Adjustment of Muscle Mechanics Model Parameters to Simulate Dynamic Contractions in Older Adults

Darryl G. Thelen
Department of Mechanical Engineering,
University of Wisconsin-Madison,
Madison, WI 53706-1572

The generation of muscle-actuated simulations that accurately represent the movement of old adults requires a model that accounts for changes in muscle properties that occur with aging. An objective of this study was to adjust the parameters of Hill-type musculo-tendon models to reflect nominal age-related changes in muscle mechanics that have been reported in the literature. A second objective was to determine whether using the parametric adjustments resulted in simulated dynamic ankle torque behavior similar to that seen in healthy old adults. The primary parameter adjustment involved decreasing maximum isometric muscle forces to account for the loss of muscle mass and specific strength with age. A review of the literature suggested the need for other modest adjustments that account for prolonged muscular deactivation, a reduction in maximum contraction velocity, greater passive muscle stiffness and increased normalized force capacity during lengthening contractions. With age-related changes incorporated, a musculo-tendon model was used to simulate isometric and isokinetic contractions of ankle plantarflexor and dorsiflexor muscles. The model predicted that ankle plantarflexion power output during 120 deg/s shortening contractions would be over 40% lower in old adults compared to healthy young adults. These power losses with age exceed the 30% loss in isometric strength assumed in the model but are comparable to 39–44% reductions in ankle power outputs measured in healthy old adults of approximately 70 years of age. Thus, accounting for age-related changes in muscle properties, other than decreased maximum isometric force, may be particularly important when simulating movements that require substantial power development. [DOI: 10.1115/1.1531112]

Introduction

Many studies have documented changes in the mechanical output of skeletal muscle with aging. For example, compared to young adults, healthy old adults (approximately 70 years old) exhibit a substantial loss of muscle strength [1–3], prolonged twitch contractions [2,4], increased passive stiffness [5,6] and slowing of the rate of muscle force development [7,8]. Such changes are believed to be the cumulative result of age-related muscle atrophy and remodeling, which seems to more adversely affect fast twitch fibers than slow twitch fibers [1–3,9–12].

Changes in muscle mechanics may affect, and in some cases limit, how older adults perform certain movement tasks. For example, ankle plantarflexor weakness may be an underlying cause of slower gait speeds in healthy older adults [13,14]. In addition, functional young-old differences in movement performance become more pronounced when tasks require the development of substantial muscle strengths in a short period of time [15]. Forward dynamic simulation is a valuable tool to gain insight into how specific age-related changes in muscle mechanics can impact movement performance, since parameters can be selectively altered and the resulting effect on performance predicted. Dynamic simulation models, consisting of a multi-body representation of a human driven by Hill-type musculo-tendon actuators, have been used to realistically simulate a variety of movements such as pedaling [16] and gait [17]. Characteristic musculo-tendon model parameters have been established to represent the muscles of young adults [18,43]. How to adjust these parameters to represent the muscle contraction mechanics of healthy old adults is not as well understood.

The objectives of this study were twofold. One objective was to adjust the parameters of Hill-type musculo-tendon models to reflect nominal aging effects on muscle mechanics that have been found in previous experimental studies of animal and human muscle. A second objective was to determine whether using the parametric adjustments resulted in simulated dynamic ankle torque behavior similar to that seen in studies of healthy old males and old females.

Methods

This study follows the approach proposed by Zajac [18] of using a generic musculo-tendon model that is scaled to individual muscles. A brief review of the generic model is given followed by a justification and description of how model parameters were adjusted to represent aging effects.

Musculo-Tendon Model. Two nonlinear differential equations were used to describe activation and musculo-tendon contraction dynamics. Activation dynamics, which relates muscle excitation to activation, was modeled by a non-linear first-order differential equation with a faster time constant during activation ($\tau_{act}=15$ ms) than deactivation ($\tau_{deact}=50$ ms) [19]. A first-order differential equation of contraction dynamics was used to relate activation to the force developed by the musculo-tendon actuators [18]. Contraction dynamics accounted for the interaction of the force-length-velocity properties of muscle and the elastic properties of tendon [Fig. 1]. See the Appendix for details of the constitutive equations of muscle and tendon, and for the specific equations used to describe activation and contraction dynamics.

Please address correspondence to: Darryl G. Thelen, Ph.D., Department of Mechanical Engineering, University of Wisconsin-Madison, 1513 University Avenue, Madison, WI 53706-1572.

Contributed by the Bioengineering Division for publication in the JOURNAL OF BIOMECHANICAL ENGINEERING. Manuscript received Sept. 2000; revised manuscript received Jul. 2002. Associated Editor: M. L. Hull.

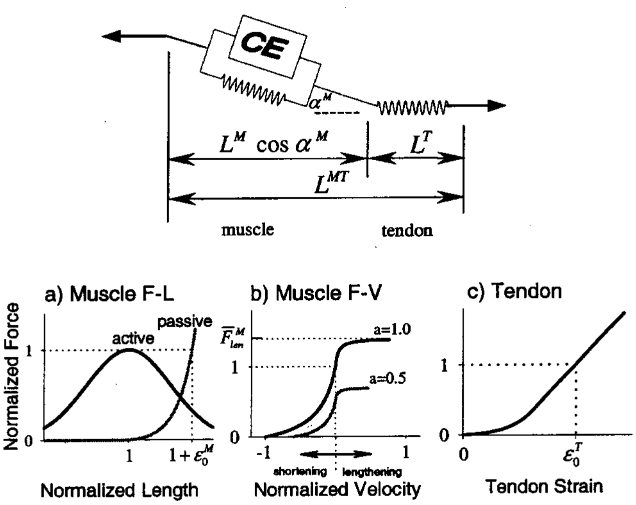

Fig. 1 A Hill-type model was used to describe musculo-tendon contraction mechanics. The model consists of a muscle contractile element in series and parallel with elastic elements. (*a*) A Gaussian curve was used to describe the active force-length relationship of muscle. (*b*) The muscle force-velocity function was scaled with activation such that the unloaded contraction velocity was reduced during sub-maximal activation. (*c*) Tendon force was assumed to increase exponentially with strain during an initial toe region, and linearly with strain thereafter.

Effects of Age on Muscle Mechanics. Age-related changes incorporated into the musculo-tendon model [Table 1] were those considered representative of muscle atrophy and remodeling that occur between the ages of 30 and 70 years of age.

