@mail.utexas.edu (C.P. McGowan).

cyclic locomotor tasks such as human walking or pedaling. Musculoskeletal modeling and forward dynamics simulations provide an ideal framework for examining the influence of muscle properties that cannot be measured directly (Gerritsen et al., 1998; Umberger et al., 2006; van Soest and Bobbert, 1993). A large number of muscle models have been developed to estimate force output ranging in complexity, with the classic Hill-type model being used most frequently in forward dynamics simulations due to its relative simplicity (Erdemir et al, 2007). The need to explore the influence of history-dependent effects on muscle models has often been recognized (e.g., Huijing, 1995; Winters, 1995); however, relatively few models have incorporated them into their estimates of force output (Ettema and Meijer, 2000; Forcinito et al., 1998; Meijer et al., 1998; Tamura et al., 2005; Wu and Herzog, 1999). Even fewer studies have used these models to examine the influence of history-dependent effects on muscle coordination during dynamic movements (e.g., Ettema, 2002).

The overall goal of this study was to develop a phenomenological model of shortening-induced force depression based on a Hill-type muscle model that could easily be incorporated into forward dynamics simulations of human movement to assess the potential influence of force depression on human locomotor performance. The accuracy of the model was evaluated by comparing simulation output with experimental measurements of force depression at the single muscle and muscle group levels. At the single muscle level, simulations were developed that emulated *in situ* muscle ergometer experiments on cat soleus muscles, and at the muscle group level, simulations were developed that emulated a human leg extension exercise. To examine the potential effects of force depression on locomotor performance, a theoretical analysis was conducted, in which simulations of maximum power pedaling with and without force depression were generated and compared.

2. Methods

2.1. Hill-type muscle model

Simulations of muscle force were generated using a standard two-state (activation, fiber length) Hill-type muscle model where the magnitude of the force is dependent primarily on the level of activation and the intrinsic muscle force–length–velocity relationships (Zajac, 1989) (Fig. 1). The musculotendon unit (MTU) is composed of a contractile element (CE) in parallel with an elastic element (PEE), both of which are in series with a tendon, or series elastic element (SEE; Fig. 1).

2.2. Force depression model

Studies have shown force depression likely occurs instantaneously with active muscle shortening and is maintained until the muscle is no longer active (e.g., Herzog et al., 2000). Further, when active shortening stops, there is a period over which the force returns exponentially to a steady-state value (Fig. 2). In this study, the difference between the steady-state isometric force following shortening and the corresponding isometric force without shortening is termed static force depression (ΔF_{static}) and the component of force depression during the period in which force returns to steady-state is termed transient force depression (ΔF_{trans}) (Fig. 2).

The magnitude of static force depression is cumulative while the muscle is active and is a function of the net work (W_{net}) done during shortening (Herzog et al., 2000). This relationship is defined as

$$\Delta F_{static} = W_{net}c \tag{1}$$

The relationship between ΔF_{static} and W_{net} is assumed to be linear, with the regression coefficient (c=9.43) determined from Herzog et al. (2000). Instantaneous muscle work (W_i) is the product of instantaneous muscle force (F_i) and velocity (v_i), and time step (dt) and is calculated as
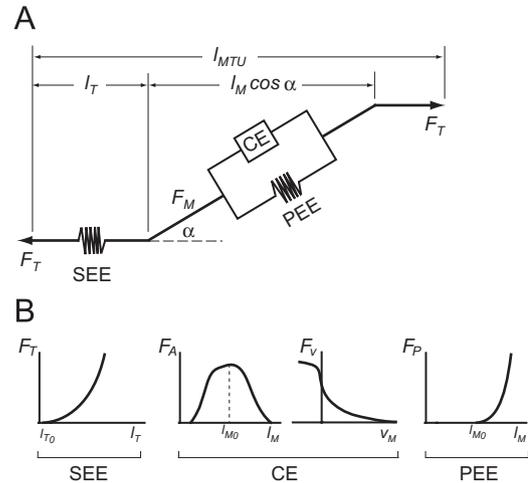
$$W_i = F_i v_i dt \tag{2}$$

Net work (W_{net}) is the cumulative sum of W_i over the entire time the muscle is active and set to zero when the muscle is inactive. Net work is calculated as

$$W_{net} = W_{net} + W_i \quad \text{if } a > 0$$
$$W_{net} = 0, \quad \text{if } a = 0 \tag{3}$$

where a is muscle activation.

