A comparison of two Hill-type skeletal muscle models on the construction of medial gastrocnemius length-tension curves in humans in vivo

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Hoffman BW, Lichtwark GA, Carroll TJ, Cresswell AG. A comparison of two Hill-type skeletal muscle models on the construction of medial gastrocnemius length-tension curves in humans in vivo. J Appl Physiol 113: 90–96, 2012. First published May 10, 2012; doi:10.1152/japplphysiol.00070.2012.—Human length-tension curves are traditionally constructed using a model that assumes passive tension does not change during contraction (model A) even though the animal literature suggests that passive tension can decrease (model B). The study’s aims were threefold: 1) measure differences in human medial gastrocnemius length-tension curves using model A vs. model B, 2) test the reliability of ultrasonography constructed length-tension curves, and 3) test the robustness of fascicle length-generated length-tension curves to variations between the angle and fascicle length relationship. An isokinetic dynamometer manipulated and measured ankle angle while ultrasound was used to measure medial gastrocnemius fascicle length. Supramaximal tibial nerve stimulation was used to evoke resting muscle twitches. Length-tension curves were constructed using model A [angle-torque (A-T(A)], length-torque (L-T(A))] or model B [length-torque (L-T(B))] in three conditions: baseline, heel-lift (where the muscle was shortened at each angle), and baseline repeated 2 h later (+2 h). Length-tension curves constructed from model B differed from those produced via model A, indicated by a significant increase in maximum torque (≈23%) when using L-T(B) vs. L-T(A). No parameter measured was different between baseline and +2 h for any method, indicating good reliability when using ultrasound. Length-tension curves were unaffected by the heel-lift condition when using L-T(A) or L-T(B), but were affected when using A-T(A). Since the muscle model used significantly alters human length-tension curves, and given animal data indicate model B to be more accurate when passive tension is present, we recommend that model B should be used when constructing medial gastrocnemius length-tension curves in humans in vivo.

force-length relationship; ultrasonography; muscle fascicle; torque-angle relationship

THE LENGTH-TENSION RELATIONSHIP of muscle is one of the most well-known and important functional properties of muscle. To explore this relationship, length-tension curves can be constructed from empirical data to provide a graphical description of the relationship between the muscle’s length and the force that it can produce at that length. The length-tension relationship can be an important marker of alterations in muscle mechanics. For example, the presence or amount of exercise-induced muscle damage can be determined through changes to the shape of both active and passive length-tension curves after a bout of damaging exercise (3, 11, 12). Therefore, it is imperative that empirically determined length-tension curves accurately represent the length-tension relationship of the muscle investigated.

In animal research, the length-tension relationship has been clearly established using isolated myofibril, muscle fiber, and whole muscle preparations (5, 7, 8, 11). Attempts to quantify this relationship in humans in vivo usually rely on plotting the joint angle against the active joint torque over a range of muscle lengths (11). When constructing active length-tension curves, the skeletal muscle model chosen to describe how the passive and active elements within the muscle interact influences the calculation of active torque. It has been common practice to select a muscle model where both the series elastic component (tendon and aponeurosis) and the contractile element (actin and myosin filaments) lie in parallel to the parallel elastic component (titin, membrane, and interstitial connective tissue) (model A, Fig. 1A) (15, 22–24). As such, this model assumes that passive torque does not change during a shortening contraction, and thus active torque is calculated by subtracting the passive torque prior to the active contraction away from the total torque during the contraction (Fig. 2A).

However, recent nonhuman studies suggest an alternative model where only the contractile element lies in parallel to the parallel elastic component (model B; Fig. 1B) (15, 22, 24). As such, this model assumes that passive torque will decrease during an isometric contraction due to shortening of the contractile element against the series elastic component, and thus active torque is calculated by subtracting the passive torque during the active contraction from the total torque (Fig. 2A). The data suggest that model B is better able to account for changes in active and passive torque than model A under various conditions, especially for muscles with long tendons (e.g., triceps surae) or when large amounts of passive torque are present (i.e., when muscle is stretched to long lengths) (15, 22, 24).