Isometric Strength. Loss of isometric strength by the 7th decade of life is reported to be 20 to 40%, depending on the study and muscles considered [1–3]. This loss in strength is primarily attributed to muscle atrophy due to a decrease in the total number and size of muscle fibers with aging [1,3,9]. In addition to atrophy, the decrease in strength with age seems to also result from a decrease in the specific strength (force/area) of muscle [4,20], though this issue is less clear [21,22]. In the current study, isometric strength of individual muscles was reduced 30% from values used for young adults, which is comparable to the loss of isometric strength measured in muscles of the lower extremities [2].

Force-velocity. In old human muscle, reductions in maximum contraction velocity likely occur because of a preferential loss of fast twitch motor units [2] and fast twitch fiber cross-sectional area [10], as well as changes in the contraction characteristics of specific fiber types [12,23,24]. Larsson et al. [25] measured a slight (7%) decrease in maximum knee extension velocity between the ages of 25 and 65. While the maximum contraction velocity ($V^M_{\max}$) of whole muscles from mice and rats is unaltered or only slightly diminished with age [26,27], single muscle fibers [12,23,24] often exhibit substantial (up to 50%) age-related reductions in $V^M_{\max}$. Based on the data available, it was assumed that maximum contraction velocity of human muscle is decreased with age, but that the overall change is probably less than the loss in isometric strength [1]. Therefore $V^M_{\max}$ was decreased by 20% from the value used for young adults, from 10 to 8 optimal fiber lengths per second.

During lengthening contractions, the relative weakness in old age is not as substantial as during isometric contractions. Studies of isolated mice muscles have found that lengthening muscle forces, normalized to isometric strength, are 15–30% higher in old animals compared to young animals [28,29]. Similarly studies of humans show that lengthening muscle strength is better preserved with age than isometric or concentric muscle strength [8,30,31]. To reflect this difference, the maximum normalized force achievable during lengthening ($\bar{F}^M_{len}$) was increased from 1.4 for young adults [19] to 1.8 for older adults.

Active Force-Length. Studies of isolated rat muscles and human skeletal muscle cells have found that both the optimal fiber length and shape of the active force-length relationship are relatively unchanged with age [12,32]. Therefore the active force-length relationship of the contractile element was assumed to be the same for both the young and old adult muscle models.

Passive Force-Length. Passive muscle tension accounts for a greater proportion of total tension (active plus passive) in old muscles during stretch [32], which may result from an age-related increase in the amount of noncontractile tissue contained in muscle [33,34]. In the model, the passive muscle strain due to maximum isometric force, ε^M_0, was reduced from 0.60 for young adults [19] to 0.50 for older adults to account for the relative increase in passive stiffness.

Activation Dynamics. The rate of muscle deactivation, i.e. the rate of uptake of calcium ions by the sarcoplasmic reticulum, is slowed in old muscles [35,36,37]. In rats, the magnitude of the slowing of calcium uptake rate with age varies from 0% to 50%, depending on the muscle considered [36]. In humans, the estimated rate of calcium ion uptake in the quadriceps was 37% lower in old females compared to young females, a difference that was partially reduced through high resistance training [37]. Slowing of calcium uptake rate with age was reflected in the model by increasing the deactivation time constant (τ_{deact}) from 50 to 60 ms.

How the rate of muscle activation changes with age is not well understood so τ_{act} was left unchanged in the older adult muscle model. It is noted that activation dynamics, i.e. calcium release and diffusion, are relatively fast compared to contraction dynamics in muscles with tendon length/fiber length ratios greater than five [18]. Thus, changes in τ_{act} that may arise with age would likely have little affect on the dynamic contractions of plantarflexor muscles (which have tendon length/fiber length ratios greater than eight, Table 2) but may influence the dynamic characteristics of muscles with shorter tendons such as the dorsiflexors.

Tendon Stiffness. The tendon strain due to maximum isometric force (ε^T_0) was set to 0.04 in the old adult musculo-tendon model, the same value used for the young adults [38]. Since maximum isometric force is lower for the old adults, this assumes that the old adult tendon is more compliant in absolute terms. This is consistent with biomechanical tests of tendon specimens, which have found that the tensile modulus (slope of the linear region of the tendon stress-strain curve) of tendon tends to decrease with age [39,40], though the decrease is not always significant [41,42].

Ankle Simulations. Four muscles were included in an ankle model: dorsiflexors, soleus, gastrocnemius and other plantarflex-

Table 1 Parameters of the musculo-tendon model were adjusted to reflect nominal changes in muscle mechanics that occur between the ages of 30 and 70. In addition to the parameter adjustments shown, maximum isometric muscle forces were also reduced 30% from values used for young adults.

	τ_{deact} (ms)	$V^M_{\max}$ (L^M_o/s)	ε^M_0	$\bar{F}^M_{len}$
Young	50	10	0.6	1.4
Old	60	8	0.5	1.8

τ_{deact}-deactivation time constant, $V^M_{\max}$-maximum muscle contraction velocity expressed in optimal fiber lengths (L^M_o) per second, ε^M_0-passive muscle strain due to maximum isometric force, $\bar{F}^M_{len}$-ratio of maximum lengthening muscle force to isometric force.

Table 2 Muscle specific parameters used for the young males in the simulation of ankle exertions. For females, fiber lengths were scaled by the female-to-male height ratio and maximum isometric muscle forces were scaled by 0.75. Maximum isometric muscle forces assumed for old adults were 30% lower than those used for young adults.

Muscle	L_0^M (m)	$\overline{L_s^T}$	F_0^M (N)	α^M (deg)
Dorsiflexors	0.090	2.4	1400	7
Soleus	0.030	8.8	3150	25
Gastrocnemius	0.050	8.3	1750	14
Other Plantarflexors	0.031	10.0	3150	12

L_0^M-optimal muscle fiber length; $\overline{L_s^T}$-tendon slack length normalized to optimal muscle fiber length; F_0^M-maximum isometric muscle force; α^M-muscle fiber pennation angle.