Fig. 1. (A) Generalized Hill-type muscle model consisting of a contractile element (CE), parallel elastic element (PEE) and series elastic element (SEE) with a pennation angle (α) (Zajac, 1989). (B) Muscle force is determined from the active force–length (F_A–l_M) and force-velocity (F_V–V_M) relationships in the contractile element and the non-linear spring properties of the passive elastic (F_P–l_M) and series elastic (F_T–l_T) elements. The relationships were normalized by the corresponding maximal isometric force, optimal fiber length, maximal shorting velocity and tendon slack length for each muscle.
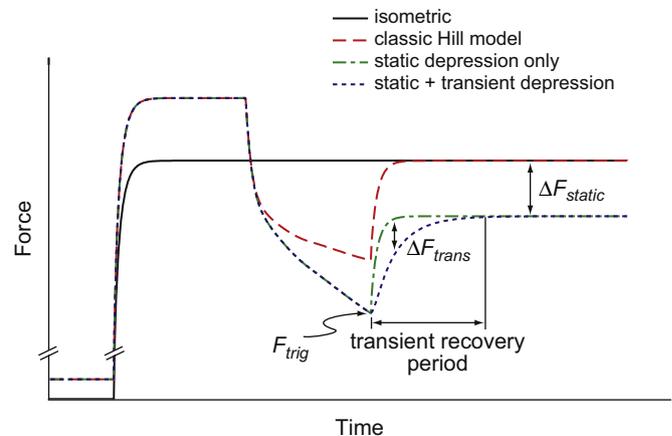
Fig. 2. A schematic showing force traces from different muscle models from the simulated muscle ergometer test. The classic Hill-type muscle model does not reproduce any aspects of shortening-induced force depression. Static force depression (ΔF_{static}) occurs throughout the test, while transient force depression (ΔF_{trans}) occurs during the transient recovery period which begins when the muscle stops shorting (F_{trig}). In order to accurately reproduce experimental data, both ΔF_{static} and ΔF_{trans} are included.

Because force depression is related to net work, if the muscle is stretched after shortening while still active, the amount of force depression is decreased. If the muscle is stretched to a greater degree than it had previously shortened, the resulting isometric force is increased (stretch-induced force enhancement) relative to isometric force with no previous length change (e.g., Herzog and Leonard, 2002). However, the relationship between muscle stretch and force enhancement is less well characterized and it is not clear if muscle work is also a reliable predictor of increased force. Therefore, in this study, if W_{net} became negative (active stretching), total force depression was set to zero.

Transient force depression (ΔF_{trans}) describes the delayed force recovery between when the muscle stops shortening and when the force returns to a steady-state (Fig. 2). The nature of this delayed force response has been previously characterized for cat soleus muscle with an exponential force recovery rate (k) that is also a function of W_{net} (Corr and Herzog, 2005). Studies of the cat soleus have shown that the delayed force recovery occurs for a short time following a rapid change in fiber velocity (e.g., Herzog et al., 2000). Therefore, ΔF_{trans} was set to zero until initiated by a decrease in contraction velocity ($dv/dt < 0$), at which point it

was calculated as

$$\Delta F_{trans} = Ae^{-kt} \tag{4}$$

where A is the difference between the current force (including ΔF_{static}) and the force at the time when ΔF_{trans} was initiated and defined as

$$A = F_i - F_{trig} \tag{5}$$

The resulting muscle force (F') is expressed as the muscle force without force depression (F) minus the sum of the static and transient force depression using the equation

