

Contractile and Elastic Ankle Joint Muscular Properties in Young and Older Adults

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Abstract

The purpose of this study was to investigate age-related differences in contractile and elastic properties of both dorsi- (DF) and plantarflexor (PF) muscles controlling the ankle joint in young and older adults. Experimental data were collected while twelve young and twelve older male and female participants performed maximal effort isometric and isovelocity contractions on a dynamometer. Equations were fit to the data to give torque-angle ($T\theta$) and torque-angular velocity ($T\omega$) relations. Muscle series-elasticity was measured during ramped dynamometer contractions using ultrasonography to measure aponeurosis extension as a function of torque; second order polynomials were used to characterize the torque-extension (TAL) relation. The results showed no age differences in DF maximal torque and none for female PF; however, older males had smaller maximal PF torques compared to young males. In both muscle groups and genders, older adults had decreased concentric force capabilities. Both DF and PF TAL relations were more nonlinear in the older adults. Older PF, but not DF muscles, were stiffer compared to young. A simple antagonism model suggested age-related differences in $T\theta$ and $T\omega$ relations would be magnified if antagonistic torque contributions were included. This assessment of static, dynamic, and elastic joint properties affords a comprehensive view of age-related modifications in muscle function. Although many clinical studies use maximal isometric strength as a marker of functional ability, the results demonstrate that there are also significant age-related modifications in ankle muscle dynamic and elastic properties.

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Introduction

The functional capabilities of the dorsi- (DF) and plantarflexor (PF) muscles controlling the ankle joint are important in many activities of daily living. Age-related degradations of muscular properties such as a decline in maximal isometric ankle torque can impact these activities [1]. However, maximal isometric torque capability is only one of several joint properties that may change with advancing age. Ankle torque production also depends on the joint position or angle (the torque-angle relation; $T\theta$), the joint angular velocity (the torque-angular velocity relation; $T\omega$), and the series elasticity (the torque-extension relation; TAL) of the muscles crossing the joint. Together, these three relations reflect the active contractile and elastic properties of the muscles controlling the ankle joint.

To date, studies investigating age-related changes in DF and PF joint $T\theta$ relations have produced equivocal results. Lanza et al. [2] have reported an angle-dependent decrease in torque for older adults; however, this might simply be due to their decreased range of motion [2]. Other studies have found no $T\theta$ changes for DF [3] or PF [4]. Studies on the $T\omega$ relation have generally shown reduced torque capability for concentric velocities for older DF [2,5] and PF [5,6] muscles, but some have found that eccentric torque production is preserved in older adults [7,8]. Technical aspects of $T\omega$ determination may play a role in variations between studies. Many studies select the peak torque values generated at a range of joint angular velocities,

and scale the data to the maximal value of the isometric $T\theta$ curve [5,9]. However, these peak torque data points may occur at different joint angles, therefore appropriate adjustments should be made to account for the shape of the underlying $T\theta$ relation [10].

Although the $T\theta$ and $T\omega$ relations reflect the force-length [11] and force-velocity [12] relations of human muscle, the exact relation between joint and muscle properties also depends on the stiffness of the muscular series elastic elements, which are characterized by the TAL relation. Studies on DF stiffness are scarce, while PF stiffness findings are equivocal. Quick-release studies [13,14,15] suggest an increase in PF stiffness with age, but an ultrasonography study showed a decrease [16]. This inconsistency may be due to measurement methods; the quick-release technique measures total muscle-tendon stiffness (K_{MT} ; including external tendon, aponeurosis, and within sarcomeres), while the ultrasonography study measured the stiffness of the external tendon K_{ET} . Animal studies have indicated that K_{ET} is greater than stiffness of the aponeurosis K_{AP} ([17,18,19]; although see [20,21]), so greater K_{MT} in older adults could result from an increase in K_{AP} , which can be measured in humans using ultrasonography.

It is important to recognize that the joint $T\theta$, $T\omega$, and TAL relations are closely intertwined, and that age-related changes in series elasticity may occur in tandem with $T\theta$ and $T\omega$ modifications, thereby complicating interpretations based on $T\theta$ and/or $T\omega$ measurements alone. The $T\theta$ relation affects the shape of the $T\omega$

relation [22,23], and series elastic stiffness (TAL) influences muscle fiber length and velocity, altering the shapes of the $T\theta$ and $T\omega$ relations [24]. Therefore, measuring $T\theta$ and $T\omega$ characteristics in parallel with the TAL relation may offer additional insight into age-related differences in functional capability.

Accordingly, the purpose of this study was to investigate age-related differences in static ($T\theta$), dynamic ($T\omega$), and elastic (TAL) characteristics of both dorsi- (DF) and plantarflexor (PF) muscles controlling the ankle joint in young and older adults. Based on evidence from previous studies, we anticipated that active community dwelling older adults would have smaller isometric torque capacities, slower concentric muscular properties (i.e. less torque at a given velocity on the $T\omega$ relation), and stiffer series elasticity in the aponeurosis TAL relation when compared to active young adults. We also expected to find greater age-related differences for the PF muscle group than in the DF, based on more atrophy of Type II fibers in the gastrocnemius [25]. Measuring all three $T\theta$, $T\omega$, and TAL properties in the DF and PF antagonist muscle groups provided a comprehensive snapshot of age-related differences in ankle joint function.

Methods

Twelve young and twelve older independent community-dwelling adults without musculoskeletal or neurological impairments participated in the study (balanced for gender, Table 1). Physician's clearance was obtained for all older subjects. Prior to participating, subjects read and signed an informed consent document approved by the University of Massachusetts Amherst Institutional Review Board. Subjects performed two experimental protocols, with all measurements taken on the left leg.

Torque-Angle ($T\theta$) and Torque-Angular Velocity ($T\omega$) Measurements

Experimental Setup. To measure the $T\theta$ and $T\omega$ relations, a series of isometric and isovelocity muscular efforts were performed on a Biodex System 3 dynamometer [26,27] (Biodex Medical Systems, Shirley, NY). Ankle torque and angular displacement were sampled from the dynamometer at 1000 Hz and 16-bit resolution with software written in Visual Basic 6.0 (Microsoft Corporation, Redmond, WA).