While the nonhuman literature suggests that model B better describes active and passive torque production, to our knowledge, no studies have used model B when constructing active length-tension curves in humans in vivo. It has been a common approach in human research to use dynamometer or joint angle as an indirect measure of muscle fascicle length (e.g., 11, 19). This technique cannot determine the muscle fascicle length change during an isometric contraction, and subsequently model A has been inherently assumed. Another disadvantage of using dynamometer or joint angle, especially when investigating the triceps surae, is that changes in muscle fascicle length can occur independently of changes in dynamometer or joint angle, such as when the ankle is not firmly attached to the dynamometer rotating the foot, or when there are changes in knee angle.
Shown there to be a significant difference between change in the PEC and thus no change in passive tension. As such, during a shortening contraction, there is no component (PEC) parallel to both the contractile element (CE) and the series elastic component (SEC). As such, during a shortening contraction, the PEC will also shorten and passive tension will decrease as a function of the length change during the contraction.

One technique researchers have used to directly measure muscle fascicle length in humans is ultrasonography. Not only can this help overcome issues when muscle length changes independently of joint angle, but it can also provide information about the length change during a contraction, thus allowing the use of model B. However, studies that have used ultrasound to plot active length-tension curves have used the passive torque prior to contraction to calculate the active torque, which is essentially using model A (10, 16). While animal studies have shown there to be a significant difference between model A and model B curves (15, 22, 24), length-tension properties can potentially differ between species as well as between muscles due to things such as the experimental set-up, length and compliance of the tendon, the effect of antagonists, and the range of motion available. Therefore, it is important to determine the skeletal muscle model that is most appropriate for the muscle being investigated. Furthermore, as length-tension curves are often repeated after some intervention (such as after a bout of damaging exercise), it is therefore important to determine how reliable the use of ultrasound is to construct multiple curves hours apart.

Therefore, the aim of this study was threefold. First, we measured the change in shape of medial gastrocnemius length-tension curves constructed from the two skeletal muscle models in humans in vivo. Second, we tested the reliability of using ultrasound measurements to construct length-tension curves. Third, we compared the robustness of length-tension curves constructed using either dynamometer angle or muscle fascicle length when dynamometer angle was changed independently from muscle length.

**METHODS**

Subjects. Ten subjects (7 men, 27.4 ± 4.1 yr, 1.77 ± 0.07 m, 72.6 ± 7.9 kg) who were healthy, had no history of neuromuscular disease, or illness and were not participating in regular, strenuous exercise, volunteered to participate in this study. The protocol was approved by the local university ethics committee and conducted according to the Declaration of Helsinki. All subjects provided written, informed consent.

Experimental set-up. Subjects lay prone on a bench with their right foot securely strapped to a foot plate that was attached to a commercially available isokinetic dynamometer (Biodex System 3 Pro, Biodex Medical Systems, Shirley, NY). The secure strapping for each subject was considered the neutral ankle position and defined as 0°, with any dorsiflexion positions considered positive. Ankle joint angle was measured directly from the dynamometer, and analog signals were low-pass filtered at 9 Hz and converted using a 16-bit analog-to-digital converter at 1 kHz (Power 1401, Cambridge Electronic Design, UK).

Peripheral nerve stimulation. Plantar flexion torque produced by the triceps surae was measured directly from the dynamometer. The signal was low-pass filtered at 5 Hz and analog-to-digital converted at 1 kHz with the same equipment described above. The torque produced by gravity acting on the foot plate and foot was estimated for each joint angle prior to testing. Using previous anatomic data (17), we created a model foot that simulated the mass of an average person’s

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**Fig. 1.** Schematic of the Hill-type skeletal muscle models used in this study and corresponding calculation of active torque. A: model A has the parallel elastic component (PEC) parallel to both the contractile element (CE) and the series elastic component (SEC). As such, during a shortening contraction, there is no change in the PEC and thus no change in passive tension. B: in contrast, model B has only the CE in parallel with the PEC. As such, during a shortening contraction, the PEC will also shorten and passive tension will decrease as a function of the length change during the contraction.