$$F' = F - (\Delta F_{static} + \Delta F_{trans}) \tag{6}$$

2.3. Simulations

2.3.1. Single muscle in situ simulation

To validate the muscle model's ability to reproduce empirical measurements of force depression at the single muscle level, the protocol from the experimental study of Herzog et al. (2000) analyzing the cat soleus was simulated. The experimental muscle ergometer from that study was modeled using SIMM/Dynamics Pipeline (MusculoGraphics, Inc) with two blocks mounted horizontally on a frictionless surface with the modified Hill-type muscle mounted between them. One block was fixed while the other block underwent prescribed linear motion in which velocity was controlled. Briefly, the experiment was designed to compare the isometric force following a constant velocity contraction with the isometric force of a muscle that did not shorten. To account for force–length effects, all contractions ended at the same length (4 mm less than optimal). In each simulation, the muscle was fully activated prior to shortening and remained fully activated until well after the muscle returned to constant force. Two sets of experiments were conducted to examine the effects of shortening length and shortening velocity. In the first set of experiments, shortening velocity was held constant (4 mm/s) and the initial muscle length was varied such that the muscle shortened over different lengths (2, 4, 6, 8 and 10 mm). In the second set of experiments, the muscle shortened a fixed distance (8 mm) over a range of constant velocities (4, 8, 16, 32 and 256 mm/s). Values for the optimal muscle fiber length (36 mm), tendon slack length (74 mm, including aponeurosis), maximum shorting velocity (3.3 lengths/s) and maximum isometric force (22.4 N) were set to approximate values for a cat soleus muscle used in the experimental study (Herzog et al., 2000).

2.3.2. Leg extension simulation

To validate the muscle model's ability to reproduce empirical measurements of force depression at the muscle group level, the protocol from the experimental study of Lee et al. (1999) analyzing an isometric human knee extension exercise was simulated. A previously described linked segment musculoskeletal model (e.g., Neptune et al., 2008) was modified and consisted of a trunk and single leg comprised of a foot, shank, patella and thigh segment and included 25 modified Hill-type muscle actuators. However, only the four quadriceps muscles (rectus femoris and three vastii) were activated during the simulations. The model was configured in a seated position with the hip and ankle angles fixed and the knee controlled using prescribed motion (Fig. 4). Simulations were performed which emulated the experiments conducted by Lee et al. (1999). Similar to the ergometer experiments, force output was compared between isometric contractions following active shortening and contractions with no prior shortening. This was accomplished by comparing the knee joint torque measured during a maximal contraction with the knee fixed at 60° flexion with the isometric joint torque measured following a constant velocity extension from 100° to 60°. This protocol was replicated in the simulation and the corresponding changes in knee joint torque were compared.

2.3.3. Maximum power pedaling simulation

To examine the potential effects of force depression on human locomotor performance, simulations of maximum power pedaling with and without force
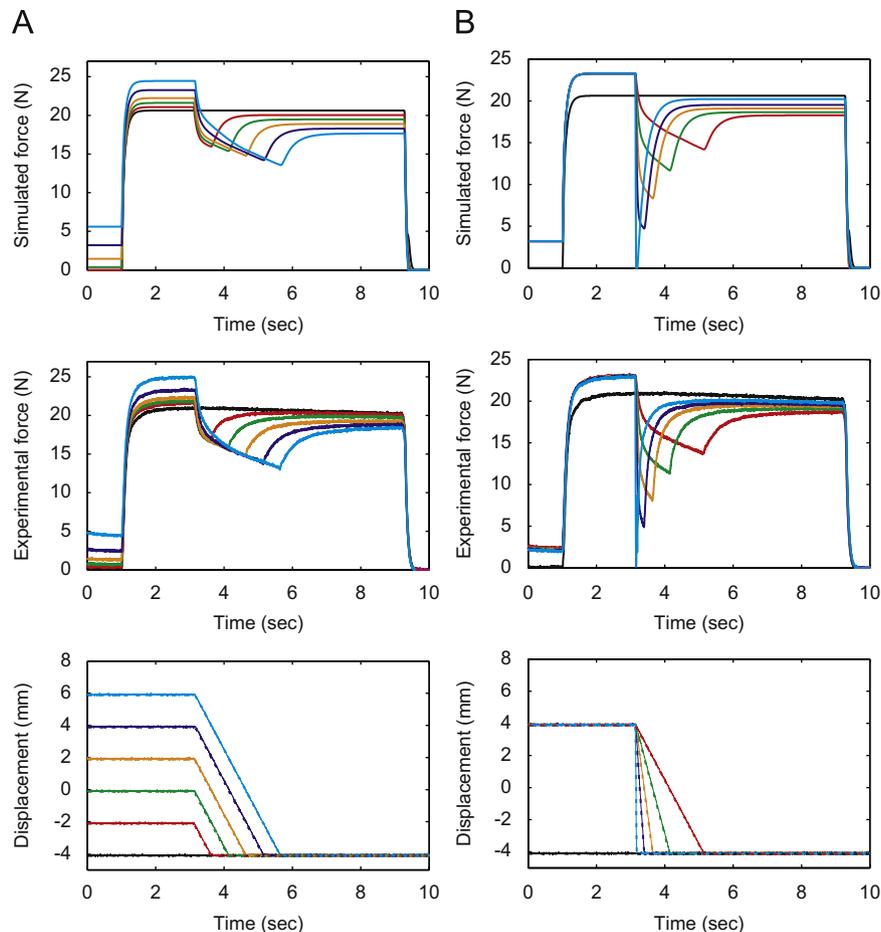