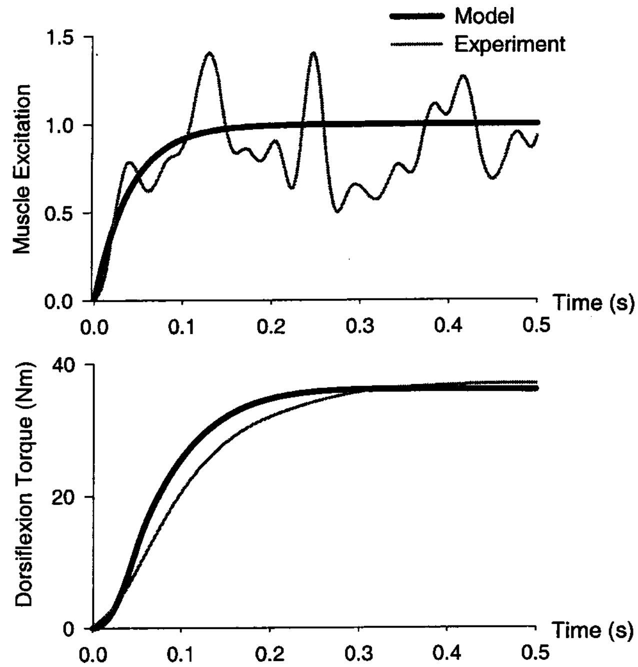

Fig. 2 Simulated muscle excitations and ankle torques during a rapid isometric contraction (thick lines). The experimental data (thin lines) are a representative tibialis anterior myoelectric signal and ensemble-averaged torque-time curve recorded from young adult males [7].

ors. The dorsiflexor muscle represented the tibialis anterior, extensor digitorum, peroneus tertius and extensor hallucis longus muscles. The gastrocnemius muscle included the medial and lateral components. The other plantarflexors muscle group included the tibialis posterior, flexor digitorum longus, flexor hallucis longus, peroneus brevis and peroneus longus. Muscle-specific parameters were based on the lower extremity musculo-skeletal model of Delp et al. [43] (Table 2). The four muscles were implemented into a 3-segment (foot, ankle, knee) model of the lower leg with segments connected by frictionless pin joints.

Because of the known gender differences in stature and muscle strength [e.g., 4,7], musculo-tendon model parameters were separately established to represent four subject groups: healthy young males (YM), young females (YF), old males (OM) and old females (OF). Segment lengths were scaled to body height [44], with heights set to represent average males (1.75 m) and females (1.62 m). Muscle fiber lengths, origins and insertions were scaled to stature, such that origins and insertions occurred at the same relative locations on the segments. Tendon length/fiber length ratios were assumed invariant. Maximum isometric muscle forces of females were set to 75% of the values used for males which, coupled with differences in stature, resulted in female/male torque ratios comparable to those measured experimentally (Table 3).

All modeling and analysis was conducted using ADAMS (Mechanical Dynamics Inc.; Ann Arbor, MI) a commercial dynamic simulation package. Custom subroutines were written and linked to ADAMS to simultaneously solve the differential equations describing activation and contraction dynamics.

Unit pulse muscle excitations of 5 ms duration were input to the models in order to estimate contraction times and one-half relaxation times of the young and old muscle models. Contraction time was defined as the time interval from the start of muscle excitation to the time of peak torque. One-half relaxation time was defined as the interval between peak torque and a decrease to one-half of peak torque.

In rapid isometric and isokinetic exertions, muscle excitation signals were obtained by passing a step function through a first order low-pass filter with a time constant of 40 ms (Fig. 2). The first order filter was used to represent the finite amount of time required to voluntarily recruit and fully excite all the motor units of a muscle [44,45,46]. Agonistic muscles were assumed to be fully excited. Antagonistic muscles were assumed to be partially excited (5%) since some antagonism is observed in maximal ankle exertions [45].

Joint angles were set to represent those prescribed experimentally. In all simulations, the knee was kept at 20 degrees of flexion. Isometric contractions in dorsiflexion and plantarflexion were simulated with the ankle at 10 degrees of plantarflexion and 5 degrees of dorsiflexion, respectively [7]. Isokinetic exertions were

Table 3 Simulated contraction times (CT) and one-half relaxation times ($\frac{1}{2}$RT) in response to unit pulse muscle excitations of 5 ms duration. Both simulations and experimental data reflect an age-related slowing in contraction and relaxation. The model predicted contraction times that tended to be slightly faster than experimental data, while predicted $\frac{1}{2}$RT were of comparable magnitude with measured values.

	Ankle Angle	CT (ms)		$\frac{1}{2}$RT (ms)	
		Young	Old	Young	Old
Dorsiflexion (DF)					
Simulated	10 deg PF	50	60	73	94
Vandervoort and McComas, 1986	30 deg PF	96 (8)	113 (10)	110 (12)	119 (28)
Van Schaik et al., 1994	10 deg PF	55 (9)	73 (5)	55 (8)	63 (6)
Plantarflexion (PF)					
Simulated	5 deg DF	88	104	87	122
Davies et al., 1983	10 deg PF	113 (11)	148 (15)	78 (4)	99 (13)
Vandervoort and McComas [1986]	10 deg DF	146 (21)	183 (23)	123 (12)	143 (27)

The ages (in years) of subjects included in the representative studies were: Davies et al., 1983: Young=20–24, Old=69.7±1.3
van Shaik et al., 1994: Young=20–40, Old=60–80 Vandervoort and McComas, 1986: Young=20–32, Old=70–80

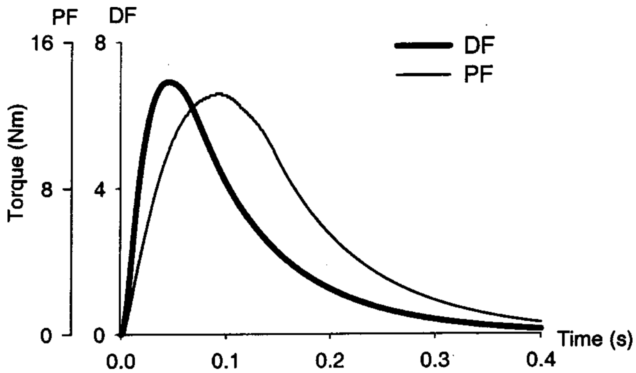

Fig. 3 Simulated contractions in dorsiflexion (DF) and plantarflexion (PF) in response to unit pulse muscle excitations of 5 ms duration. Model parameters representative of young adults were used. Contractions are prolonged in plantarflexion due to larger tendon length/fiber length ratios in the plantarflexor muscles.

simulated at velocities ranging from 240 deg/s shortening to 240 deg/s lengthening. All isokinetic exertions were simulated between 15 degrees of dorsiflexion and 45 degrees of plantarflexion, with the onset of muscle excitation occurring at the start of the simulation.