Protocol. Subjects sat upright with their trunk inclined backwards 45° from the vertical and arms crossed in front of their chest. After sub-maximal warm-up efforts, passive joint torque was measured by having the dynamometer slowly ($20^\circ/s$) move the ankle joint through its range of motion without active subject resistance. Isometric ($T\theta$) and isovelocity ($T\omega$) dynamometer trials were done on separate days to minimize fatigue. Two trials were performed at each joint angle (θ) and angular velocity (ω), with trial order randomized and a one-minute rest between trials. The knee

remained fixed at 100° for DF and 90° for PF. For isometric trials the ankle position was varied at five different angles evenly spaced throughout each subject's full range of motion. Concentric isovelocity trials were performed at $20^\circ/s$, and from 30 to $240^\circ/s$ in $30^\circ/s$ increments. Eccentric trials were performed at -150 , -60 , and $-30^\circ/s$. In all trials, passive elastic, gravitational, and inertial torque contributions were assessed to calculate the active muscular torque [28]. The passive torque-angle data were averaged across dorsi/plantarflexion trials (typically three per subject); a third-order polynomial was fit to these mean data to generate a passive torque-angle relationship. In the active trials, the polynomial was evaluated at the each instantaneous joint angle and subtracted from the measured torque. Torque contributions due to the weight and inertia of the foot, estimated from de Leva [29], and dynamometer arm, measured experimentally, were also subtracted. We did not account for joint viscosity and friction, as these make negligible contributions to the net joint torque compared with passive elastic, gravitational, and inertial effects [30].

Data Processing – Torque Angle ($T\theta$). For each subject, the larger of the two maximal isometric joint torque measurements at each ankle angle (T_{IM}) was used to construct a $T\theta$ relationship. The $T\theta$ relationship for each subject was expressed as a second order polynomial fit to the DF and PF T_{IM} vs. θ data using a least squares approach. The maximum of the polynomial within the measured range of motion was used to define the maximum isometric torque T_0 and the optimal angle θ_0 .

Data Processing – Torque Angular Velocity ($T\omega$)

The peak torque T_{IV} and corresponding ω from each isovelocity trial were used to construct a $T\omega$ relation. At peak torque all shortening/lengthening occurs via the contractile component, i.e. elastic component velocity is momentarily zero. Measured $T\omega$ data were also adjusted to account for $T\theta$ effects [2,10,31]. For each subject, the relation between θ and ω coinciding with the T_{IV} data points was established using linear regression, and used with the $T\theta$ relation to predict the isometric torque capability corresponding to each T_{IV} value. Each original $T\omega$ data point was divided by its angle-specific isometric torque capability to give scaled isovelocity peak torque (\bar{T}_{IV}) values (if $\bar{T}_{IV} = 1$ then T_{IV} was equal to the isometric torque at that angle). A rectangular hyperbola was fit to these scaled $T\omega$ data. Based on Hill [32], if ω (rad/s) is positive (concentric), then

$$\bar{T}_{IV} = \frac{(1 + A_{T\omega})B_{T\omega}}{\omega + B_{T\omega}} - A_{T\omega}$$

where $A_{T\omega}$ and $B_{T\omega}$ are coefficients describing the shape of the scaled $T\omega$ relation (Figure 1). For eccentric conditions, when ω is negative, based on FitzHugh [33]

Table 1. Subject characteristics.

Subject Group	N	Age (yrs)		Height (m)		Mass (kg)	
		Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range
Young Male	6	27 \pm 3	21–30	1.81 \pm 0.06	1.70–1.85	76.9 \pm 8.2	68.3–87.5
Young Female	6	26 \pm 3	21–31	1.65 \pm 0.08	1.52–1.74	57.2 \pm 6.6	49.9–65.8
Older Male	6	73 \pm 5	67–79	1.77 \pm 0.08	1.68–1.88	91.7 \pm 10.3	74.0–102
Older Female	6	70 \pm 5	66–78	1.66 \pm 0.09	1.60–1.70	72.6 \pm 17.0	59.3–77.4

N = number of subjects; SD = between-subjects standard deviation.
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$$\bar{T}_{IV} = T_{ECC} - \frac{s(T_{ECC} - 1)}{s - \omega}$$

where

$$s = \frac{B_{T\omega}(T_{ECC} - 1)}{1 + A_{T\omega}}$$

and T_{ECC} defines the eccentric plateau.

Torque-Extension (TAL) Measurements

Experimental Setup. To estimate DF and PF TAL relationships, ankle torque was measured as subjects performed a series of ramped maximal isometric efforts on the dynamometer. The tibialis anterior, lateral head of the gastrocnemius, and soleus muscles were imaged using an Acuson 128XP real-time ultrasonic scanner with a linear-array probe (7.5 MHz, 50 mm scanning length, B-mode). The ultrasound probe was orientated along the mid-sagittal axis of each muscle, with transmission gel used for improved acoustic coupling [34,35]. Ultrasound images (Figure 2A) were sampled at 30 Hz and saved to magnetic tape. With the knee extended, the ankle was positioned at 90° where passive contributions are minimal [36]. The torque data were sampled at 900 Hz with 16-bit resolution, using a 5V analog pulse for synchronization with the ultrasound data.

Protocol. Subjects performed two blocks of trials (DF, PF), with block order balanced across subjects. Within each block, two maximal voluntary contractions (MVCs) were performed to establish maximal isometric ankle torque, followed by five trials with torque and ultrasound measurements. In each 30-second trial, subjects were asked to match their ankle torque to a predefined green target force template that increased exponentially from 0 to 30% MVC, and linearly from 30 to 100% MVC (Figure 2C, solid line). The initial exponential increase was to ensure a slow rate of extension to facilitate subsequent image analysis. Red lines defined acceptable torque variation (Figure 2C, broken lines). During each trial, the subject's actual ankle torque appeared in real time. Subjects were instructed

to follow the green line as closely as possible. Trials were separated by two-minute rest periods.

Video Capture and Preprocessing. The ultrasound video was parsed into individual trials and converted to digital format (AVI, 720×480 pixels) using a video capture system (Studio MovieBox USB, Pinnacle Systems). Subsequent processing was done using MATLABTM (Version 7, The MathWorks, Natick MA). The 900 Hz torque data were downsampled to 30 Hz and synchronized with the ultrasound video using the rising edge of the analog pulse.

Tracking of Aponeurosis Extension. To measure extension, multiple points on the ultrasound images were identified: one set of eight superficial reference points evenly spaced near the skin, and a cluster of eight points along the aponeurosis (see Figure 2A). The movement of all points was automatically tracked using a two-dimensional cross-correlation tracking algorithm [37]. The tibialis anterior aponeurosis extension was assumed to represent the DF muscles (including the tibialis anterior, extensor hallucis longus, extensor digitorum longus, and peroneus tertius), while the extension of the combined gastrocnemius and soleus aponeuroses represented the PF muscles.