Fig. 3. Simulated (top row) and experimental (middle row) data from (A) constant velocity and (B) variable velocity *in situ* experiments. Muscles were fully activated at 1 s and deactivated at ~9.5 s. The constant velocity experiments were conducted at 4 mm s^{-1} and shortened 2, 4, 6, 8 and 10 mm. Variable velocity experiments were conducted at 4, 8, 16, 32 and 256 mm s^{-1} with a fixed displacement of 8 mm. Simulated displacements (large dashed lines) are plotted over experimental displacements (thin lines) on the same graphs (bottom row).

depression were generated and compared. The modified Hill-type model with force depression was incorporated into a previously described pedaling simulation (for details, see Rankin and Neptune, 2008). Briefly, the musculoskeletal model consisted of nine segments (pelvis, two legs with a thigh, shank, patella and foot), a crank and pedal system, and 15 musculotendon actuators per leg. The pelvis and crank segments were fixed to the ground and the foot segments were fixed to the pedals resulting in three rotational degrees of freedom (crank and two pedals). The motion of the crank segment was prescribed in order to emulate an isokinetic ergometer. Simulations of 90 rpm pedaling with and without force depression were generated using a simulated annealing algorithm (Goffe et al., 1994) that fine tuned the muscle excitation patterns to maximize average crank power. The influence of force depression was assessed by comparing the results for maximal average crank power between the two simulations.

