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Maximum voluntary joint torque as a function of joint angle and angular velocity: model development and application to the lower limb

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Abstract

Measurements of human strength can be important during analyses of physical activities. Such measurements have often taken the form of the maximum voluntary torque at a single joint angle and angular velocity. However, the available strength varies substantially with joint position and velocity. When examining dynamic activities, strength measurements should account for these variations. A model is presented of maximum voluntary joint torque as a function of joint angle and angular velocity. The model is based on well-known physiological relationships between muscle force and length and between muscle force and velocity and was tested by fitting it to maximum voluntary joint torque data from six different exertions in the lower limb. Isometric, concentric and eccentric maximum voluntary contractions were collected during hip extension, hip flexion, knee extension, knee flexion, ankle plantar flexion and dorsiflexion. Model parameters are reported for each of these exertion directions by gender and age group. This model provides an efficient method by which strength variations with joint angle and angular velocity may be incorporated into comparisons between joint torques calculated by inverse dynamics and the maximum available joint torques.

Keywords

muscle strength; force-length; force-velocity; joint torque; dynamometer

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Introduction

Voluntary muscle strength is a fundamental component of human physical capabilities. In an effort to understand the importance of strength in selected activities, numerous studies have determined joint torques via inverse dynamics analysis and compared these torques to strength values (Grabiner, Owings, and Pavol 2005; Gross et al. 1998; Hughes, Myers, and Schenkman 1996; Kotake et al. 1993; Pavol et al. 2002; Schultz, Alexander, and Ashton-Miller 1992; Wojcik et al. 2001). Strength has been expressed in a variety of ways, including maximum weight lifted (Gross et al. 1998), angle-specific maximum isometric torque (Hughes, Myers, and Schenkman 1996; Kotake et al. 1993; Pavol et al. 2002), angle-specific maximum isokinetic torque (Pavol et al. 2002), non-angle-specific maximum isometric torque (Grabiner, Owings, and Pavol 2005; Wojcik et al. 2001) and non-angle-specific maximum isokinetic torque (Grabiner, Owings, and Pavol 2005; Wojcik et al. 2001). While such values provide valid quantitative estimates of strength, strength cannot be fully expressed by any single value. Maximum voluntary joint torque changes substantially with joint angle and angular velocity, due in part to the muscle force-length (Sale et al. 1982) and force-velocity (Westing, Seger, and Thorstensson 1990) relations. Accounting for strength variations with joint angle and angular velocity could lead to a better understanding of the role of strength in human movement activities.

Muscle force-length (F-L) and joint torque-angle relations in humans have been widely studied in the past (see Kulig, Andrews, and Hay 1984, for a review), as have force-velocity (F-V) and torque-angular velocity relations, both in vitro and using isokinetic dynamometers (Cabri 1991; Gulch 1994). A number of studies have addressed both length and velocity (or angle and angular velocity) contributions together when examining muscle force or joint torque (Caldwell, Adams, and Whetstone 1993; Chow et al. 1999; Connelly and Vandervoort 2000; James et al. 1994; King and Yeadon 2002; Krylow and Sandercock 1997; Lanza et al. 2003; Sutarno and McGill 1995; Thorstensson, Grimby, and Karlsson 1976; Westing and Seger 1989; Abbott and Wilkie 1953; Fuglevand 1987; Marshall, Mazur, and Taylor 1990). However, few studies have united both into a single mathematical model. King et al. (2002) extended a six parameter model of torque-angular velocity to include joint angle by making each of the parameters a quadratic function of angle, giving a total of 18 parameters. Chow et al. (1999) modeled muscle forces for the four quadriceps muscles with the Hill F-V model (Hill 1938) in which the three Hill parameters were made polynomial functions of muscle length. Resultant knee torque was determined by summing these muscle forces and then multiplying by the effective moment arm of the quadriceps.

The purpose of the model presented here is to provide a practical and widely applicable method for estimating maximum voluntary joint torque given joint angle and angular velocity. With this goal in mind, care was taken to maximize the utility of the model. The model uses only 10 parameters, several of which have simple physical interpretations. Furthermore, the model was developed in a general form that can be applied to a variety of joints and motions. This flexibility is shown by using the model to fit data from six different lower extremity exertion directions: hip extension (HE), hip flexion (HF), knee extension (KE), knee flexion (KF), ankle plantar flexion (PF), and ankle dorsiflexion (DF). Mean

model parameters are reported for these six exertion directions for three age groups: 18-25, 55-65, and >65 years old.