Data Processing. Horizontal and vertical point displacements and the torque data were smoothed using a Butterworth digital filter with optimal cut-off frequencies determined through residual and power spectral analyses [38]. The multiple reference and aponeurosis point displacements were averaged to give a single reference and aponeurosis time-series (Figure 2B). After subtraction of reference point motion to account for possible probe movement relative to the skin, the magnitude of the aponeurosis displacement vector was expressed as extension (ΔL) from the rest position. Highly variable data above 60% MVC torque were excluded from the subsequent fitting of a second order polynomial [16,39,40] to the ankle torque (T) vs. ΔL data (Figure 2D):

$$T = \alpha_{T\Delta L} \Delta L^2 + \beta_{T\Delta L} \Delta L$$

where $\alpha_{T\Delta L}$ and $\beta_{T\Delta L}$ are shape coefficients. The linear stiffness (K) was calculated as the slope of the fitted polynomials (i.e. $K = 2\alpha_{T\Delta L} \Delta L + \beta_{T\Delta L}$) at three different torque levels ($K_{Low} = 5$ Nm [DF], 15 Nm [PF]; $K_{Med} = 15$ Nm [DF], 30 Nm

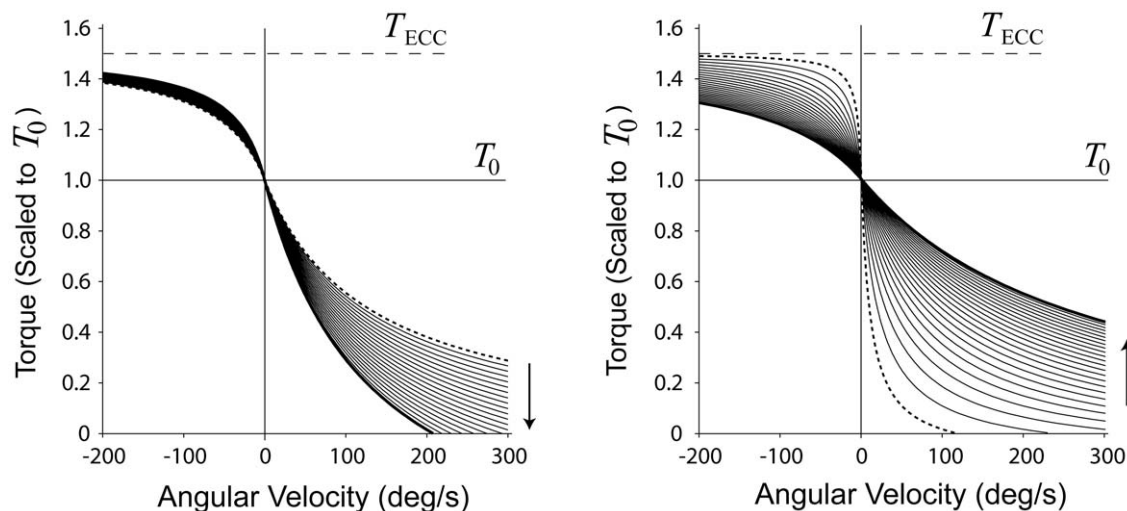


Figure 1. Effects of changing the coefficients describing the torque-angular velocity relation ($T\omega$). Left: effect of varying $A_{T\omega}$ from 0.02 to 0.62 while keeping $B_{T\omega} = 2.25$. Right: effect of varying $B_{T\omega}$ from 0.2 to 5.0 while keeping $A_{T\omega} = 0.1$. The eccentric plateau (T_{ECC}) was set to $1.5 T_0$. Dashed and thick solid lines indicate small and large values for each coefficient, respectively. doi:10.1371/journal.pone.0015953.g001