3. Results

3.1. Single muscle in situ simulation

The simulated muscle ergometer tests incorporating the modified Hill-type model were able to accurately reproduce both the length- and velocity-dependent characteristics of shortening-induced force depression observed experimentally (Figs. 3 and 4). The constant velocity experiments exhibited both an increase in steady-state force depression and a decrease in the rate of force recovery during the transient recovery period (Fig. 2) with an increase in length change (Fig. 3A). The average root mean square error (RMSE) between the simulation and experimental data for the constant velocity trials was 0.66 N (range: 0.58–0.94 N). The
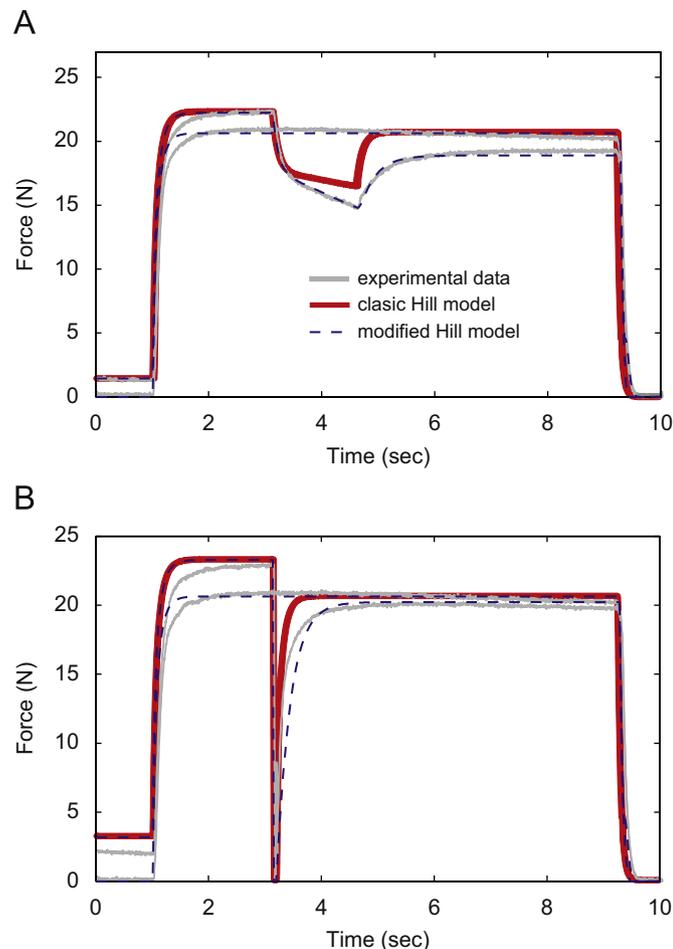
variable velocity experiments exhibited a decrease in steady-state force depression and an increase in rate of force recovery with an increase in shortening velocity (Fig. 3B). The average RMSE for the variable velocity trials was 0.86 N (range: 0.35–1.45 N).

3.2. Leg extension simulation

The simulation of a seated knee extension exercise showed that isometric torque following a knee extension of 40° (from 100° to 60° flexion) was reduced by 6% relative to an isometric contraction at 60° with no previous shortening (Fig. 5). This result is comparable to the previous experimental study of human subjects, which showed an average reduction in torque of 6.5% under the same conditions (Lee et al., 1999).
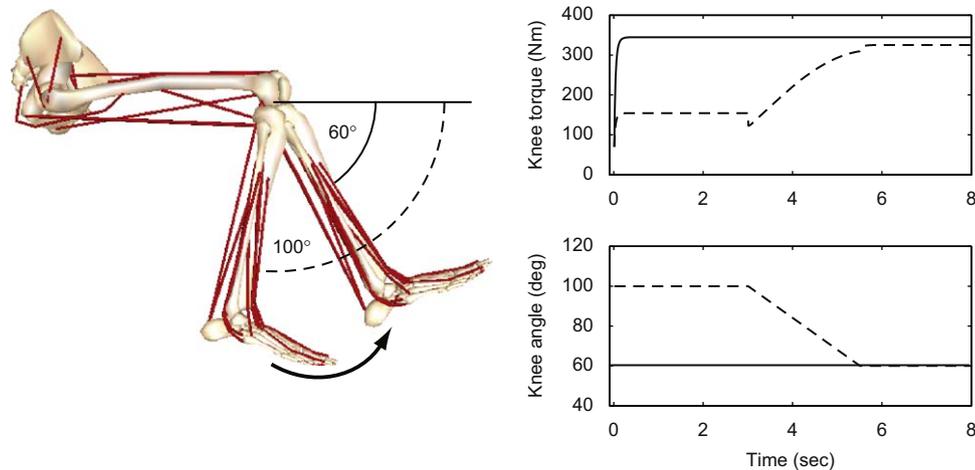
3.3. Maximum power pedaling simulation

The maximal average crank power in the pedaling simulation with and without force depression was 649 and 966 W, respectively, yielding a reduction in average power of ∼ 28%. Not surprisingly, force depression had the greatest impact on the major power producing muscles (i.e. the vastii and gluteus maximus). Force depression in these muscles resulted in a reduction in average muscle power of 45.6 and 13.6 W, respectively. Both simulations utilized similar activation patterns (Fig. 6) and had similar muscle fiber lengths and velocities. Thus, the reduction in muscle power was almost exclusively due to force depression, especially during the second half of the power stroke (∼90° to 180°; Fig. 6).