Methods

Model Development

A joint torque is the sum of passive and active torques. Passive torques are produced by tension developed as muscle tissue, tendons and ligaments are stretched. Passive torque-angle relationships have previously been modeled using exponential equations (Yoon and Mansour 1982; Hoang et al. 2005), and in this case, the passive joint torque was modeled as:

$$T_{PASSIVE} = B_1 e^{k_1 \theta} + B_2 e^{k_2 \theta} \quad (1)$$

The two terms in this equation represent the passive joint torque at either end of the range of motion. Since the passive torque function is independent of muscle activation, the same passive torques are present in both directions of exertion (e.g. knee extension and knee flexion).

There are two main ways that the active torque depends on joint angle: the variation of moment arm length with angle (Ito, Akima, and Fukunaga 2000; Maganaris 2001; Krevolin 2004) and the muscle F-L relation, as muscle length depends on joint angle. *In vivo*, active joint torque is produced by multiple agonist and antagonist muscles acting on muscle specific moment arms about the joint axis. In developing the active torque model, it was assumed that active torques were produced by a single representative muscle force, F , acting about a moment arm, r . Thus, the isometric active torque will have the form:

$$T_{ISO}(\theta) = r(\theta) \cdot F(\theta) \quad (2)$$

However, if both moment arm and muscle force are independent functions of angle, the model is overspecified, leading to inconsistent parameter values. Furthermore, torque-angle curves have similar profiles to F-L curves, which may be seen in Kulig et al. (1984). Thus, the model was simplified by limiting the angle dependence to muscle force, making moment arm a constant.

Measured strength variations with joint angle behave in one of three general ways, ascending, descending, and ascending-descending (Kulig, Andrews, and Hay 1984). Theoretically, the F-L relation for active muscle force peaks at an optimal sarcomere length, with force decreasing to zero at longer and shorter lengths (Gordon, Huxley, and Julian 1966; Winter 2005). A variety of mathematical models have been used to describe this relation including a quadratic equation (Chow et al. 1999), a normal curve (Audu 1985), a combination sine-exponential equation (Hatze 1977) and cubic spline interpolation (Lloyd and Besier 2003). Unfortunately, no single definitive model of the F-L relation has emerged. However, in creating a function of angle that could model all three behaviors noted above, a sinusoidal function seemed a natural form to examine. Based on this, the following model for isometric torque was created:

$$T_{ISO}(\theta) = r \cdot F_{MAX} \cdot \cos\left(\pi \frac{\theta - \theta_0}{\theta_{MAX} - \theta_{MIN}}\right) \quad (3)$$

where F_{MAX} is the maximum muscle force, θ_0 is the joint angle where maximum torque occurs, and θ_{MAX} and θ_{MIN} are joint angles where the cosine function goes to zero.

The active torque dependence on angular velocity arises from the muscle F-V relation. The concentric F-V relation of muscle indicates a decrease in muscle force as muscle shortening velocity increases. The hyperbolic Hill equation (Hill 1938) is perhaps the most widely used expression for this relation:

$$F(V) = \frac{F_{ISO}b - aV}{b + V} \quad (4)$$

where F_{ISO} represents the isometric muscle force, and a and b are constants defining the curvature of the hyperbola. Changing the form of this equation gives:

$$F(V) = F_{ISO} \frac{2V_1V_2 + V(V_2 - 3V_1)}{2V_1V_2 + V(2V_2 - 4V_1)} \quad (5)$$

where the constants V_1 and V_2 represent the muscle velocities at which muscle force is 75% and 50% of F_{ISO} , respectively.

In general, muscle velocity can be a function of both angle and angular velocity. However, it follows from the previous assumption of constant moment arm that muscle length is a linear function of angle. Therefore, muscle velocity depends on angular velocity alone:

$$V(\dot{\theta}) = r\dot{\theta} \quad (6)$$

This means that the shape of the torque-angular velocity curve will be independent of angle. It has been noted previously that the magnitude of torque-velocity curves changes with joint angle, while the shape of the curves remains similar (Westing and Seger 1989; Abbott and Wilkie 1953).