Experimental Data. Isometric and isokinetic simulations were compared with ankle torques recorded from 24 healthy young (age 19–29) and 24 healthy old (age 65–86 years) adults, equally divided into males and females [7]. All subjects performed isometric and isokinetic exertions (30, 60, 120, 180 and 240 deg/s) in dorsiflexion and plantarflexion on an isokinetic dynamometer (MERAC, Universal Gym Equipment; Cedar Rapids, IA). Subjects lay supine with body motions other than ankle rotation restricted by straps over the lower leg, upper leg, waist and shoulders. The preferred foot, defined as the foot that the subject selected to kick a ball, was strapped to a footplate attached to a dynamometer. Footplate angular position and exerted ankle torque were continuously monitored, the former using an optical encoder with a 90 count/deg resolution and the latter using a torque cell mounted on the dynamometer axis. Myoelectric signals were recorded from the tibialis anterior, soleus, and medial and lateral gastrocnemius muscles using bipolar surface electrodes. Further details of the experimental setup and data analysis can be found elsewhere [7,45].

Results

Contraction and Relaxation Times. The simulated contractions in response to the unit pulse excitations demonstrated a twitch-like response, with a fast rise to a peak torque and relatively slow fall off of torque thereafter (Fig. 3). As found experimentally, simulated contraction times and one-half relaxation times were prolonged for old adults compared to young adults (Table 3).

Rapid Isometric Exertions. Simulated maximum plantarflexion and dorsiflexion torques were generally within one standard deviation of mean isometric strengths measured experimentally for each subject group (Table 4). The estimated time required to reach 50% of maximum torque from rest was prolonged in old adults, by 8% in dorsiflexion and 12% in plantarflexion.

Isokinetic Exertions. The simulated torque-angle and torque-velocity curves were within one standard deviation of mean experimental values recorded during isokinetic dorsiflexion and plantarflexion exertions (Figs. 4 and 5). The percentage losses in strength with age were predicted to be larger during concentric contractions than during isometric or eccentric contractions. For example, young males were estimated to develop 253, 193 and 75 Nm during lengthening (120 deg/s), isometric and shortening (120 deg/s) contractions, respectively. Corresponding peak torques of old males were 18, 30 and 43% smaller, with the greatest percentage losses occurring during the highest speed shortening contractions.

Power Outputs. Compared to young adults, average power outputs of old adults during 120 deg/s shortening contractions were estimated to be 42 and 49% lower in dorsiflexion and plantarflexion, respectively. These differences are greater than the 30% loss in isometric strength assumed in the model, but in relative agreement with the 39–44% reductions in power outputs measured in old adults (Table 5).

Discussion

An objective of this study was to review how to adjust Hill-type muscle model parameters to reflect age-related changes in muscle mechanics. A second objective was to assess whether using the parameter adjustments results in simulated ankle torque behavior that is consistent with measurements from healthy old adults. The primary parameter adjustment is to decrease maximum isometric muscle forces to account for the substantial loss of isometric strength in older adults. A review of the literature suggests other modest parameter adjustments are needed to account for prolonged muscular deactivation (τ_{deact}), a reduction in maximum

Table 4 Maximum isometric ankle torques and times required to reach 50% of maximum torque (T_{50}) during simulations of rapid isometric contractions from rest. The mean (SD) maximal isometric torques and T_{50} values from experimental studies are shown for comparison. T_{50} values are not shown separately for males and females since simulated values were identical for each gender.

	Max Isometric Torque (Nm)				T_{50} (ms)	
	Young Females	Old Females	Young Males	Old Males	Young	Old
Dorsiflexion						
Simulated	34	24	49	35	62	67
Vandervoort and McComas, 1986	27 (5)	22 (4)	44 (7)	32 (9)		
Thelen et al., 1996	28 (4)	22 (3)	43 (8)	37 (5)	83 (20)	91 (20)
Plantarflexion						
Simulated	134	94	193	143	102	114
Vandervoort and McComas, 1986	113 (35)	94 (27)	171 (34)	121 (31)		
Thelen et al., 1996	130 (27)	88 (21)	181 (38)	137 (32)	142 (23)	152 (55)

The ages (in years) of subjects included in the representative studies were: Vandervoort and McComas, 1986: Young=20–32, Old=70–80
Thelen et al., 1996: Young=19–29, Old=65–86

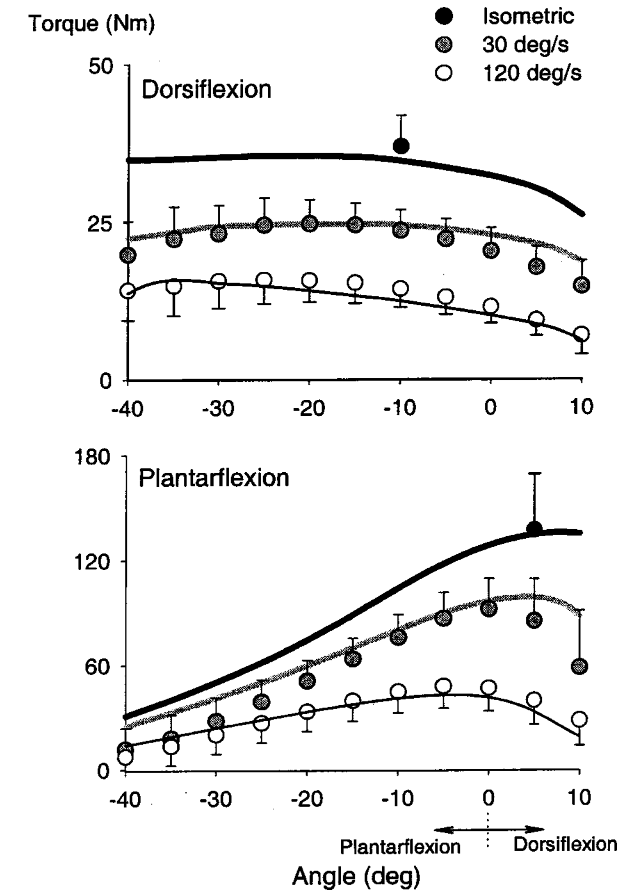

Fig. 4 Simulated torque-angle curves for isometric (thick black lines), 30 deg/s (thick gray lines) and 120 deg/s (thin black lines) isokinetic contractions using model parameters representative of older males. The superimposed points are the mean (error bar=1 SD) torques recorded experimentally from old males during isometric and isokinetic exertions [7].