**Fig. 2.** Raw data traces from a single-stimulation contraction and calculation of active torque using either model A or B. A: raw total torque (solid line), passive torque (dashed line), and fascicle length traces (dotted line) from a typical subject for a single-twitch contraction. Each dot of the fascicle length trace indicates the frame rate used to capture the rapid change in fascicle length. B: for methods assuming model A, the passive torque corresponding to the muscle length before the contraction occurs [P(A)] is subtracted from the total torque (T) during the contraction to calculate active torque [A(A)]. For methods assuming model B, the passive torque corresponding to the shortened muscle length during the contraction [P(B)] is subtracted from the total torque to determine active torque [A(B)]. To determine the passive torque during a contraction (for model B), the passive length-torque curve is first established from model A data. Then the value along the passive curve that corresponds to the shortened muscle fascicle length during the contraction is used as the passive torque during the contraction.
foot and then measured the combined foot plus foot plate torque value at every angle. It is possible that by using this approach variations in subjects’ foot size will cause either an underestimation or overestimation in calculating the torque due to gravity acting on the foot. However, this error is likely to be mostly negligible compared with the large torque value of gravity acting on the foot plate. We then subtracted these values off the torque values measured during the experiments to determine the active and passive torque. Torque tweches were evoked by application of electrical peripheral nerve stimulation (pulse width of 500 μs) to the tibial nerve with the subject at rest (termed resting torque tweches). Current was delivered with a constant-current stimulator (model D77AH, Digitimer, UK) and passed from a cathode (Ag-AgCl electrode, 24-mm diameter; Tyco Healthcare Group) placed on the optimal site of stimulation within the popliteal fossa to an anode (Ag-AgCl electrode, 24-mm diameter; Tyco Healthcare Group) positioned proximal to the cathode on the midline of the popliteal fossa. The size of the resting torque tweches were measured as the difference between the peak torque value of the twitch and the torque directly preceding the twitch. Current was gradually increased until the twitch amplitude failed to increase, at which point the intensity was further increased by up to 50% to ensure a maximal response throughout. This supramaximal intensity was used for the remainder of the experiment; however, a double pulse with an interstimulus interval of 20 ms was used to produce the measured response.

Ultrasound measurements. Muscle fascicle length was measured by using a flat shaped ultrasound probe tightly strapped to the medial aspect of the medial gastrocnemius. A 96-element, linear, multifrequency probe (LV7.5/6096, Teledem, Vilnius, Lithuania) was used at a frequency of 6 MHz, a field of view of 65 mm, and with a focus range of 18–26 mm in B-mode. The probe was attached to a PC-based ultrasound system (Echoblastar 128, UAB, Telemed) running software (EchoWaveII, Telemed) for recording of the ultrasound images at a frame rate of 80 frames/s. The location of the probe relative to the skin was marked with indelible marker for consistent placement of the probe throughout the experiment. A custom-written optical flow tracking algorithm implemented in Matlab (Mathworks) was used offline to track muscle fascicle length on the ultrasound recording (4, 6).