We are now able to construct a torque-angle-angular velocity function for concentric motions. Substituting Equation 6 into Equation 5 defines force as a function of angular velocity. Furthermore, multiplying the isometric muscle force, F_{ISO} , by moment arm, r , gives T_{ISO} , the isometric joint torque, which is defined in Equation 3. Combining Equations 3, 5 and 6 gives:

$$T_{CON}(\theta, \dot{\theta}) = r \cdot F_{MAX} \cdot \cos\left(\pi \frac{\theta - \theta_0}{\theta_{MAX} - \theta_{MIN}}\right) \cdot \left(\frac{2\omega_1\omega_2 + \dot{\theta}(\omega_2 - 3\omega_1)}{2\omega_1\omega_2 + \dot{\theta}(2\omega_2 - 4\omega_1)}\right) \quad (7)$$

where ω_1 and ω_2 are angular velocity analogs of V_1 and V_2 .

Eccentric torque was defined by scaling the concentric torque. Dudley (1990) showed the ratio of eccentric to concentric knee extensor torques to continuously increase with angular velocity. Thus, the scaling factor was made a linear function of velocity, resulting in:

$$T_{ECC}(\theta, \dot{\theta}) = T_{CON}(\theta, -\dot{\theta}) \cdot (1 - E\dot{\theta}) \quad (8)$$

where E is a constant. The major advantage of this approach is that only one additional parameter is required to define eccentric torque.

Combining constants into independent parameters, the final model for active muscle torque is:

$$T_{ACTIVE}(\theta, \dot{\theta}) = \begin{cases} C_1 \cos(C_2(\theta - C_3)) \left(\frac{2C_4C_5 + \dot{\theta}(C_5 - 3C_4)}{2C_4C_5 + \dot{\theta}(2C_5 - 4C_4)} \right) & \dot{\theta} \geq 0 \\ C_1 \cos(C_2(\theta - C_3)) \left(\frac{2C_4C_5 - \dot{\theta}(C_5 - 3C_4)}{2C_4C_5 - \dot{\theta}(2C_5 - 4C_4)} \right) (1 - C_6\dot{\theta}) & \dot{\theta} < 0 \end{cases} \quad (9)$$

where positive velocity indicates concentric motion, and negative velocity indicates eccentric motion. This model produces a surface in the torque-angle-angular velocity space that represents the maximum voluntary torque. Table 1 describes the six parameters in the active torque model. The total joint torque is the sum of the active (Equation 9) and passive (Equation 1) torques.

Application to the Lower Limb

A total of 34 healthy, active adults were recruited from the university population and local community including 14 subjects aged 18-25, 14 aged 55-65, and 6 aged over 65 (Table 2). Each age group contained an equal number of males and females. Criteria for inclusion in the study were lack of injury or illness that could confound results or endanger the subject, and participation in physical activities (aerobic or strengthening) 2-4 times per week. In addition, older subjects were required to pass a medical screening administered by a physician prior to participation. The medical screening was used to exclude subjects with any neurological, cardiac, respiratory, otological, or musculoskeletal disorders. The study was approved by the Virginia Tech Institutional Review Board, and all subjects provided informed consent prior to participation.

The protocol for measuring maximum voluntary muscle strength included isometric and isokinetic (concentric and eccentric) maximum voluntary contractions (MVCs), each performed in six exertion directions: HE, HF, KE, KF, PF and DF. All testing was done on the right leg with a Biodex System 3 dynamometer (Biodex Medical Systems, Inc., Shirley, New York, USA). Subjects were instructed to give maximum effort, and were verbally encouraged throughout the protocol.

The protocol was similar for each joint and exertion direction. A passive torque profile was first recorded by moving the dynamometer slowly (5 deg/s) through the entire range of motion while the subject was relaxed. Next, an isometric MVC was recorded at each of six

joint angles spaced evenly throughout the subject-specific range of motion, going from one end of the range of motion to the other (e.g. flexion through extension). All six isometric MVCs were first performed for one direction (e.g. extension), and then the six for the other direction (e.g. flexion) were performed. Following this, a five minute rest was taken. Four isokinetic concentric MVCs were recorded for both movement directions at each of two velocities (60 and 120 deg/s for the ankle and hip, and 75 and 150 deg/s for the knee). A second five minute rest was then taken. Four high speed concentric MVCs were also recorded for both movement directions. In these tests, the maximum isokinetic velocity of the Biodex (500 deg/s) was used, effectively minimizing resistance, and the subject was encouraged to move as quickly as possible. Following the high speed movements, four isokinetic eccentric MVCs were performed at a single velocity (60 deg/s for the ankle and hip, and 75 deg/s for the knee) for both movement directions. A final five minute rest period was then observed. Last, a second set of isometric MVCs was taken. This procedure was identical to the first set of isometric measurements, except that the order of testing angles was reversed (e.g. extension through flexion).