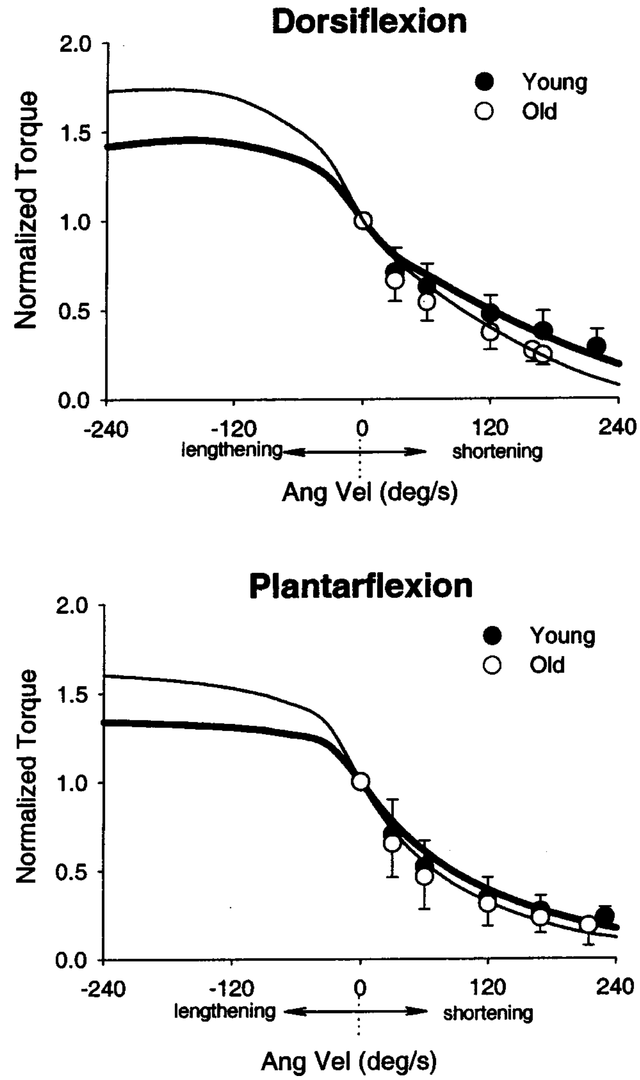

Fig. 5 Simulated peak ankle torques, normalized to maximal isometric torque, as a function of velocity during isokinetic dorsiflexion and plantarflexion exertions for young (thick lines) and old (thin lines) adults. Superimposed are the mean (error bar=1 SD) normalized torques recorded from healthy young and old adults [7].

contraction velocity ($V^M_{\max}$), greater passive muscle stiffness (ε^M_0) and increased normalized force capacity ($\overline{F}^M_{len}$) during lengthening contractions. With the parameter adjustments incorporated, a muscle-actuated model predicted age-related changes in dynamic ankle torque behavior that were consistent with experimental observations. More specifically, the model predicted the reduced ankle power output [7] and prolonged contraction and relaxation times [4,47,48] that are commonly observed in old adults.

Methodological Issues. Some limitations of this study should be considered. While the proposed parameter adjustments are qualitatively consistent with observed age-related changes in muscle, the quantitative magnitudes of the adjustments are less definitive. For example, maximum contraction velocities of muscle fibers have been found to slow with age [12] and a preferential reduction in fast-twitch muscle mass is often reported in humans [2,10]. However how these factors combine to contribute to slowing of the maximum contraction velocity of whole human muscle is difficult to measure and consequently not as well documented. In the model, a 20% reduction in maximum contraction velocity was assumed to occur with aging. This adjustment produced isokinetic torque-velocity relationships that were within one standard deviation of experimental data (Fig. 5). However, it is possible that other changes, e.g. a change in the curvature of the force-velocity relationship, could produce similar results. Given the parameter uncertainty, sensitivity studies are important when using musculo-tendon models in whole body movement simulations to better understand functional implications of specific changes in muscle properties on performance.

It is also noted that muscle mechanics changes with age can vary substantially across muscles [20,49]. For example, age-related losses in isometric strength in the lower extremity tend to be slightly more pronounced than in the upper extremity [3]. Consequently, further study is needed to ascertain how well the proposed global adjustments in a generic muscle model reflect age-related changes in torque development at joints other than the ankle.

Interpretation of Results. Parameter adjustments, other than simple scaling of isometric strength, were necessary to reflect observed age-related changes in dynamic muscle contractions. That is, if only maximum isometric forces are scaled for older subjects, then activation and contraction dynamics are unaltered and the dynamic muscle properties would be the same for young and old muscles. However it is known that this is not true and thus other parameter adjustments are necessary. For example, the proposed model predicted that contraction and one-half relaxation times

Table 5 Average power outputs (Watts) developed between 5 deg of dorsiflexion and 25 deg of plantarflexion during 120 deg/s isokinetic exertions. Mean (SD) experimental data for young and old adults are given for comparison. Simulated power outputs were 49% lower in dorsiflexion and 42% lower in plantarflexion when using the old adult muscle model parameters, which is comparable to the 39–44% power reductions measured in healthy old adults.

	Young Females (W)	Old Females (W)	Old/ Young (%)	Young Males (W)	Old Males (W)	Old/ Young (%)
Dorsiflexion						
Simulated	35	18	51	50	26	51
Thelen et al., 1996	21 (5)	12 (4)	56	36 (9)	22 (9)	60
Plantarflexion						
Simulated	96	56	58	139	80	58
Thelen et al., 1996	86 (28)	49 (19)	57	113 (41)	69 (30)	61

would be prolonged in older adults in response to a pulse excitation, which is consistent with experimental observations of stimulated twitch contractions [4,47,48]. A sensitivity study was conducted and found that the prolonged contractions predicted by the model were primarily a result of the assumed decrease in maximum contraction velocity and increase in the deactivation time constant.