A brief outline of the tracking process follows. Initially the muscle fascicle length was defined on the first frame of the ultrasound recording by selecting two points: one on each of the superior and inferior borders of the medial gastrocnemius muscle that represented the average muscle fascicle length across the middle of the image. The visible area of the medial gastrocnemius was then defined by manually selecting a polygon area that represented the tracking region of interest. An optical flow algorithm was then used that assessed the shape change of the muscle by a least-squares fit of an affine transformation to the optical flow of the region of interest. This tracking algorithm has been shown to be robust and accurate compared with manual tracking for passive and isometric contractions (6). The affine transformation is then applied to the two tracking points representing the fascicle, which effectively moves the end points to match the measured shape change of the muscle from one frame to the next. As this is an iterative process there is some potential of drift of the tracking points due to accumulation of very small errors across many tracking frames. To account for this, a small correction was made in each trial. Keyframes were selected where angle and torque were the same across the trial (i.e., before and after a contraction). If torque is the same between two keyframes, then length should also be similar and therefore it is possible to track the movement of the fascicles between the keyframe images only and estimate the drift that occurs as the difference between the tracked movement and keyframe movement. A linear correction across time was then applied to correct for the small amount of drift. The order of the ultrasound videos tracked was the same order as the angles used during the stimulations. As each ultrasound recording began from the previous trial’s muscle fascicle length, the defined fascicle from the previous trial was used with minimal error for the proceeding trial and any movement between the two videos could be tracked sufficiently due to the very small amount of muscle movement. This was done to prevent redefining the fascicle for each trial, which can be prone to error.

Experimental protocol. Supramaximal peripheral nerve stimulation was applied randomly at 12–16 preselected joint angles across each subject’s range of motion. The range of angles selected ensured accurate construction of the active length-tension curve, especially for determining the plateau region and descending limb. Stimulations were made at the 11 most dorsiflexed joint angles for the subject’s range of motion in 1° increments (e.g., for a subject whose maximum dorsiflexion range of motion joint angle was 22°, stimulations were applied between 12 and 22°, inclusive). Outside of this range, further stimulations were applied in dorsiflexion at 5° increments, beginning at the neutral ankle position (e.g., for the same subject who had stimulations applied between 12 and 22°, further stimulations were applied outside of this range at 0°, 5° and 10°). Approximately 2–3 s prior to each stimulation, but after repositioning the ankle joint angle, subjects’ performed a brief (1–2 s), submaximal [<30% maximal voluntary contraction (MVC)] plantar flexion contraction to minimize anythiostropic effects within the muscle (20). Each joint angle was randomly tested three times for a total of 36–48 stimulations.

Using this stimulation procedure, length-tension data were collected under three conditions. Initially, control length-tension curves were constructed where the above protocol was followed, which will be referred to as the “baseline” condition. Immediately after, we then created a condition that simulated the effects of when the ankle is not tightly strapped to the dynamometer. Ensuring the ankle is tightly strapped to the dynamometer is critical in research that uses joint angle as a proxy for muscle-tendon unit length. If the ankle is not tightly strapped and becomes loose, not only can this affect torque production, but also the dynamometer angle no longer reflects the same relative joint configuration and muscle length. However, direct fascicle length measures should be insensitive to joint configuration changes. Therefore, we used this scenario to test how robust the length-tension curves are to a change in muscle fascicle length without the same relative change in dynamometer angle. To do this, a 2-cm block of wood was placed under the subject’s heel pad to lift the heel from the dynamometer foot plate. This set-up ensured that the medial gastrocnemius muscle fascicle length was systematically shorter for a given dynamometer angle compared with the baseline condition. Length-tension curves were then constructed using this modified set-up, referred to as the “heel-lift” condition. Subjects were then released from the dynamometer and a minimum of 2 h was given before a third length-tension curve was constructed using the same positioning as the baseline condition. This third condition was referred to as the +2-h condition.

Length-tension curve construction. For each condition (i.e., baseline, heel lift, and +2 h), active length-torque (L-T) or angle-torque (A-T) curves were constructed via three methods. The first method consisted of plotting the dynamometer angle against the active torque according to model A, herein referred to as the angle-torque(A) [A-T(A)] method. The second method consisted of plotting the muscle fascicle length against the active torque also according to model A, herein referred to as the length-torque(L) [L-T(L)] method. For these two methods, active torque was calculated by subtracting the average passive torque over a 0.5-s window prior to the stimulation from the peak torque value of the twitch (Fig. 2A). The third method consisted of plotting muscle fascicle length against the active torque according to model B, herein referred to as the length-torque(L) [L-T(B)] method. For this method, the active torque was calculated by subtracting the passive torque during the contraction away from the peak value during the twitch (Fig. 2A). To determine the passive torque during the twitch contraction, the passive length-torque curve was determined (see below) and then the passive value was estimated corresponding to the length the muscle shortened to during the contraction (Fig. 2B). The corresponding muscle fascicle length was the shortest...
fascicle length measured by the ultrasound recordings during the twitch contraction. Second-order exponential curves were fit according to previous physiologically appropriate models (1, 18):