All subjects were positioned similarly during tests. Ankle and knee testing was performed using standard manufacturer attachments in a seated position. Ankle testing was performed with the hip flexed 80 deg and the knee flexed 50 deg. Knee testing was performed with the hip flexed about 70 deg. Hip testing was performed in a standing position with a custom-built rigid frame, in a manner similar to Dean et al. (2004). The knee was held in a slightly flexed position using a knee immobilizer.

Angle, angular velocity, and torque were sampled at 200 Hz during all exertions. The raw data were low pass filtered at 5 Hz (fourth order Butterworth filter). The isokinetic portions of the motion data, where acceleration was negligible, were determined. Torque due to the weight of the limb and apparatus can cause significant errors in dynamometer data (Herzog 1988). This gravitational torque was estimated (in concert with the passive joint torques) by a least squares fit of the passive torque profile and subtracted from the data. An arbitrary number of joint angles (10 for hip and knee, 8 for ankle) evenly spaced across the range of motion defined the data points used in fitting the model. Isometric torques were found at these joint angles using a cubic spline interpolation, and maximum isokinetic torques at these angles were taken directly from the data. From the high speed motion, the point of maximum speed attained (i.e. when angular acceleration was zero) was included.

Parameters for the passive joint torque function were estimated (in concert with the gravitational torque) from the passive torque profile using a least squares fit. When the knee was flexed, the recorded passive torque was thought to be largely due to compression of the Biodex seat, so this portion was not included as a passive joint torque. When the ankle was plantar flexed, the Biodex generally limited the range of motion, rather than the subject. For most of the younger subjects, passive joint torques at this position were too small to determine parameters reliably.

To calculate the parameters of the active torque function for each subject, a simulated annealing algorithm, based largely on that detailed by Corana et al. (1987), was created in Matlab (The MathWorks Inc., Natick, Massachusetts, USA). The model parameters for each

subject were found by minimizing the sum of the squared residuals. The first five parameters of the function were determined using only the isometric and concentric data points. The residuals were weighted so that the four velocities (isometric, two isokinetic, and high speed) made equal contributions to the fit. The sixth parameter was determined in a second simulated annealing run, in which the eccentric data was included and the first five parameters held constant.

While the six parameters in the model were initially presumed to be independent, it was found that the two parameters defining the velocity relation, C4 and C5, were linearly related within each exertion direction. Thus, the ratio C5/C4 was set constant for each different exertion direction. The value of this ratio was 2.020 for HE, 2.037 for HF, 2.606 for KE, 2.605 for KF, 3.602 for PF, and 2.777 for DF. The final model parameters were calculated including this constraint, and thus subject-specific fits of the active torque had only five independent parameters, with the sixth depending on exertion direction.

Results

The model was able to produce a maximum voluntary joint torque surface in the joint angle-angular velocity space. Representative knee extensor dynamometer data from an individual subject are shown in Figure 1, along with the corresponding surface calculated by the model. To assess the predictive ability of the model, model-predicted torques were correlated with measured torques from the dynamometer using data from all subjects (Figure 2). In addition, the model fit the data from each individual subject well in most cases (mean R^2 of 0.89, range 0.46 to 0.99). The general shape of the surface was similar between subjects for each exertion direction, but there were marked differences between exertion directions (Figure 3). It is important to note that for this model, angular velocity defined as negative for eccentric motions, regardless of the actual direction of joint motion. Joint angles were defined as positive for joint flexion (including dorsiflexion) in all joints. Approximate ranges of motion were -0.5 rad (hyperextended) to 1.3 rad (flexed) for the hip, 0 rad (fully extended) to 1.8 rad (flexed) for the knee, and -0.6 rad (plantar flexed) to 0.5 rad (dorsiflexed) for the ankle, where 0 rad represents the anatomic position in each joint.

The model parameters were estimated for each subject in all six exertion directions. Mean parameter values for the different exertions are presented by age and gender in Table 3. Reported values of C_1 (maximum isometric torque in N-m) were normalized by body weight $\times$ height. With the parameters reported here, the model can predict maximum voluntary torque for three different age groups given the instantaneous joint angle and angular velocity.