The model also predicted that ankle power development during high-speed shortening is adversely compromised with aging. This effect resulted from the assumed changes to the normalized force-velocity function with age: i.e., a decrease in the maximum contraction velocity and increase in the maximum normalized force during lengthening. The result of these parameter adjustments was a larger percentage loss in joint torque, and correspondingly power, development at high contraction velocities that that seen during isometric or lengthening contractions. This prediction is consistent with isokinetic strength studies, which have found that eccentric strength is better preserved in old age than isometric or concentric strength [5,8,31,50].

In summary, accounting for changes in muscle properties is an important consideration when using forward dynamic models to interpret movement performance of older adults, particularly when simulating tasks that require large strengths, rapid changes in force or substantial power development.

Acknowledgments

The financial support of the National Science Foundation (BES-9702275), the National Institute on Aging (AG13759-01) and the contributions of the University of Michigan Biomechanics Research Laboratory to the experimental portion of this study are gratefully acknowledged.

Appendix

Following is a description of the state equations used to describe activation dynamics, musculo-tendon contraction dynamics, and the constitutive relationships assumed for muscle and tendon. Note that force and length quantities are normalized to maximum isometric muscle force (F_0^M) and optimal muscle fiber length (L_0^M), respectively.

Activation Dynamics. An idealized muscle excitation signal (u), a dimensionless quantity between 0 and 1, is used as the input to each of the muscles. The muscular excitation is related to the muscular activation (a) by a non-linear first order differential equation:

$$\frac{da}{dt} = \frac{u-a}{\tau_a(a,u)} \tag{1}$$

where $\tau_a(a,u)$ is a time constant that varies with activation level and whether the muscle activation level is increasing or decreasing [19]:

$$\tau_a(a,u) = \begin{cases} \tau_{act}(0.5+1.5a); & u > a \\ \tau_{deact}/(0.5+1.5a); & u \leqslant a \end{cases} \tag{2}$$

where τ_{act} is the activation time constant and τ_{deact} is the deactivation time constant. This relationship predicts that the activation slows as activation level increases due to less efficient calcium release and diffusion. Similarly deactivation slows when muscle activation level decreases due to there being less calcium ions available for uptake by the sarcoplasmic reticulum [19].

Muscle and Tendon Properties. The passive force-length relationship of muscle is represented by an exponential function:

$$\bar{F}^{PE} = \frac{e^{k^{PE}(\bar{L}^M - 1)/\varepsilon_0^M} - 1}{e^{k^{PE}} - 1} \tag{3}$$

where $\bar{F}^{PE}$ is the normalized passive muscle force, k^{PE} is an exponential shape factor, and ε_0^M is the passive muscle strain due to maximum isometric force. The shape factor, k^{PE}, was set equal to five, while ε_0^M was set differently for young and old adults as described in the Methods.

The active force-length relationship of muscle is represented by a Gaussian function [46]

$$f_l = e^{-(\bar{L}^M - 1)^2/\gamma} \tag{4}$$

where f_l is an active force-length scale factor, $\bar{L}^M$ is the normalized muscle fiber length, and γ is a shape factor. A value of 0.45 was selected for γ which approximates the force-length relationship of individual sarcomeres [51].

The force-strain relationship of tendon is represented by an exponential function during an initial nonlinear toe region and by a linear function thereafter:

$$\bar{F}^T = \begin{cases} \dfrac{\bar{F}_{toe}^T}{e^{k_{toe}} - 1}(e^{k_{toe}\varepsilon^T/\varepsilon_{toe}^T} - 1); & \varepsilon^T \leqslant \varepsilon_{toe}^T \\ k_{lin}(\varepsilon^T - \varepsilon_{toe}^T) + \bar{F}_{toe}^T; & \varepsilon^T > \varepsilon_{toe}^T \end{cases} \tag{5}$$

where $\bar{F}^T$ is the tendon force normalized to maximum isometric force, ε^T is the tendon strain, ε_{toe}^T is the tendon strain above which the tendon exhibits linear behavior, k_{toe} is an exponential shape factor and k_{lin} is a linear scale factor. A value of 3 was used for k_{toe}. The transition from nonlinear to linear behavior was prescribed to occur for normalized tendon forces greater than $\bar{F}_{toe}^T = 0.33$ [38]. Requiring continuity of slopes at the transition resulted in $\varepsilon_{toe}^T = 0.609\varepsilon_0^T$ and $k_{lin} = 1.712/\varepsilon_0^T$.

Musculo-Tendon Contraction Dynamics. Musculo-tendon contraction dynamics accounts for the interaction of the activation-force-length-velocity properties of muscle and the elastic properties of tendon. In particular, the muscle fiber velocity (V^M) is assumed to be a unique function of the muscle fiber length ($\bar{L}^M$), muscle activation (a) and active muscle force ($\bar{F}^M$):

$$V^M = (0.25 + 0.75a) V^M_{\max} \frac{\overline{F}^M - af_l}{b} \quad (6)$$

where $V^M_{\max}$ is the maximum contraction velocity and the parameter b is computed differently depending on whether the muscle fiber is shortening ($\overline{F}^M \leqslant af_l$) or lengthening ($\overline{F}^M > af_l$):

$$b = \begin{cases} af_l + \overline{F}^M / A_f; & \overline{F}^M \leqslant af_l \\ \dfrac{(2 + 2/A_f)(af_l \overline{F}^M_{len} - \overline{F}^M)}{(\overline{F}^M_{len} - 1)}; & \overline{F}^M > af_l \end{cases} \quad (7)$$

In Eq. (7), $\overline{F}^M_{len}$ is the maximum normalized muscle force achievable when the fiber is lengthening and A_f is a force-velocity shape factor, which was set to 0.25 [19]. At zero velocity, the slope of the force-velocity curve for lengthening contractions was assumed to be twice as large as that for shortening [52]. Values for $V^M_{\max}$ and $\overline{F}^M_{len}$ were set differently for young and old adults as discussed in the Methods.

In each of the simulations, the equations describing activation and contraction dynamics (Eq. 1 & 6) were numerically integrated along with the equations of motion in order to compute the time-varying activations and muscle fiber lengths. At each time step in the stimulation, the muscle fiber length was used along with the musculo-tendon length and pennation angle to compute the normalized tendon length ($\overline{L}^T = \overline{L}^{MT} - \overline{L}^M \cos \alpha^M$) and corresponding tendon force ($\overline{F}^T$) that was applied to the segments in the model.