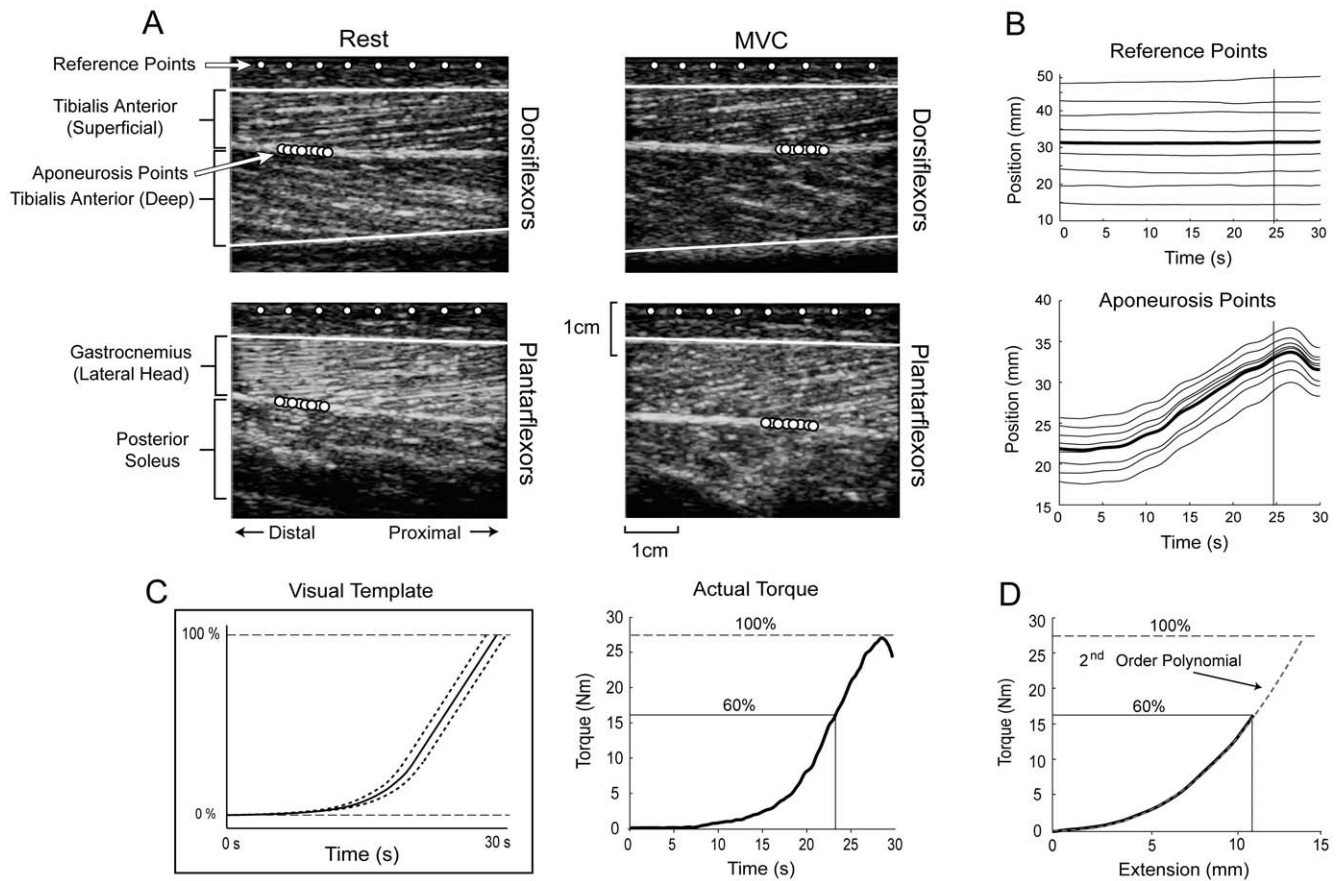


Figure 2. Methodology for measuring musculotendon series elasticity. A: Ultrasound stills from the start (left) and end (right, at MVC) of a dorsi- (top) and plantarflexion (bottom) ramped trial. The white dots indicate points of interest, including a set of reference points near the skin, and a set of points on the aponeurosis of each muscle. The motion of the points was tracked using an automated cross-correlation algorithm. B: Example of the horizontal displacements of the reference points (top) and aponeurosis points for a dorsiflexion trial (thick line = average). C: The visual torque-time template (left) and the actual dorsiflexion torque produced (right). D: The resulting torque vs. extension plot. A second order polynomial was fit to the torque up to 60% MVC, and then extended up to MVC (dashed line).
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[PF]; $K_{High} = 30$ Nm [DF], 60 Nm [PF]). The maximum extension of the series elastic components (ΔL_{MAX}) was assessed by evaluating the polynomial equation at MVC.

Statistics

Due to technical issues affecting torque measurement, one of the young male subjects was excluded from the $T\theta$ and $T\omega$ analysis. Separate three-way ANOVAs (age [Y,O] x gender [M,F] x muscle [PF,DF]) were performed on each dependent variable. The dependent variables included two $T\theta$ variables (T_0 , θ_0) and three $T\omega$ variables ($A_{T\omega}$, $B_{T\omega}$, and T_{ECC}). For the TAL relations, the three dependent variables were α_{TAL} , β_{TAL} and ΔL_{MAX} . Separate two-way ANOVAs (age x gender) were performed for DF and PF linear stiffness measures (K_{Low} , K_{Med} , K_{High}); an additional one-way ANOVA was performed to test for muscle group difference at the same absolute torque level (15 Nm). Outliers were defined as data points that exceeded the mean by more than three times the interquartile range. Statistical significance for all tests was set at $p \leq .05$.

Results

Torque-Angle ($T\theta$)

Individual subject $T\theta$ and $T\omega$ relations are shown in Figure 3; summary statistics are given in Table 2, with age group mean curves shown in Figure 4. For maximal isometric torque T_0 , there

was a main effect of age, with T_0 greater in the young compared to old ($p = .028$), and a main effect of muscle, with PF greater than DF ($p < .001$). There was also a three-way interaction between age, gender, and muscle ($p = .034$) (Figure 5). No age-related differences were found in females for DF T_0 ($p = .794$) or PF T_0 ($p = .161$), or for DF T_0 in males ($p = .587$), but older males had significantly weaker PF compared to younger males ($p < .001$). There was a main effect of muscle for optimal angle θ_0 ($p < .001$), with θ_0 occurring at a more plantarflexed position for DF (at $+14^\circ$ of plantarflexion) than for PF (at -14° of dorsiflexion), but there were no θ_0 effects for age ($p = .834$) or gender ($p = .201$).

Torque-Angular Velocity ($T\omega$)

Compared to the younger individuals, older adults produced less torque relative to T_0 for concentric velocities, as indicated by the smaller $T\omega$ shape coefficient $B_{T\omega}$ (Table 2 and Figures 3 and 4; age main effect $p = .003$). There were no main effects of gender ($p = .935$) or muscle ($p = .977$). There were no effects of age, gender, or muscle on the $T\omega$ parameters $A_{T\omega}$ ($p > .110$ for all tests) or T_{ECC} ($p > .192$ for all tests).

Torque-Extension (TAL)

Individual subject TAL relations are shown in Figure 6. For these second order polynomial relations, older subjects had larger