Discussion

A model for calculating maximum voluntary joint torque as a function of joint angle and angular velocity has been presented. It has been shown to be a generalized form that is applicable to multiple joints/movement directions of the lower extremity, and it is reasonable to suppose that it could be applied to other joints as well. The model has a total of 10 parameters, including a passive torque component with four independent parameters, and an

active torque component with five subject-specific independent parameters and a sixth parameter dependent on exertion direction. A useful feature of the active torque model is that several of the parameters have easily understood physical interpretations. Specifically, C_1 is the maximum isometric active joint torque, C_3 the corresponding joint angle, and C_4 and C_5 the concentric angular velocities at which joint torque is reduced to 75% and 50% of the isometric torque, respectively.

Model parameters can be derived from a reasonable regimen of strength tests on an isokinetic dynamometer to determine a subject-specific torque-angle-angular velocity relation. Alternatively, mean model parameters (such as those presented in Table 3) can be used to estimate the torque-angle-angular velocity relation for a given subject demographic. Once the model parameters have been determined, instantaneous joint angle and joint angular velocity measurements can be used to determine the instantaneous maximum voluntary joint torque for comparison with joint torques calculated via inverse dynamics.

There are several limitations inherent in the data collection protocol that could affect the data, and hence the resulting models. Although we used only isokinetic/isometric torque data and exercised care in joint alignment on the dynamometer, inertial effects and misalignment of the joint axis may introduce errors in dynamometer data (Herzog 1988). In addition, actual joint angle and angular velocity may differ from dynamometer recordings (King and Yeadon 2002). Subjects were encouraged to provide their maximum effort during testing, although no measurements of muscle activation, such as EMG, were made, and the data were assumed to be reasonably good representations of the maximum voluntary joint torques. Lanza et al. (2004) and Kent-Braun et al. (2002) showed that isometric dorsiflexor MVCs were within a few percent of actual maximum activation, which indicates that properly collected MVCs will provide good representations of the maximum voluntary torques. However, it should be noted that maximum voluntary muscle force may be limited by maximum voluntary muscle activation, and thus be less than the theoretical maximum force. Hence, there remains some reserve of muscle strength which could possibly be called upon in exceptional circumstances (Gandevia 2001). In such cases, measured maximum voluntary joint torques may be lower than actual strength.

While the model presented was successful in fitting measured joint torque data, some limits of the model are worth noting. The presence of two-joint muscles, such as the biceps femoris and the gastrocnemius, means that maximum torque at one joint is dependent on the position of another joint. Because of the complexity this would introduce, two-joint muscles were not considered in the current model. However, this is an important aspect of musculoskeletal anatomy that could be included in future improvements of this model. The torque-angular velocity relation is based on the Hill equation. While this equation is widely used, it may not be fully representative of torqueangular velocity behavior. Specifically, a plateau region has been noted in torques at lower velocities, before it drops off (James et al. 1994; King and Yeadon 2002; Perrine and Edgerton 1978; Wickiewicz et al. 1984). As this behavior was seen in some of the data in the current study, modifying the model to account for this should be explored. In calculating model parameters, a least-squares approach was used to fit the data. As a result, the torque predicted by the model is sometimes less than the measured torque. At these points, the model is clearly underestimating the maximum voluntary torque.

An alternative method for fitting the data that would reduce the chance of underestimating the measured torques may result in more accurate predictions of maximum voluntary torques.

Visual inspection of the torque-angle-angular velocity surfaces revealed some notable characteristics that may vary between exertion directions (Figure 3). For some exertions, torque displayed a parabolic-like behavior as a function of joint angle (e.g. KE), while some increased continuously over the range of motion (e.g. PF). Joint torques decrease with increasing concentric velocity, due to fluid viscosity and the breaking and reforming of actin-myosin cross bridges (Winter 2005). The concentric torque-velocity curves showed differences between joints, with the hip torques decreasing to zero in an essentially linear manner, while the knee and ankle torques have more curvature, and decrease in an asymptotic manner. The maximum joint torques during eccentric exertions did not necessarily increase from the isometric torque, unlike muscle force in *in vitro* tests (Joyce, Rack, and Westbury 1969). However, several studies, as reviewed by Yeadon et al. (2006), indicate that muscle activation is suppressed during eccentric contractions, an effect believed to be an injury prevention mechanism (Seger and Thorstensson 2000; Westing, Seger, and Thorstensson 1990). Thus, it is possible that eccentric maximum voluntary torques were suppressed by neurological factors that act to prevent injury to the muscle, joint or bone.