\[ T_{\text{active}} = e^{-|L - L_0|^a} \]

where \( T \) is torque, \( L \) is fascicle length or dynamometer angle at which maximum torque occurs (i.e., the optimal muscle fascicle length, \( L_0 \)), and \( a \) is roundness, \( b \) is skewness, and \( s \) is width.

Passive L-T/A-T curves were also constructed for each of the three methods by fitting a standard exponential expression:

\[ T_{\text{passive}} = A e^{kL} \]

where \( k \) is the stiffness of the curve.

Data and statistical analysis. From the fitted active L-T/A-T curves, the maximum torque \( (T_{\text{max}}) \), the muscle fascicle length or dynamometer angle at which maximum torque occurs (i.e., the optimal muscle fascicle length, \( L_0 \)), and the passive stiffness \( (k) \) were determined. Two-way repeated-measures ANOVA tests were performed to examine the effect of the method used and the curve condition on \( T_{\text{max}} \) and \( L_0 \) [for L-T(A) and L-T(B) methods only]. The same effects were examined using one-way ANOVA tests on \( k \) and \( L_0 \) [for the A-T(A) method only]. Bonferroni post hoc tests were performed when significant main effects were found. All group data presented in RESULTS are presented as means \( \pm \) SD; group data in Figs. 4–6 are presented as means \( \pm \) SE. Significant differences were established at \( P \leq 0.05 \).

RESULTS

Comparing curve construction methods. To compare the effect of the model used on the shape of the active length-tension curve, parameters \( T_{\text{max}} \) and \( L_0 \) were compared across the methods at baseline. A significant main effect of method was found for maximum torque production at baseline \( (F_{2,27} = 4.95, P \leq 0.05) \), which is exemplified by a single subject’s data in Fig. 3. \( T_{\text{max}} \) calculated using the L-T(B) method was 64.16 \( \pm \) 8.99 N·m and was significantly greater than both the L-T(A) method \( (51.99 \pm 9.33) \) and the A-T(A) method \( (52.59 \pm 9.08) \) N·m; Fig. 4). This indicates that the calculation of maximum torque from the active length-tension curve was greater when model B rather than model A was used. Conversely, there was no significant main effect found for optimal muscle length at baseline between the two ultrasound methods \( (F_{2,18} = 0.28, P = 0.60) \). \( L_0 \) in the baseline condition was 58.14 \( \pm \) 10.10 and 61.87 \( \pm \) 11.25 mm for the L-T(A) and L-T(B) methods, respectively (Fig. 5A).

Effect of the heel-lift condition. To examine the effect of changing dynamometer angle independent of muscle fascicle length, parameters \( T_{\text{max}}, L_0, \) and \( k \) were compared between the baseline and heel-lift conditions for each method. There was no significant main effect of curve condition found for maximum torque production for the three methods used \( (F_{2,54} = 1.49, P = 0.24) \) (Fig. 4). For L-T(A) and L-T(B) methods, \( T_{\text{max}} \) in the baseline condition was similar to that for the heel-lift condition \( (52.94 \pm 10.77 \) and 62.45 \( \pm \) 9.93 N·m, respectively). This indicates that maximum torque production was not affected by the heel-lift condition regardless of the method used to construct the curves. A significant main effect of curve condition was found for optimal muscle length \( (F_{2,36} = 6.43, P \leq 0.05) \). However, there was no interaction effect for optimal muscle length between baseline and heel lift, where \( L_0 \) was 58.04 \( \pm \) 12.88 and 60.09 \( \pm \) 12.85 mm in the heel-lift condition for methods L-T(A) and L-T(B), respectively (Fig. 5A). Furthermore, there was no significant main effect of curve condition found for passive stiffness for the ultrasound methods used \( (F_{2,18} = 2.70, P = 0.09) \) (Fig. 6A). For either the L-T(A) or L-T(B) methods, \( k \) in the baseline condition \( (0.190 \pm 0.118) \) was similar to that for the heel-lift condition \( (0.246 \pm 0.121) \).