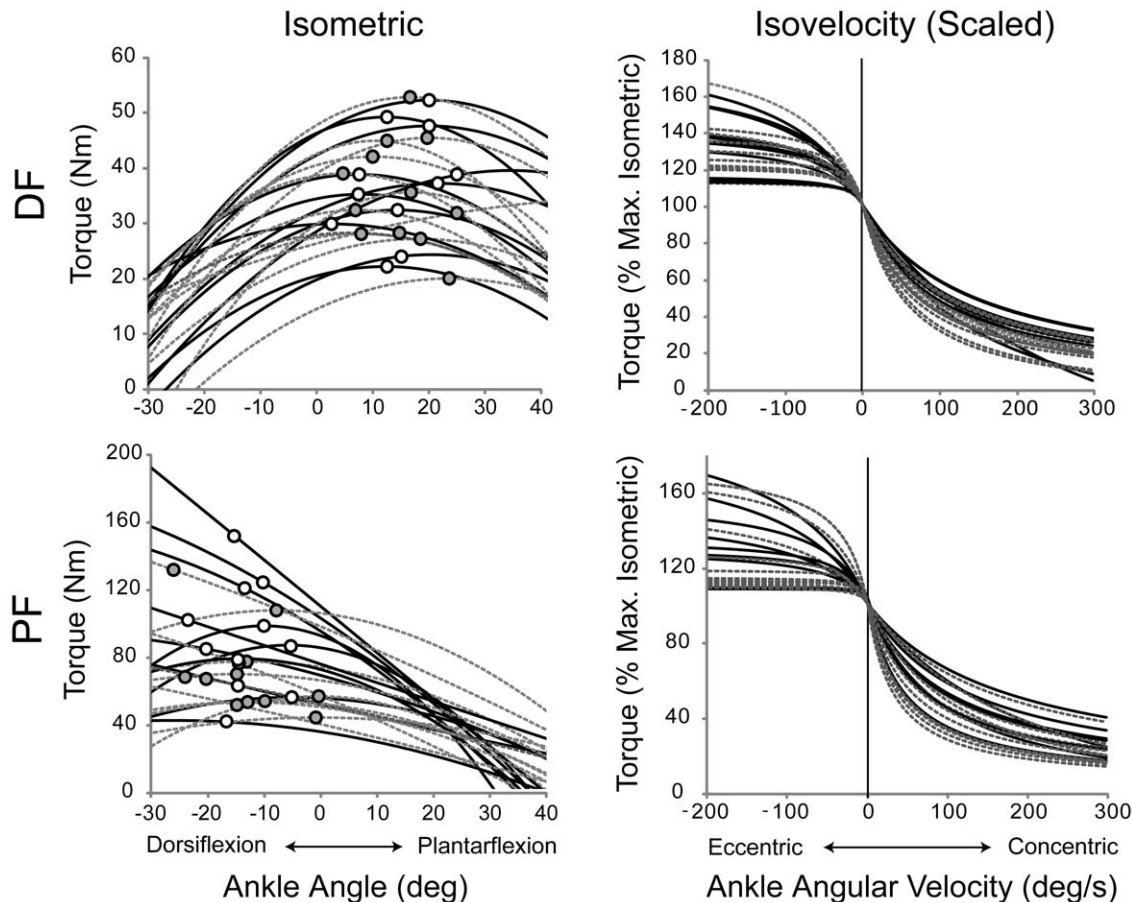


Figure 3. Equations representing the best fit between the experimental data and second order polynomials (torque-angle relation; isometric) and rectangular hyperbolas (torque-angular velocity relation; isovelocicity) for young (solid black lines) and older (dashed gray lines). The solid circles positioned on the isometric curves represent the peak isometric torque. For some subjects, the peak did not occur within the subject's range of motion, in these cases the solid circle is positioned at the end of the range of motion. The isovelocicity fits are scaled to the peak isometric torques.
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α_{TAL} coefficients (Table 3; $p = .009$), but no differences for β_{TAL} ($p = .457$). Both coefficients were larger for PF compared to DF (α_{TAL} ; $p = .002$; β_{TAL} ; $p < .001$). There were no gender differences for either coefficient (α_{TAL} ; $p = .706$; β_{TAL} ; $p < .343$). There were no age effects for DF at any linear stiffness level (K_{Low} , K_{Med} , K_{High}) ($p > .691$), and none for PF at K_{Low} ($p = .143$) and K_{Med} ($p = .058$). However, K_{High} was greater for the older subjects ($p = .031$). There were no gender differences at any K for DF ($p > .538$) or PF ($p > .231$). When comparing K at the same absolute torque level (15 Nm), the PF muscles were stiffer than the DF ($p < .001$). Older adults had smaller maximal aponeurosis extensions (5.7 mm) than the younger subjects (8.8 mm) (ΔL_{MAX} ; $p < .001$). There was an age by muscle interaction for maximal extension ($p = .015$), with PF ΔL_{MAX} smaller than DF ($p = .017$) for the older subjects, but not for the young ($p = .388$).

Discussion

The hypothesis of lower maximal isometric torques (T_0) in the older adults was supported partially; only the older male subjects had lower T_0 , and only in the PF muscle group. There was stronger support for the hypotheses of decreased concentric force capabilities and increased series elastic stiffness in the older adults; however, the latter was observed only for PF. We also expected to

find greater age-related differences for PF compared to DF due to previous reports of Type II fiber atrophy in the gastrocnemius in older adults. This was observed for the male PF T_0 as well as the PF stiffness; however, age-related reductions in concentric force capabilities were found for both DF and PF. No differences were found between age groups in the optimal joint angle of the $T\theta$ relation, or in eccentric torque capabilities.

Torque-Angle

As in prior studies [1,2,41], we found age-related deficits in maximal isometric joint strength (T_0), but only for PF in male subjects; females showed no age-related differences. Kent-Braun and Ng [42] reported a similar interaction for DF, with T_0 greater in young men than older, but not in the females. Other support for an age and gender interaction is provided by Winegard et al. [4], in which older female subjects had larger PF T_0 values than older males, and did not show significant age-related deficits in strength. These findings could be related to age-related decreases in male testosterone concentrations [43], which is associated with decreased muscle mass and strength [44,45]. We saw no age-related differences for the angle of peak torque (θ_0), consistent with Simoneau and colleagues [46], who found no variations with age in the DF and PF $T\theta$ relations. We also observed that the angle at maximum torque (θ_0) was not different between the age/gender

Table 2. Parameters characterizing torque-angle ($T\theta$) and torque-angular velocity ($T\omega$) data (mean \pm between-subjects standard deviation).

Group	Muscle Group	$T\theta$		$T\omega$		
		T_0 (Nm)	θ_0 ($^\circ$)	$A_{T\omega}$	$B_{T\omega}$	T_{ECC}
Young Male ^a	DF	42.1 \pm 8.70	14.3 \pm 5.28	0.030 \pm 0.078	2.12 \pm 0.43	1.48 \pm 0.31
	PF	114 \pm 28.1	-12.7 \pm 2.48	0.350 \pm 0.585	3.19 \pm 3.04	1.37 \pm 0.35
Young Female	DF	30.9 \pm 7.40	13.6 \pm 8.25	0.241 \pm 0.358	2.81 \pm 1.27	1.43 \pm 0.20
	PF	70.9 \pm 22.8	-14.3 \pm 7.65	0.240 \pm 0.535	2.15 \pm 1.58	1.35 \pm 0.41
Young Average	DF	36.5 \pm 8.10	13.9 \pm 6.77	0.136 \pm 0.218	2.47 \pm 0.85	1.46 \pm 0.26
	PF	92.5 \pm 25.5	-13.5 \pm 5.07	0.295 \pm 0.560	2.67 \pm 2.31	1.36 \pm 0.38
Older Male	DF	35.2 \pm 7.20	16.0 \pm 6.15	0.029 \pm 0.044	1.31 \pm 0.28	1.30 \pm 0.12
	PF	61.4 \pm 9.72	-12.8 \pm 7.74	0.034 \pm 0.068	1.53 \pm 0.82	1.21 \pm 0.20
Older Female	DF	34.1 \pm 11.5	12.4 \pm 6.74	0.008 \pm 0.014	1.59 \pm 0.29	1.39 \pm 0.27
	PF	78.5 \pm 34.3	-13.8 \pm 8.94	0.050 \pm 0.123	1.41 \pm 1.05	1.35 \pm 0.33
Older Average	DF	34.7 \pm 9.35	14.2 \pm 6.45	0.019 \pm 0.029	1.45 \pm 0.29	1.35 \pm 0.20
	PF	69.9 \pm 22.0	-13.3 \pm 8.34	0.042 \pm 0.096	1.47 \pm 0.94	1.28 \pm 0.27
Main Effects ^b		A, M	M	-	A	-
Interactions ^b		A X G X M	-	-	G X M	-

^aOne outlier is excluded.