In conclusion, this model provides an efficient method by which strength variations with joint angle and angular velocity may be incorporated into comparisons between joint torques calculated by inverse dynamics and the maximum available joint torques. For such analyses, the model parameters may be determined from isometric and isokinetic strength measurements using a simulated annealing algorithm, as was done here. However, this may not always be a desirable option. Alternatively, an estimate of the torque-angle-angular velocity relation can be made using parameters presented here along with subject age, gender, height and weight.

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Figure 1.

Maximum knee extension torque measurements from a single subject (left), and the corresponding maximum torque surface estimated by the model (right). Positive joint angle indicates flexion. Positive angular velocity indicates concentric motion, while negative indicates eccentric motion.

Figure 2.

To quantify the overall predictive abilities of the model, linear regression was performed between the predicted and measured joint torques for all subjects. The data and regression line for knee extension torques are shown. R² values are given for all six exertion directions.

Figure 3.

Torque surfaces created using means of parameters reported in Table 3. These surfaces illustrate the variation of maximum joint torque (N-m) with joint angle (deg) and angular velocity (deg/s) as well as the marked differences between joints and exertion directions. Positive joint angle indicates flexion (dorsiflexion). Positive angular velocity indicates concentric motion, while negative indicates eccentric motion.

Table 1

Descriptions of the six parameters in the active torque equation

Parameter	Interpretation
$C_1 = F_{MAX}r$	Maximum isometric joint torque (N-m)
$C_2 = \pi/(\theta_{MAX}-\theta_{MIN})$	π divided by the (theoretical) range of joint angles in which active muscle force is present.
$C_3 = \theta_0$	Joint angle at maximum isometric joint torque (rad)
$C_4 = \omega_1$	Angular velocity when torque is 75% of isometric torque (rad/s)
$C_5 = \omega_2$	Angular velocity when torque is 50% of isometric torque (rad/s)
$C_6 = E$	Defines eccentric torque relative to concentric torque. A positive value indicates eccentric > concentric.

Table 2

Summary of mean(SD) subject characteristics.

Age Group	18-25		55-65		>65	
Gender	M	F	M	F	M	F
Age (years)	19.6 (1.1)	19.6 (1.3)	61.3 (3.3)	58.1 (3.3)	71.7 (2.3)	68.3 (2.5)
Height (cm)	174.8 (5.2)	160.6 (5.0)	174.7 (4.9)	162.6 (1.9)	174.3 (8.6)	161.7 (4.7)
Mass (kg)	72.8 (7.2)	62.1 (6.3)	87.7 (13.2)	66.0 (10.6)	86.2 (11.4)	64.5 (2.9)

Table 3

Mean (SD) parameter values by age and gender for six exertions.