The shape of A-T curves constructed using dynamometer angle was affected by the heel-lift condition. While there was no difference in \( T_{\text{max}} \) between baseline and heel lift \( (52.59 \pm 9.08) \) N·m, a significant main effect of curve condition was found for optimal angle using the A-T(A) method \( (F_{2,18} = 8.22, P \leq 0.05) \) (Fig. 5B). \( L_0 \) in the baseline condition was 19.10 \( \pm \) 4.42° and this increased significantly in the heel-lift condition to 22.08 \( \pm \) 3.83°. No significant main effect of curve condition was found for passive stiffness \( (F_{2,18} = 0.09, P = 0.91) \) for the A-T(A) method (baseline \( k = 0.109 \pm 0.058 \), heel lift \( k = 0.110 \pm 0.028 \)) (Fig. 6B).

Reliability of the curve construction methods. To test the reliability of the curve construction methods, parameters \( T_{\text{max}}, L_0, \) and \( k \) were compared between the baseline and \( +2\)h conditions for each method. Irrespective of the method used, there were no differences between baseline and \( +2\)h parameters. For the \( +2\)h condition, \( T_{\text{max}} \) was 51.70 \( \pm \) 8.92, 51.42 \( \pm \) 8.41, and 62.04 \( \pm \) 8.56 N·m for methods A-T(A), L-T(A), and L-T(B), respectively (Fig. 4). These values were not signifi-
compared with using techniques that assumed tension was found to be significantly larger when assuming human medial gastrocnemius in vivo. Maximal torque production on the construction of active length-tension curves of the human medial gastrocnemius. Furthermore, active length-tension curves constructed using ultrasound to measure fascicle length compared with their corresponding baseline values. Optimal muscle length in the +2-h condition for the L-T(A) and L-T(B) methods was 55.71 ± 12.18 and 58.32 ± 12.44 mm (Fig. 5A), respectively, while optimal angle using the A-T(A) method was 18.96 ± 2.81° (Fig. 5B). Similar to maximum torque production, optimal length/angle was no different between baseline and the +2-h conditions. For k using method L-T(A) or L-T(B), there was again no significant difference in the +2-h condition (0.205 ± 0.069; Fig. 6A) compared with the baseline condition. Furthermore, no change was evident in k between baseline and +2-h conditions (0.104 ± 0.024) using the A-T(A) method (Fig. 6B).

DISCUSSION

The present study investigated the implications of the choice of two popular Hill-type skeletal muscle models (models A and B) on the construction of active length-tension curves of the human medial gastrocnemius in vivo. Maximal torque production was found to be significantly larger when assuming model B compared with using techniques that assumed model A. These results indicate that the choice of model has a significant effect on the shape of active length-tension curves of the human medial gastrocnemius. Furthermore, active length-tension curves constructed using ultrasound to measure fascicle length changes can be reliably reconstructed and are not compromised by changes in the relationship between muscle length and dynamometer angle. As previous nonhuman literature has indicated that model B better describes the interaction between active and passive components, particularly for muscles with long tendons and when passive tension is high (15, 22, 24), we recommend the use of model B for these conditions when constructing medial gastrocnemius active length-tension curves in humans in vivo.