4. Discussion

The goal of this study was to develop a phenomenological model of shortening-induced force depression that could easily be incorporated into forward dynamics simulations. The results of the simulations showed that the modified Hill-type model could more accurately reproduce experimental data than the classic Hill-type model alone (Fig. 4). Experimental data were matched for single muscle in situ preparations (Fig. 3) and whole muscle groups in vivo (Fig. 5), thus validating the model's use in more complex whole-body movements. The results from incorporating the modified model into a forward dynamics simulation of maximal power pedaling suggest that shortening-induced force depression has the potential to substantially reduce muscle power output.

The agreement between our simulations and experimental muscle ergometer data was comparable to that found by previous models incorporating shortening-induced force depression (e.g., Ettema and Meijer, 2000; Forcinito et al., 1998; Meijer et al., 1998; Wu and Herzog, 1999) indicating a similar ability to account for this history-dependent effect. The model developed by Wu and Herzog (1999) is based on a modified cross-bridge model, which can accurately reproduce both the static and transient aspects of force depression, but is relatively complex and cannot be easily incorporated into computationally intensive forward dynamics simulations. Simpler modified Hill-type muscle models (Ettema and Meijer, 2000; Meijer et al., 1998) and exponential decay models (Ettema and Meijer, 2000) have been developed that are better suited for use in forward dynamics simulations, but these are limited in their ability to reproduce the transient component of force depression (Meijer et al., 1998). Building on this previous work, the present model reproduces both the transient and long lasting force depression, similar to the

Fig. 4. A comparison of experimental data with a simulation using the classic Hill model the modified Hill model during (A) a 6 mm shortening trial at 4 mm s^{-1} and (B) a 8 mm shorting trial at 256 mm s^{-1}.

Fig. 5. Simulations of a knee extension exercise during isometric (solid line) and isometric-shortening-isometric (dashed line) contractions. The quadriceps muscles were fully activated at 0 sec and remained active throughout the simulation. The isometric test was conducted at 60° and the isometric-shortening-isometric test began at 100° and underwent constant velocity shortening to 60°.

model of Wu and Herzog (1999), while being simple enough to use in forward dynamics simulation analyses.

With the model validated at the single muscle and muscle group levels, we could pursue our primary goal of assessing the potential influence of force depression on human locomotor performance. During normal cyclic movements such as walking or pedaling, muscles typically undergo repeated cycles of shortening and lengthening with little or no isometric activity. However, studies suggest that force depression begins at the instant that the muscle begins to shorten (e.g., Herzog et al., 2000), and therefore should affect the muscle's ability to generate force during cyclic movements with no isometric phase. The results from our simulation of maximal power pedaling support this conclusion. The maximal average crank power was reduced by ∼28%, primarily due to a reduction in force during the second half of the power stroke, when cumulative muscle work, and thus depression, is greatest (Fig. 6). It is important to note that force depression would likely not have as great of an effect during sub-maximal activities, where increased muscle recruitment can offset any force depression. However, increased recruitment would be associated with greater fatigue and higher metabolic cost.

The model presented in this study only accounts for shortening-induced force depression. However, other history-dependent effects such as active, stretch-induced force enhancement may play an equally important role during cyclic movements. Force enhancement was not included in the current model because, to date, there has not been an established relationship between force enhancement and a simple scalar variable such as muscle work and it appears force enhancement may depend greatly on the current muscle length (e.g., Hisey et al., 2009). Other studies have incorporated force enhancement by generally using the same function for enhancement and depression (Ettema and Meijer, 2000; Forcinito et al., 1998). This approach is reasonable, provided that the cumulative effects are taken into account. Specifically, the effects of a stretch following shortening appear to be cumulative; whereas the effects of shortening following stretch are not (Herzog and Leonard, 2000). In the present study, it is likely that stretch-induced force enhancement would have a limited influence during our simulation of pedaling since active stretch only occurs for a short period of time during the transition between the power (downstroke) and recovery

(upstroke) regions in the pedaling cycle when the activation level is low. However, in activities such as running, where several muscles are actively stretched during the first part of stance, stretch-induced force enhancement may have a greater influence than shortening depression. Future work is needed to examine the relative roles of force depression and enhancement in other types of locomotion.