Age	18-25		55-65		>65	
Gender	M	F	M	F	M	F
Hip Extension						
C ₁ [*]	0.161 (0.049)	0.181 (0.047)	0.171 (0.043)	0.140 (0.032)	0.144 (0.039)	0.138 (0.003)
C ₂	0.958 (0.201)	0.697 (0.130)	0.922 (0.155)	0.830 (0.246)	0.896 (0.124)	0.707 (0.173)
C ₃	0.932 (0.358)	1.242 (0.418)	1.176 (0.195)	1.241 (0.365)	1.125 (0.077)	1.542 (0.279)
C ₄	1.578 (0.286)	1.567 (0.268)	1.601 (0.306)	1.444 (0.223)	1.561 (0.184)	1.613 (0.135)
C ₅	3.190 (0.586)	3.164 (0.542)	3.236 (0.622)	2.919 (0.450)	3.152 (0.372)	3.256 (0.273)
C ₆	0.242 (0.272)	0.164 (0.175)	0.320 (0.189)	0.317 (0.140)	0.477 (0.368)	0.360 (0.237)
B ₁	-1.210 (0.660)	-1.753 (1.930)	-2.160 (1.297)	-1.361 (1.294)	-2.671 (0.271)	-0.758 (0.613)
k ₁	-6.351 (0.970)	-6.358 (2.828)	-8.073 (2.701)	-7.128 (2.541)	-7.850 (3.402)	-7.545 (0.741)
B ₂	0.476 (0.547)	0.239 (0.292)	0.108 (0.091)	0.013 (0.020)	0.092 (0.111)	0.018 (0.031)
k ₂	5.910 (4.955)	3.872 (1.895)	4.593 (0.854)	6.479 (2.924)	5.192 (1.691)	6.061 (2.265)
Hip Flexion						
C ₁ [*]	0.113 (0.025)	0.127 (0.033)	0.107 (0.020)	0.091 (0.016)	0.101 (0.025)	0.081 (0.008)
C ₂	0.738 (0.217)	0.650 (0.178)	0.712 (0.248)	0.812 (0.244)	0.762 (0.151)	0.625 (0.062)
C ₃	-0.214 (0.245)	-0.350 (0.232)	-0.192 (0.274)	-0.196 (0.209)	-0.269 (0.234)	-0.422 (0.214)
C ₄	2.095 (0.489)	2.136 (0.345)	2.038 (0.318)	2.145 (0.375)	1.875 (0.164)	2.084 (0.321)
C ₅	4.267 (0.995)	4.349 (0.702)	4.145 (0.652)	4.366 (0.765)	3.819 (0.335)	4.245 (0.654)
C ₆	0.218 (0.225)	0.156 (0.179)	0.206 (0.088)	0.186 (0.262)	0.296 (0.102)	0.196 (0.280)
B ₁	1.210 (0.660)	1.753 (1.930)	2.160 (1.297)	1.361 (1.294)	2.671 (0.271)	0.758 (0.613)
k ₁	-6.351 (0.970)	-6.358 (2.828)	-8.073 (2.701)	-7.128 (2.541)	-7.850 (3.402)	-7.545 (0.741)
B ₂	-0.476 (0.547)	-0.239 (0.292)	-0.108 (0.091)	-0.013 (0.020)	-0.092 (0.111)	-0.018 (0.031)
k ₂	5.910 (4.955)	3.872 (1.895)	4.593 (0.854)	6.479 (2.924)	5.192 (1.691)	6.061 (2.265)
Knee Extension						
C ₁ [*]	0.163 (0.040)	0.159 (0.028)	0.156 (0.031)	0.128 (0.016)	0.137 (0.017)	0.124 (0.018)
C ₂	1.258 (0.073)	1.187 (0.084)	1.225 (0.063)	1.286 (0.094)	1.310 (0.127)	1.347 (0.044)
C ₃	1.133 (0.073)	1.274 (0.181)	1.173 (0.048)	1.141 (0.077)	1.067 (0.024)	1.140 (0.124)
C ₄	1.517 (0.593)	1.393 (0.380)	1.518 (0.363)	1.332 (0.319)	1.141 (0.046)	1.066 (0.128)
C ₅	3.952 (1.546)	3.623 (0.989)	3.954 (0.947)	3.469 (0.832)	3.152 (0.040)	2.855 (0.221)
C ₆	0.095 (0.171)	0.173 (0.270)	0.266 (0.060)	0.233 (0.133)	0.386 (0.124)	0.464 (0.129)
B ₁ [†]	0	0	0	0	0	0
k ₁ [†]	0	0	0	0	0	0
B ₂	-6.250 (2.617)	-8.033 (3.696)	-12.830 (2.541)	-6.576 (1.958)	-10.519 (1.896)	-8.800 (6.141)