The skeletal muscle model used to describe how muscle force is produced relative to length influences the interpretation of passive tension during a contraction. We found that maximum torque was larger using L-T(B) (model B) compared with L-T(A) (≈23%) and A-T(A) (≈22%) (model A). To our knowledge, this is the first time a change in the shape of the length-tension curve due to the muscle model used has been reported in human research. While the change in optimal fascicle length for the present study was not statistically significant, it is likely that a significant difference was hidden due to difficulties in determining L0 when the muscle acted entirely on the ascending limb (as discussed in detail below).

Previous nonhuman literature has shown the maximum force to be greater and the optimal fascicle length to be significantly longer when using model B. MacIntosh and MacNaughton (15) showed greater active force values for fascicle lengths equal to and above resting length when using model B, which corresponds to a significant lengthening of the optimal fascicle length compared with model A. They also designed a number of experiments to test the assumptions of both model A and model B and found that model B better described the force-length relationship of the rat medial gastrocnemius. These findings are further supported by Siebert et al. (24) who found parameters such as isometric force and optimal fascicle length from fitted force-length curves were more closely matched to the corresponding parameters from experimental data when model B was used to fit the curve compared with model A. Finally, Rode et al. (22) supramaximally stimulated cat soleus muscle and found that maximum isometric muscle force was 10% greater and optimal fascicle length 10% longer when using model B vs. model A. These results indicate that the choice of model has a significant effect on the shape of active length-tension curves. As such, it is important for researchers to choose the model that accurately describes the interaction between active and passive components for the muscle they are investigating. It is acknowledged that length-tension curves can be affected by the interaction between stimulation fre-
quency and muscle length (21). However, as we kept our level of stimulation consistently low, this had no effect on the differences found between model A and model B. Furthermore, the shape of our L-T curves appear similar to L-T curves produced during MVC when model B is applied.

While the present study did not directly examine which model more accurately describes the length-torque relationship of the triceps surae, the findings from MacIntosh and MacNaughton (15) combined with a large shortening of the muscle fascicle during the contractions observed here would suggest that passive tension decreases during isometric contractions of the human triceps surae muscles. Thus model B would better describe how torque is produced between the active and passive components. Furthermore, because of differences in muscle passive tension, the contributions of surrounding muscles and the associated joint range of motion between muscles and between species, it should be noted here that our recommendation that model B should be used to construct L-T curves only applies to the human medial gastrocnemius. However, it is likely that many muscles in the body will have similar passive properties that model B can only correctly account for. As such we also recommend that any research that measures length-tension curves should correctly determine the most appropriate skeletal muscle model for the muscle they are measuring before analyzing length-tension curves.

We acknowledge that the fascicle length of only one (medial gastrocnemius) of the three muscles that comprises the triceps surae was recorded while total plantar flexor torque was measured. A limitation of this design is that it is unknown what relative contribution the medial gastrocnemius makes to the net passive torque at the ankle. During our experiments we observed from one subject that the proximal soleus fascicles (visible deep to the medial gastrocnemius) shortened by a large amount (=5–15%) that was also comparable to the length change in medial gastrocnemius (=10–20%). This is expected given that the muscles attach to the same compliant Achilles tendon and suggests model B should be used for both medial gastrocnemius and soleus.

It is not possible from our data to determine whether one muscle has a greater reduction in passive force than the other. However, for the same example subject we constructed soleus and medial gastrocnemius L-T curves and analyzed two hypotheses regarding passive torque. In one hypothesis we constructed the medial gastrocnemius L-T curve assuming medial gastrocnemius provided 100% of triceps surae passive torque while in the other we constructed soleus L-T curves assuming soleus provided the entire contribution. We found that for contractions occurring at the longest muscle length (i.e., highest passive torque), the passive torque values during contraction for both muscles were quite low, similar to each other and significantly reduced from the passive values prior to the contraction occurring (~75%). As such, we believe that passive torque will be reduced significantly in both muscles and we are confident that the results from medial gastrocnemius are accurate and reflect what is occurring within the entire triceps surae muscle group. Further work to partition the forces of the muscles (9) is required to precisely determine the active and passive force length curves of each muscle.