^bSignificant main effects and interactions for age (A), gender (G), and muscle (M).

DF, PF: dorsiflexors, plantarflexors.

T_0 : maximal isometric joint torque.

θ_0 : ankle angle at T_0 (DF = Negative; PF = Positive).

$A_{T\omega}$, $B_{T\omega}$: shape coefficients for $T\omega$ relation; units for $B_{T\omega}$ are rad/s.

T_{ECC} : eccentric plateau of $T\omega$ relation (relative to T_0).

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groups. Relative to neutral (0°), both DF θ_0 ($+14^\circ$ of plantarflexion) and PF θ_0 (-14° of dorsiflexion) were similar to other studies [2,22,47,48,49,50].

Our estimates of T_0 were based on a second order polynomial that represented the $T\theta$ relation. Average DF T_0 values were ~ 37 Nm for the younger subjects and ~ 35 Nm for the older subjects. These data agree with literature values that range from ~ 22 to 44 Nm for both young and older adults [1,2,5,46,51,52]. For PF T_0 , values averaged 93 Nm for young and 70 Nm for older males, while literature values range from 104 to 232 Nm for young males and from 100 to 125 Nm for older males [1,4,5,46,51,53]. Our relatively low results could be due to several factors, including the use of a knee angle of 90° , at which the gastrocnemius is shorter than optimum length [50], reducing the net plantarflexor torque. We also report active torque after subtracting for passive torque contributions, and were stringent concerning proper joint alignment and/or upper body fixation during the experimental trials [54].

Torque-Angular Velocity

The $T\omega$ relation was characterized by the shape parameters $A_{T\omega}$ and $B_{T\omega}$, akin to the dynamic constants of the Hill force-velocity equation [12] and independent of T_0 . Figure 1 illustrates that independently increasing $A_{T\omega}$ produces lower torque at any given concentric velocity, while increasing $B_{T\omega}$ leads to greater concentric, but decreased eccentric force capability.

The shape of the $T\omega$ relation differed between age groups, with weaker/slower concentric force capabilities (lower $B_{T\omega}$) in older DF and PF, but without a concomitant deficit in eccentric strength as indicated by the eccentric torque plateau (T_{ECC}). These data are consistent with other reports that concentric capability is reduced

with aging [2,5,6,55], but that eccentric torque production is preserved [7,8,9,56,57,58]. Because we accounted for individual subject differences in strength, muscle moment arms, and muscle torque-angle relations, our $T\omega$ findings represent a difference in the intrinsic force-velocity properties of the ankle muscles. This may be related to an age-related decrease in the size and/or number of fast-twitch Type II muscle fibers in the dorsiflexor tibialis anterior and the plantarflexor gastrocnemius [59]. With aging the percentage of Type IIa fibers decreases by about 9% in the tibialis anterior [60]. Although gastrocnemius Type IIa and Type IIb fiber number remains stable with increased age, these fibers shrink by about 13–31% in comparison with sedentary young adults [25].

Series Elasticity

The change in series elastic component length as a function of joint torque (i.e. the TAL relation) was represented by a second order polynomial with shape coefficients α_{TAL} and β_{TAL} . The squared coefficient α_{TAL} has a large influence on the rate of torque increase with increasing extension, and this coefficient was larger for the older subjects, indicating greater non-linearity in the TAL relation. There were no age differences in the β_{TAL} coefficient, which has a smaller role in determining the shape of the TAL relation. To determine linear stiffness, we computed the slope of the non-linear TAL relation at three different relative torque levels (K_{Low} , K_{Med} , K_{High}). Although we found no age differences among DF linear stiffness values at any torque level, older PF muscles had greater stiffness when evaluated at the high torque level (K_{High}). Greater PF stiffness in older adults agrees with other studies [13,14,61], and may offset the age-related decrement in velocity-dependent force capabilities, as force can rise faster if the