Age	18-25		55-65		>65	
Gender	M	F	M	F	M	F
k_2	-4.521 (0.553)	-5.250 (1.512)	-5.127 (2.148)	-4.466 (1.630)	-5.662 (1.517)	-6.763 (0.742)
Knee Flexion						
C_1^*	0.087 (0.015)	0.080 (0.015)	0.081 (0.017)	0.060 (0.015)	0.069 (0.022)	0.060 (0.005)
C_2	0.869 (0.163)	0.873 (0.191)	0.986 (0.138)	0.967 (0.210)	0.838 (0.084)	0.897 (0.145)
C_3	0.522 (0.317)	0.635 (0.287)	0.523 (0.212)	0.402 (0.273)	0.437 (0.357)	0.445 (0.210)
C_4	2.008 (1.364)	1.698 (0.825)	1.830 (0.795)	1.693 (0.718)	1.718 (0.716)	1.121 (0.052)
C_5	5.233 (3.554)	4.412 (2.139)	4.777 (2.067)	4.410 (1.871)	4.476 (1.866)	2.922 (0.135)
C_6	0.304 (0.598)	0.175 (0.319)	0.230 (0.094)	0.349 (0.143)	0.414 (0.201)	0.389 (0.078)
$B_1^{\ddagger}$	0	0	0	0	0	0
$k_1^{\ddagger}$	0	0	0	0	0	0
B_2	6.250 (2.617)	8.033 (3.696)	12.830 (2.541)	6.576 (1.958)	10.519 (1.896)	8.800 (6.141)
k_2	-4.521 (0.553)	-5.250 (1.512)	-5.127 (2.148)	-4.466 (1.630)	-5.662 (1.517)	-6.763 (0.742)
Plantar Flexion						
C_1^*	0.095 (0.022)	0.104 (0.034)	0.114 (0.029)	0.093 (0.026)	0.106 (0.035)	0.130 (0.013)
C_2	1.391 (0.089)	1.399 (0.190)	1.444 (0.136)	1.504 (0.235)	1.465 (0.136)	1.305 (0.089)
C_3	0.408 (0.083)	0.424 (0.186)	0.551 (0.103)	0.381 (0.143)	0.498 (0.132)	0.580 (0.115)
C_4	0.987 (0.595)	0.862 (0.487)	0.593 (0.165)	0.860 (0.448)	0.490 (0.262)	0.448 (0.026)
C_5	3.558 (2.144)	3.109 (1.760)	2.128 (0.578)	3.126 (1.613)	1.767 (0.944)	1.612 (0.093)
C_6	0.295 (0.214)	0.189 (0.213)	0.350 (0.133)	0.349 (0.270)	0.571 (0.313)	0.393 (0.092)
B_1	-5.781E-4 (1.193E-3)	-5.218E-3 (1.135E-2)	-1.311E-3 (3.331E-3)	-2.888E-5 (3.562E-5)	-5.693E-5 (3.164E-5)	-2.350E-5 (2.535E-5)
k_1	-5.819 (7.384)	-4.875 (6.770)	-10.943 (10.291)	-17.189 (7.848)	-21.088 (1.786)	-12.567 (10.885)
B_2	0.967 (0.323)	0.470 (0.328)	0.377 (0.403)	0.523 (0.394)	0.488 (0.258)	0.195 (0.292)
k_2	6.090 (1.196)	6.425 (1.177)	8.916 (3.119)	7.888 (1.141)	7.309 (0.902)	8.846 (2.233)
Dorsiflexion						
C_1^*	0.033 (0.005)	0.027 (0.006)	0.028 (0.005)	0.024 (0.002)	0.029 (0.002)	0.023 (0.003)
C_2	1.510 (0.190)	1.079 (0.271)	1.293 (0.479)	1.308 (0.339)	1.419 (0.195)	1.221 (0.354)
C_3	-0.187 (0.067)	-0.302 (0.171)	-0.284 (0.178)	-0.254 (0.133)	-0.174 (0.056)	-0.369 (0.109)
C_4	0.699 (0.108)	0.864 (0.446)	0.634 (0.216)	0.596 (0.148)	0.561 (0.188)	0.424 (0.063)
C_5	1.940 (0.301)	2.399 (1.236)	1.759 (0.601)	1.654 (0.410)	1.558 (0.521)	1.177 (0.175)
C_6	0.828 (0.134)	0.771 (0.206)	0.999 (0.214)	1.006 (0.284)	1.198 (0.290)	1.459 (0.349)
B_1	5.781E-4 (1.193E-3)	5.218E-3 (1.135E-2)	1.311E-3 (3.331E-3)	2.888E-5 (3.562E-5)	5.693E-5 (3.164E-5)	2.350E-5 (2.535E-5)
k_1	-5.819 (7.384)	-4.875 (6.770)	-10.943 (10.291)	-17.189 (7.848)	-21.088 (1.786)	-12.567 (10.885)
B_2	-0.967 (0.323)	-0.470 (0.328)	-0.377 (0.403)	-0.523 (0.394)	-0.488 (0.258)	-0.195 (0.292)
k_2	6.090 (1.196)	6.425 (1.177)	8.916 (3.119)	7.888 (1.141)	7.309 (0.902)	8.846 (2.233)

* Values are normalized by body weight×height.

[†]Zeros indicate that passive joint torques were not determined.

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