A limitation of 2D ultrasound imaging during active contractions is the potential for movement of the fascicle out of the imaging plane during the contraction. We have attempted to limit this by ensuring correct orientation of the transducer to the plane of movement at rest (2) and also ensuring that we have good-quality images throughout the contraction (i.e., that the fascicle connective tissue is clearly visible). Given that the length changes during twitch contractions are rather small compared with MVCs (13), the potential for large-scale movement out of the plane is minimized; however, there is a potential for error in our length measurements. A method of 3D imaging the fascicles may be required to more accurately measure the dynamic length changes.

A consequence of using model B over model A is that there is a change in the active range of the active length-tension curve over which the medial gastrocnemius works. Due to the calculation of active torque using model B, the ascending limb of the curve lengthens and there is a widening of the plateau region. As such, more of the medial gastrocnemius is activated for muscle lengths corresponding to the ascending limb of the active length-tension curve. As a result of anatomical range of motion constraints, there were very few data points that formed a descending limb in the curve (as exemplified by the circle data points in Fig. 7), which made fitting curves to the data problematic for some participants (i.e., the “turning point” of the curve fell outside the range of raw data values). Quite often, this would mean the estimated $T_{\text{max}}$ value and the estimated $L_0$ value would be unrealistically large and the curves would not be physiologically correct. To deal with this, for participants where no clear descending limb was present, the upper bound of the maximum torque parameter in the model fit was constrained to the highest total torque value collected for that condition. This ensured that the curves began to decrease from the plateau region. Conservative bounds were estimated to produce a shape that typified the active length-tension relationship based on curves where there was a clear optimum and descending limb. Figure 7 shows an example of this procedure being applied to the circle data points to produce the fitted curve (dotted line). This fitting procedure is likely to have led to some variability and an underestimation of the optimum length, which is the likely reason there was no significant change in this parameter in our study.

A common approach used in human research is the measurement of dynamometer or joint angle as an indirect measure
of muscle length for the construction of active length-tension curves. Without knowledge of how the fascicles shorten during a contraction, model A must be assumed by default in these type of studies. However, another inherent problem with using dynamometer or joint angle, apart from not being able to use model B, is that changes in either measurement can occur without a subsequent change in muscle length. We simulated this particular scenario during the “heel-lift” condition by systematically shortening the triceps surae muscle length for a given dynamometer angle. The results revealed that the shape of active length-tension curves was affected by the “heel-lift” condition when constructed using dynamometer angle, whereas the curves were no different in shape from the “baseline” condition when the ultrasound methods were applied. While using direct measurements of ankle joint angle (i.e., via a goniometer) instead of dynamometer angle might reduce this particular error, changes in triceps surae muscle length are not necessarily reflected by changes in ankle joint angle. For example, changes in the fascicle length of the biarticular medial gastrocnemius can occur due to joint angle changes at the knee, which cannot be detected by measuring ankle joint angle. Therefore, the use of ultrasound allows a more accurate measurement of the change in muscle length and also allows the use of model B. More importantly, measuring fascicle length accounts for the effects of series elastic compliance that may differ between individuals (14), and therefore the use of ultrasound allows a more accurate measurement of the change in muscle length and allows the use of model B.

Our results have significant implications for human research using the medial gastrocnemius where joint torque and joint angle are used to estimate the contribution of both active and passive muscle tension, such as in exercise-induced muscle damage. During these experiments, it is typically assumed that the passive tension at a specific joint angle is constant through a contraction. However, it is clear from our data that there is significant shortening of the muscle fascicles, which likely reduces the passive tension within the muscle. In the case of muscle damage, where it has been shown that the passive tension of muscle increases in response to eccentric muscle activities (9), using model A would lead to significant reductions in the estimates of active tension at long muscle lengths compared with model B (11, 25). This would not be physiologically accurate because the passive tension during contraction would be significantly overestimated.

DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

REFERENCES