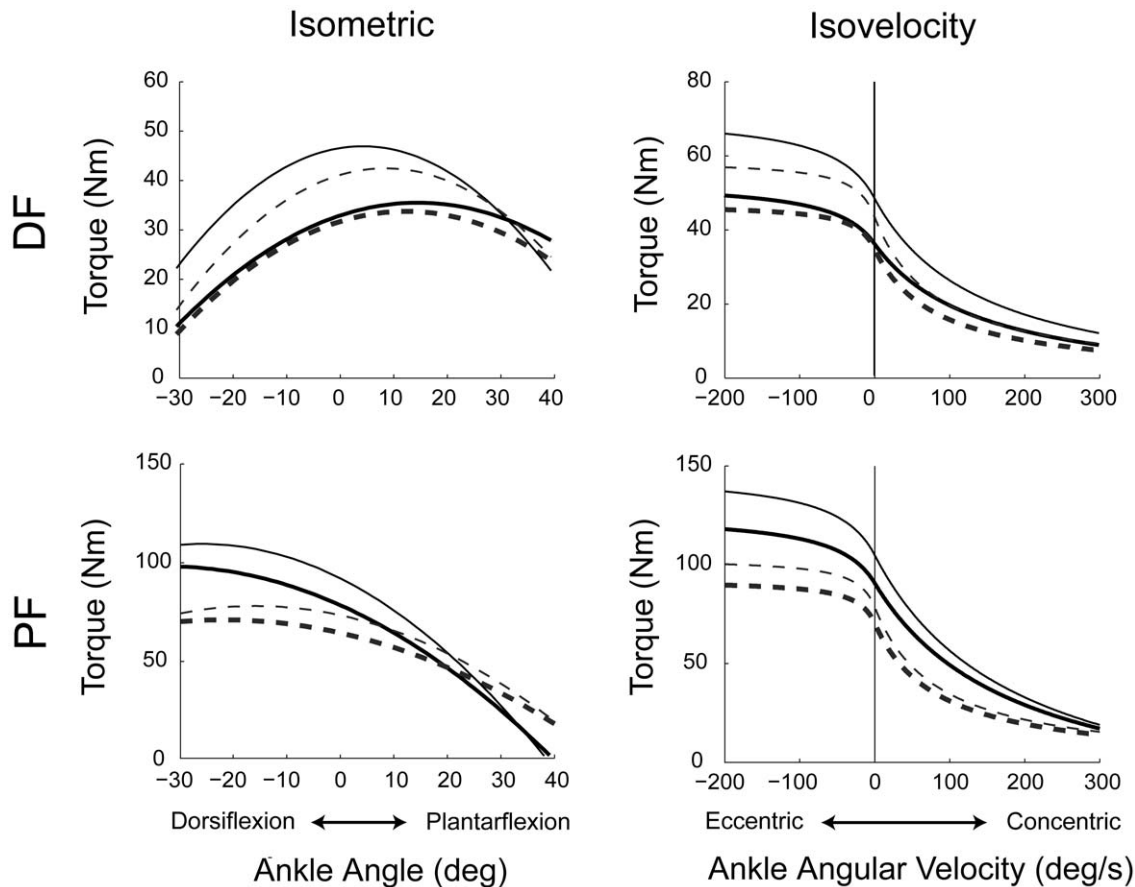


Figure 4. Average young (black solid lines) and older (gray dashed lines) torque-angle (left) and torque-angular velocity (right) curves. Both measured (thick lines) and co-activation adjusted (thin lines; see Discussion) data fits are shown.
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contractile component is attached to a stiffer series elastic component rather than a more compliant one [62].

This study also found TAL differences between the muscle groups. Compared to DF, both α_{TAL} and β_{TAL} polynomial coefficients and the linear stiffness measure at 15 Nm were greater for PF. This is supported by literature reports of aponeurosis stiffness and Young's modulus (E) (at maximal torque) *in vivo*, with lower values (stiffness = 32 N/mm; $E = 0.563$ Gpa) reported for

DF [63] than for the PF muscles (stiffness = 467 N/mm; $E = 1.474$ GPa)[39]. We did not compute E , since it requires explicit measures of series elastic component length and cross-sectional area [64]. Our findings of increased PF stiffness are also supported by evidence that muscle elastic characteristics are influenced by physiological function [65]; PF would be expected to have a higher stiffness to support much higher static and dynamic loads compared to DF [66]. This is one of the first reports on DF

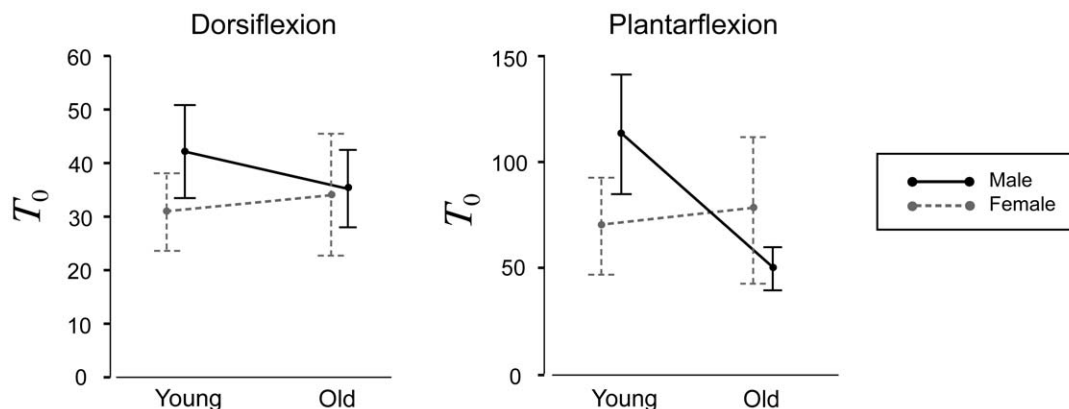


Figure 5. Interaction plots for maximal isometric torque (T_0).
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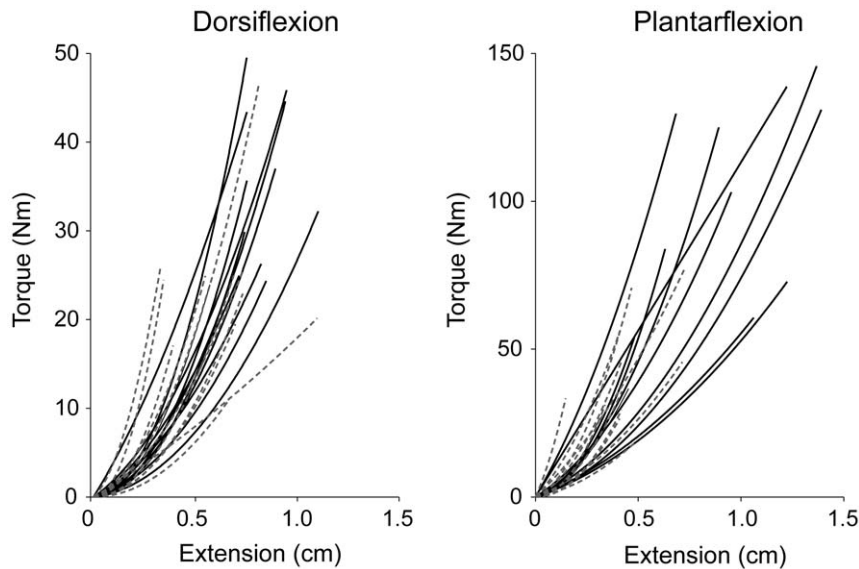


Figure 6. Second order polynomial fits to the young (solid black lines) and older (broken gray lines) torque-extension data from the ultrasound experiments.

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stiffness in older adults, as most studies focus on PF because they are purported to make a larger contribution to activities of daily living [67]. On the other hand, DF can generate significant torque and contribute to ankle joint stiffness that is important for postural stabilization [68].

It is important to note the limitations associated with these interpretations of series-elastic stiffness. Although we only measured aponeurosis extension in the longitudinal direction, the aponeurosis stretches bi-axially in the longitudinal and

transverse planes [20,69]. This complex behavior results in a variable aponeurosis stiffness [70], which we characterized with a second-order polynomial, and made linear approximations of the stiffness (K) at different torque values to facilitate group comparisons. Although we assumed that the aponeurosis acts in series with the muscle fibers and external tendon, the force expressed across these structures may differ due to the complex geometry of the musculotendon unit [71]. We did not normalize the stiffness measures by the cross-sectional area and rest length of

Table 3. Parameters describing the torque-extension ($T/\Delta L$) data (mean \pm between-subjects standard deviation).