References

[1] Aoyagi, Y., and Shephard, R. J., 1992, ''Aging and Muscle Function,'' Sports Med., **14**, pp. 376–396.
[2] Doherty, T. J., Vandervoort, A. A., and Brown, W. F., 1993, ''Effects of Ageing on the Motor Unit: A Brief Review,'' Can. J. Appl. Physiol., **18**, pp. 331–358.
[3] Brooks, S. V., and Faulkner, J. A., 1994, ''Skeletal Muscle Weakness in Old Age: Underlying Mechanisms,'' Med. Sci. Sports Exercise, **26**, pp. 432–439.
[4] Vandervoort, A. A., and McComas, A. J., 1986, ''Contractile Changes in Opposing Muscles of the Human Ankle Joint with Aging,'' J. Appl. Physiol., **61**, pp. 361–367.
[5] Vandervoort, A. A., Chesworth, B. M., Cunningham, D. A., Paterson, D. H., Rechnitzer, P. A., and Koval, J. J., 1992, ''Age and Sex Effects on Mobility of the Human Ankle,'' J Gerontol Med Sci, **47**, pp. M17–21.
[6] Gajdosik, R. L., Vander Linden, D. W., and Williams, A. K., 1996, ''Influence of Age on Concentric Isokinetic Torque and Passive Extensibility Variables of the Calf Muscles of Women,'' Eur. J. Appl. Physiol., , **74**, pp. 279–286.
[7] Thelen, D. G., Schultz, A. B., Alexander, N. B., and Ashton-Miller, J. A., 1996, ''Effects of Age on Rapid Ankle Torque Development,'' J Gerontol Med Sci, **51A**, pp. M226–232.
[8] Porter, M. M., Vandervoort, A. A., and Kramer, J. F., 1997, ''Eccentric Peak Torque of the Plantar and Dorsiflexors is Maintained in Older Women,'' J Gerontol Bio Sci, **52A**, pp. B125–B131.
[9] Lexell, J., Henriksson-Larsén, K., Winblad, B., and Sjöström, M., 1983, ''Distribution of Different Fiber Types in Human Skeletal Muscles: Effects of Aging Studied in Whole Muscle Cross-sections,'' Muscle Nerve, **6**, pp. 588–595.
[10] Lexell, J., 1993, ''Ageing and Human Muscle: Observations from Sweden,'' Can. J. Appl. Physiol., **18**, pp. 19–30.
[11] Cartee, G. D., 1995, ''What Insights into Age-Related Changes in Skeletal Muscles are Provided by Animal Models?'' J. Gerontol., Ser. A, , **50A**, pp. 137–141.
[12] Larsson, L., Li, X., and Frontera, W. R., 1997, ''Effects of Aging on Shortening Velocity and Myosin Isoform Composition in Single Human Skeletal Muscle Cells,'' Am. J. Physiol., **272**, pp. C638–649.
[13] Winter, D. A., Patla, A. E., Frank, J. S., and Walt, S. E., 1990, ''Biomechanical Walking Pattern Changes in the Fit and Healthy Elderly,'' Phys. Ther., , **70**, pp. 340–347.
[14] Kerrigan, D. C., Todd, M. K., Della Croce, U., Lipsitz, L. A., and Collins, J. J., 1998, ''Biomechanical Gait Alterations Independent of Speed in the Healthy Elderly: Evidence for Specific Limiting Impairments,'' Arch. Phys. Med. Rehabil., **79**, pp. 317–322.
[15] Schultz, A. B., Ashton-Miller, J. A., and Alexander, N. B., 1997, ''What Leads to Age and Gender Differences in Balance Maintenance and Recovery,'' Muscle Nerve Suppl., **5**, pp. S60–64.
[16] Raasch, C. C., Zajac, F. E., Ma, B., and Levine, W. S., 1997, ''Muscle Coordination of Maximum-Speed Pedaling,'' J. Biomech., **30**, pp. 595–602.
[17] Anderson, F. C., and Pandy, M. G., 2001, ''Dynamic Optimization of Human Walking,'' J. Biomech. Eng., **123**, pp. 381–390.
[18] Zajac, F. E., 1989, ''Muscle and Tendon: Properties, Models, Scaling and Application to Biomechanics and Motor Control,'' Crit. Rev. Biomed. Eng., **17**, pp. 359–411.
[19] Winters, J. M., 1995, ''An Improved Muscle-Reflex Actuator for Use in Large-Scale Neuromusculoskeletal Models,'' Ann. Biomed. Eng., **23**, pp. 359–374.
[20] Brown, M., and Hasser, E. M., 1996, ''Complexity of Age-Related Changes in Skeletal Muscle,'' J Gerontol: Biol Sci, **51A**, pp. B117–B123.
[21] Young, A., Stokes, M., and Crowe, M., 1984, ''Size and Strength of the Quadriceps Muscles of Old and Young Women,'' Eur. J. Clin. Invest., , **14**, pp. 282–287.
[22] Frontera, W. R., Hughes, V. A., Lutz, K. J., and Evans, W. J., 1991, ''A Cross-Sectional Study of Muscle Strength and Mass in 45- to 78-yr-Old Men and Women,'' J. Appl. Physiol., **71**, pp. 644–650.
[23] Xiaopeng, L., and Larsson, L., 1996, ''Maximum Shortening Velocity and Myosin Isoforms in Single Muscle Fibers from Young and Old Rats,'' Am. J. Physiol., **270**, pp. C352–C360.
[24] Thompson, L. V., and Brown, M., 1999, ''Age-Related Changes in Contractile Properties of Single Skeletal Fibers from the Soleus Muscle,'' J. Appl. Physiol., **86**, pp. 881–986.
[25] Larsson, L., Grimby, G., and Karlsson, J., 1979, ''Muscle Strength and Speed of Movement in Relation to Age and Muscle Morphology,'' J. Appl. Physiol., **46**, pp. 451–456.
[26] Fitts, R. H., Troup, J. P., Witzmann, F. A., and Holloszy, J. O., 1984, ''The Effect of Ageing and Exercise on Skeletal Muscle Function,'' Mech. Ageing Dev., **27**, pp. 161–72.
[27] Brooks, S. V., and Faulkner, J. A., 1988, ''Contractile Properties of Skeletal Muscles from Young, Adult and Aged Aice,'' J Physiol, **404**, pp. 71–82.