An important note is that the modified Hill-type model in this study calculated force depression based on the relationship between force depression and mechanical work derived from cat soleus muscle. However, Herzog et al. (2000) showed that there is considerable variability in the relationship among individual muscles tested. Because the soleus muscle is relatively small, this relationship had to be extrapolated well beyond the values measured in order to incorporate force depression in our simulation of human movement. Thus, a relatively small difference in regression constants could potentially have a large effect on force depression in muscles that produce significant muscle work. To examine this, we repeated the maximal power pedaling simulations with regression constants that represented the highest ($c = 13.3$) and lowest ($c = 6.67$) possible slopes for the data presented by Herzog et al. (2000). Maximal average crank power varied from 570 to 770 W for the high and low regression constants, respectively. Thus, depending on the relationship chosen, force depression may reduce maximal average power in pedaling between 20–40%.

The current study assumes that the relationship between mechanical work and force depression in cat soleus muscles is representative of what exists in human muscles. However, based on the few studies that have characterized this relationship, there is reason to believe this may not be the case, at least not for all muscles. Recent studies have indicated that the relationship between force depression and mechanical work may be related to fiber type (Kosterina et al., 2009; Kosterina et al., 2008). From our present study, it is clear that force depression has the potential to have a significant influence on whole-body cyclic movements in humans. But to gain a better insight into the magnitude of this influence, it is important that studies continue to examine the relationship between force depression and mechanical work in larger muscles and in muscles with different fiber type compositions, as well as trying to elucidate the mechanisms underlying this phenomenon.
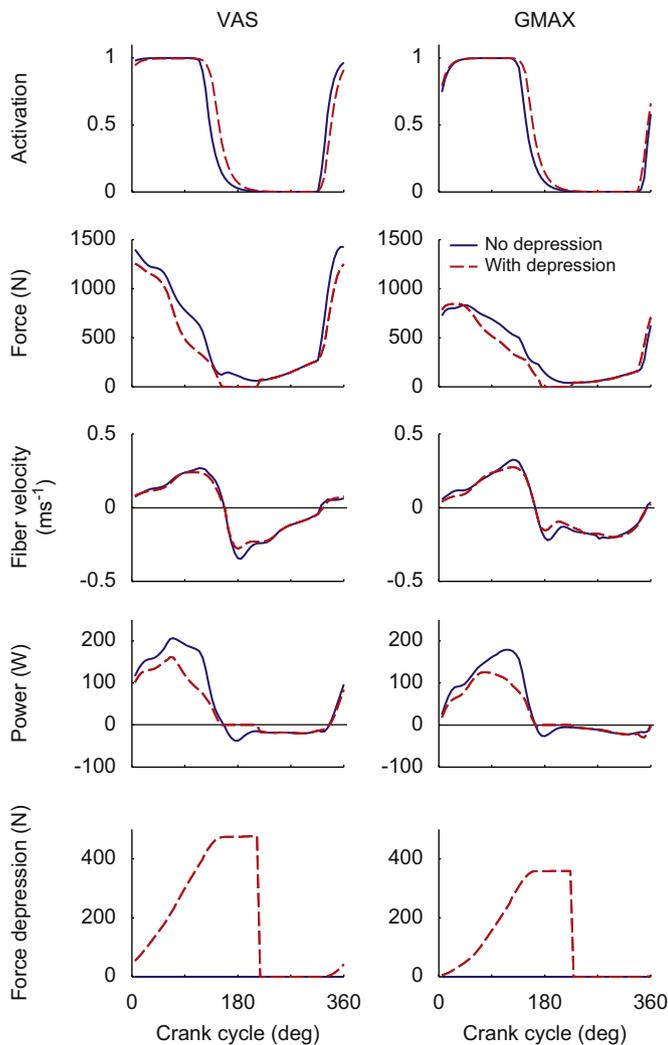
Fig. 6. Simulation data from vastus lateralis (VAS) and gluteus maximus (GMAX) from one cycle of maximum power pedaling with (dashed line) and without (solid line) shortening-induced force depression.

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