Group	Mus.	ΔL_{MAX} (mm)	$\alpha_{T,\Delta L}$	$\beta_{T,\Delta L}$	K_{Low}	K_{Med}	K_{High}
Young Male	DF	8.4 \pm 1.0	0.491 \pm 0.221	0.570 \pm 0.643	3.51 \pm 0.64	5.62 \pm 0.92	7.75 \pm 1.42
	PF	11 \pm 3.5	0.835 \pm 0.697	4.22 \pm 3.55	8.61 \pm 2.25	11.1 \pm 2.75	14.6 \pm 4.31
Young Female	DF	8.0 \pm 1.8	0.386 \pm 0.194	0.577 \pm 0.550	2.83 \pm 0.59	4.77 \pm 1.09	6.69 \pm 1.57
	PF	7.8 \pm 3.0	0.809 \pm 0.733	4.64 \pm 4.17	8.59 \pm 3.61	10.8 \pm 4.48	14.1 \pm 6.22
Young Average	DF	8.2 \pm 1.4	0.439 \pm 0.208	0.574 \pm 0.597	3.17 \pm 0.62	5.20 \pm 1.01	7.22 \pm 1.50
	PF	9.4 \pm 3.3	0.822 \pm 0.715	4.43 \pm 3.86	8.60 \pm 2.93	11.0 \pm 3.62	14.4 \pm 5.27
Older Male ^a	DF	8.5 \pm 4.7	0.578 \pm 0.617	0.893 \pm 0.816	3.22 \pm 1.75	5.34 \pm 3.02	7.45 \pm 4.28
	PF	3.5 \pm 1.4	2.10 \pm 5.11	1.42 \pm 1.35	11.3 \pm 1.41	15.9 \pm 1.96	28.5 \pm 15.2
Older Female	DF	6.0 \pm 1.8	0.809 \pm 0.678	0.197 \pm 0.403	3.81 \pm 1.48	6.57 \pm 2.59	9.27 \pm 3.67
	PF	4.7 \pm 2.0	1.64 \pm 1.73	5.52 \pm 5.59	8.55 \pm 2.67	11.9 \pm 3.40	19.1 \pm 10.1
Older Average	DF	7.3 \pm 3.3	0.694 \pm 0.648	0.545 \pm 0.610	3.52 \pm 1.62	5.96 \pm 2.81	8.36 \pm 3.98
	PF	4.1 \pm 1.7	1.87 \pm 3.42	3.47 \pm 3.47	9.93 \pm 2.04	13.9 \pm 2.68	23.8 \pm 12.7
Main Effects ^b	A		A, M	M	-	M	A (PF)
Interactions ^b	A \times M		-	-	-	-	-

^aOne outlier is excluded.

^bSignificant main effects and interactions for age (A) and muscle (M).

DF, PF: dorsiflexors, plantarflexors.

ΔL_{MAX} : maximum extension of aponeurosis.

$\alpha_{T,\Delta L}$, $\beta_{T,\Delta L}$: shape coefficients for the $T/\Delta L$ relation.

K : Linear stiffness coefficients at different absolute torque levels; for DF: [K_{Low} , K_{Med} , K_{High}] = [5, 15, 30 Nm]; For PF: [K_{Low} , K_{Med} , K_{High}] = [15, 30, 60 Nm]. Stiffness units are Nm/mm.

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the elastic structures. Additionally, the gastrocnemius and soleus aponeuroses are separate structures linked by transverse collagen fibers, which can move independently during PF torque production, i.e. there is inter-aponeurosis shear [72]. Our ultrasound machine had insufficient resolution to make this subtle distinction. Thus, our PF aponeurosis extension values represent an average for the gastrocnemius and soleus (the tracking points spanned both aponeuroses).

Antagonist Co-Activation

In measuring resultant joint torque to assess muscle function, we made the common assumption of no antagonist co-activation [2,5,14,22,51]. This assumption is likely false in maximal joint torque efforts, and could cause agonist torque capabilities to be underestimated [73], which in turn would lead to inaccurate muscular properties. To assess possible influences of antagonistic co-activation, we estimated the percentage of antagonistic co-activation ($\%CoAct$) from the isometric data of Simoneau et al. [41]

$$\%CoAct_{PF} = 0.270 T_{DF} + 2$$

$$\%CoAct_{DF} = 0.177 T_{PF}$$

where T_{DF} and T_{PF} are the agonist DF and PF torques (Nm). For each muscle group the antagonistic torque contribution (T^{Antag} , Nm) was computed as

$$T^{Antag} = T_0^{Antag} (\%CoAct^{Antag} / 100)$$

We found that including antagonistic contributions increased agonist DF T_0 by 35% in young and 26% in older subjects, and increased agonist PF T_0 by 16% in young and 12% in older subjects. The most pronounced change was for isometric DF, in which the small differences between the young and old subjects became much greater with the inclusion of antagonism (Figure 4). This was because the younger subjects had stronger PF muscles and therefore greater antagonistic torque during the isometric DF trials.

Including antagonistic contributions may also influence stiffness measurements. Agonist muscles produce more torque than the dynamometer measures when antagonist muscles produce opposing torques. Magnusson et al. [39] demonstrated that antagonistic influences are small but significant for PF in male adults (average age: 37 yrs), such that Achilles tendon force was underestimated

by ~2.6% when antagonist coactivation was ignored. Lower torques for a given tendinous extension would cause stiffness to be underestimated. However, in the present study the degree of underestimation would be smaller for the older subjects and the DF muscles, since in both cases the magnitudes of the joint torques were smaller than those measured by Magnusson and colleagues.

Our simple antagonism model assumed that antagonist co-activation is dictated by agonist torque level alone, is independent of joint angular velocity [74,75], and that the torque/co-activation relation was the same for both age groups [41]. However, the degree of antagonistic co-contraction is likely task-specific, and may be influenced by joint angle [46,76], angular velocity [77], and whether the muscular effort is isometric, concentric, or eccentric [78,79]. One possibility is to use electromyography to estimate co-activation [80], but some have questioned the reliability of antagonist torque estimated in this manner [76]. Therefore, the exact magnitude of the co-activation adjusted results should be viewed with caution, but the simple model used here demonstrates the importance of including antagonism when predicting muscular properties.

Conclusions

Many clinical studies use maximal isometric strength as a marker of functional ability [81,82]. However, the present study has shown additional age-related differences in the dynamic properties of the ankle muscles, with slower concentric force capabilities and stiffer series elasticity in the older adults. This assessment of static, dynamic, and elastic joint properties affords a comprehensive view of age-related modifications in muscle function. Future work should further investigate links between age-related differences in these properties, which together may represent adaptations to physiological and lifestyle changes in older adults. Since the subjects in the present study were all healthy and active members of the community, we speculate that these differences represent a normal aging process.

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Author Contributions

Conceived and designed the experiments: CJH RHM GEC. Performed the experiments: CJH RHM. Analyzed the data: CJH RHM. Contributed reagents/materials/analysis tools: GEC. Wrote the paper: CJH RHM GEC.

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