[28] Phillips, S. K., Bruce, S. A., and Woledge, R. C., 1991, ''In Mice, the Muscle Weakness due to Age is Absent During Stretching,'' J Physiol, **437**, pp. 63–70.
[29] Brooks, S. V., and Faulkner, J. A., 1994, ''Isometric, Shortening and Lengthening Contractions of Muscle Fiber Segments from Adult and Old Mice,'' Am. J. Physiol., **267**, pp. C507–C513.
[30] Vandervoort, A. A., Kramer, J. F., and Wharram, E. R., 1990, ''Eccentric Knee Strength of Elderly Females,'' J Gerontol Biol Sci, **45**, pp. B125–B128.
[31] Hortobagyi, T., Zheng, D., Weidner, M., Lambert, N. J., Westbrook, S., and Houmard, J. A., 1995, ''The Influence of Aging on Muscle Strength and Muscle Fiber Characteristics with Special Reference to Eccentric Strength,'' J Gerontol Biol Sci, **50A**, pp. B399–406.
[32] Brown, M., Fisher, J. S., and Salsich, G., 1999, ''Stiffness and Muscle Function with Age and Reduced Muscle Use,'' J. Orthop. Res., **17**, pp. 409–414.
[33] Alnaqeeb, M. A., Al Zaid, N. S., and Goldspink, G., 1984, ''Connective Tissue Changes and Physical Properties of Developing and Ageing Skeletal Muscle,'' J. Anat., **139**, pp. 677–689.
[34] Kent-Braun, J. A., Alexander, V. N., and Young, K., 2000, ''Skeletal Muscle Contractile and Noncontractile Components in Young and Older Women and Men,'' J. Appl. Physiol., **88**, pp. 662–668.
[35] Larsson, L., and Salviati, G., 1989, ''Effects of Age on Calcium Transport Activity of Sarcoplasmic Reticulum in Fast- and Slow-Twitch Rat Muscle Fibres,'' J Physiol, **419**, pp. 253–264.
[36] Narayanan, N., Jones, D. L., Xu, A., and Yu, J. C., 1996, ''Effects of Aging on Sarcoplasmic Reticulum Function and Contraction Duration in Skeletal Muscles of the Rat,'' Am. J. Physiol., **271**, pp. C1032–C1040.
[37] Hunter, S. K., Thompson, M. W., Ruell, P. A., Harmer, A. R., Thom, J. M., Gwinn, T. H., and Adams, R. D., 1999, ''Human Skeletal Sarcoplasmic Reticulum Ca^{2+} Uptake and Muscle Function with Aging and Strength Training,'' J. Appl. Physiol., **86**, pp. 1858–1865.
[38] Proske, U., and Morgan, D. L., 1987, ''Tendon Stiffness: Methods of Measurement and Significance for the Control of Movement. A Review.'' J. Biomech., **20**, pp. 75–82.
[39] Blevins, F. T., Hecker, A. T., Bigler, G. T., Boland, A. L., and Hayes, W. C., 1994, ''The Effects of Donor Age and Strain Rate on the Biomechanical Properties of Bone-Patellar Tendon-Bone Allografts,'' Am. J. Sports Med., , **22**, pp. 328–333.
[40] Lewis, G., and Shaw, K. M., 1997, ''Tensile Properties of Human Tendo Achillis: Effect of Donor Age and Strain Rate,'' J. Foot Ankle Surg., **36**, pp. 435–445.
[41] Johnson, G. A., Tramaglini, D. M., Levine, R. E., Ohno, K., Choi, N. Y., and Woo, S. L., 1994, ''Tensile and Viscoelastic Properties of Human Patellar Tendon,'' J. Orthop. Res., **12**, pp. 796–803.
[42] Nakagawa, Y., Hayashi, K., Yamamoto, N., and Nagashima, K., 1996, ''Age-Related Changes in Biomechanics Properties of the Achilles Tendon in Rabbits,'' Eur. J. Appl. Physiol., , **73**, pp. 7–10.
[43] Delp, S. L., Loan, J. P., Hoy, M. G., Zajac, F. E., Topp, E. L., and Rosen, J. M., 1990, ''An Interactive Graphics-Based Model of the Lower Extremity to Study Orthopaedic Surgical Procedures,'' IEEE Trans. Biomed. Eng., **37**, pp. 757–67.
[44] Winter, D. A., 1990, *Biomechanics and Motor Control of Human Movement*, 2nd Ed., Wiley, New York, NY.
[45] Thelen, D. G., Ashton-Miller, J. A., Schultz, A. B., and Alexander, N. B., 1996, ''Do Neural Factors Underlie Age Differences in Rapid Ankle Torque Development?'' J. Am. Geriatr. Soc., **44**, pp. 804–808.
[46] Winters, J. M., 1990, ''Hill-Based Muscle Models: A Systems Engineering Perspective,'' in Multiple Muscle Systems: Biomechanics and Movement Organization, edited by JM Winters and SL Woo, Springer-Verlag, New York.
[47] Davies, C. T. M., and White, M. J., 1983, ''Contractile Properties of Elderly Human Triceps Surae,'' Gerontology, **29**, pp. 19–25.
[48] van Schaik, C. S., Hicks, A. L., and McCartney, N., 1994, ''An Evaluation of

the Length-Tension Relationship in Elderly Human Ankle Dorsiflexors,'' J Gerontol Biol Sci, **49**, pp. 121–127.
[49] Staron, R. S., 1997, ''Human Skeletal Muscle Fiber Types: Delineation, Development and Distribution,'' Can. J. Appl. Physiol., **22**, pp. 307–327.
[50] Poulin, M. J., Vandervoort, A. A., Paterson, D. H., Kramer, J. F., and Cunningham, D. A., 1992, ''Eccentric and Concentric Torques of Knee and Elbow Extension in Young and Older Men,'' Can. J. Sport Sci., **17**, pp. 3–7.
[51] Gordon, A. M., Huxley, A. F., and Julian, F. J., 1966, ''The Variation in Isometric Tension with Sarcomere Length in Vertebrate Muscle Fibres,'' J Physiol, **184**, pp. 170–192.
[52] Katz, B., 1939, ''The Relation Between Force and Speed in Muscular Contraction,'' J Physiol, **96**, pp. 45–64.