The maximum shortening velocity of muscle should be scaled with activation

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Chow, John W., and Warren G. Darling. The maximum shortening velocity of muscle should be scaled with activation. J. Appl. Physiol. 86(3): 1025–1031, 1999.—The purpose of this study was to determine whether the maximum shortening velocity (Vmax) in Hill’s mechanical model (A. V. Hill. Proc. R. Soc. London Ser. B. 126: 136–195, 1938) should be scaled with activation, measured as a fraction of the maximum isometric force (Fmax). By using the quick-release method, force-velocity (F-V) relationships of the wrist flexors were gathered at five different activation levels (20–100% of maximum at intervals of 20%) from four subjects. The F-V data at different activation levels can be fitted remarkably well with Hill’s characteristic equation. In general, the shortening velocity decreases with activation. With the assumption of nonlinear relationships between Hill constants and activation level, a scaled Vmax model was developed. When the F-V curves for submaximal activation were forced to converge at the Vmax obtained with maximum activation (constant Vmax model), there were drastic changes in the shape of the curves. The differences in Vmax values generated by the scaled and constant Vmax models were statistically significant. These results suggest that, when a Hill-type model is used in musculoskeletal modeling, the Vmax should be scaled with activation.

force-velocity relationship; Hill model; wrist flexors

A NUMBER OF MUSCLE MODELS have been proposed since the 1930s. The prominent models include Hill’s mechanical model (10), the cross-bridge model (11), the molecular model (9), and the distribution-moment model (28). Among these models, Hill’s mechanical model

\[ F = \left( F_{max} b - av \right) / \left( v + b \right) \]  

(1)

where F is muscle force, Fmax is maximum isometric force, v is muscle shortening velocity, and a and b are Hill constants, has stood the test of time and still serves as the most convenient mathematical description of the force-velocity (F-V) characteristic of muscle contraction. One of the problems that has to be addressed when the Hill-type muscle model (10) is used in muscle modeling is how to modify the F-V relationship at submaximal activation (26, 30). The major issue is the maximum velocity of shortening (Vmax) at different activation levels (ALs). Some investigators assume that the Vmax is constant (2, 15, 22), whereas others assume that it decreases with activation (4, 27). In other words, the former group assumes that the constants in Hill’s characteristic equation (Hill constants a and b) are constants regardless of the activation, and the latter group considers the Hill constants functions of the activation.

In a study of the F-V relationship in cat soleus muscle at different stimulus rates, Joyce and Rack (14) found that the Vmax decreased with the stimulus rate. Similar results were also reported by Mashima et al. (18), who controlled the activation [measured by the contractile force before the quick release (QR)] of the frog semitendinosus muscle by varying the potassium concentration of the Ringer solution and the frequency of the stimulation. A review of the literature indicates that only one attempt has been made to study the F-V-activation (F-V-A) relationship by using human subjects. Zahalak et al. (29) attempted to relate the surface electromyographic (EMG) measurements to the F-V relationship in the forearm flexors. Subjects in this study were trained to move their forearms at different constant angular velocities before the experimental trials were conducted. A decrease in Vmax at submaximal activation was reported. However, these results represent values obtained by control over velocity rather than responses of the muscle to different loads at different ALs. A review of the literature indicates that only one attempt has been made to study the F-V-activation (F-V-A) relationship by using human subjects. Zahalak et al. (29) attempted to relate the surface electromyographic (EMG) measurements to the F-V relationship in the forearm flexors. Subjects in this study were trained to move their forearms at different constant angular velocities before the experimental trials were conducted. A decrease in Vmax at submaximal activation was reported. However, these results represent values obtained by control over velocity rather than responses of the muscle to different loads at different ALs. In view of the limited data on the F-V-A relationship in human muscle under voluntary contraction, the purpose of this study was to determine whether the Vmax in Hill’s mechanical model should be scaled with activation by using a technique different from the one used by Zahalak et al.

METHODS

Three male and two female paid volunteers with no history of persistent joint disorders or musculoskeletal trauma served as subjects (age 18–25 yr) in this study. Informed consent was obtained from subjects before their participation. Only the data of four subjects were considered adequate and used in subsequent analyses. See explanation in Data reduction.)

Experimental setup. During the trials, the subject sat behind a table in an upright posture, and his or her left forearm was constrained by a plastic polymer cast (Fig. 1). The left upper arm was inclined at an ~70° angle. Two openings in the cast permitted placement of EMG electrodes over the medial and lateral surfaces of the forearm. The center bore of a motor pulley was fitted to the shaft of a potentiometer (model 534, Spectrol Electronics, City of Industry, CA, nominal resistance 5 kΩ ± 5%, nonlinearity <0.25%) located underneath the tabletop. Potentiometer measurements were highly reliable in repeated tests, and the resolution of angle measurement was 0.1°.

The distance between the longitudinal axis of the handle (length = 10 cm, diameter = 2.5 cm) and the axis of rotation of the motor pulley (AOR) was adjustable, ranging from 4.5 to 7.0 cm. The shortest distance between the steel cable and the AOR was 9.5 cm. The back support and the hold-down pulley were installed to prevent lateral displacement of the wrist and upward tilt of the lateral side of the motor pulley during the course of wrist flexion, respectively. The part of the back support that made contact with the subject’s forearm was 3 cm behind the AOR. The steel cable (diameter = 2 mm) had one end fixed to the medial side of the motor pulley and the other end connected to
a load cell (model AWU250, Genesco Technology, Simi Valley, CA, nonlinearity <0.05% full scale, hysteresis <0.03% full scale, maximum capacity = 1,112 N). The load cell was in series with a weight plate holder, located directly above an electromagnet fixed to the floor. When the holder was held down by the active electromagnet and the cable was taut (i.e., before the QR), both the center of the handle and the AOR were aligned with the longitudinal axis of the cast in an overhead view. In other words, the wrist was at a neutral position during the isometric contractions before the QR.

Although it was not the purpose of this study to relate the EMG to the F−V relationship, muscular activities of the wrist flexors and extensors were monitored so that the electrical activities during the course of each trial could be examined. Two pairs of bipolar silver-silver chloride surface electrodes (diameter = 8 mm, center-to-center distance = 20 mm) were placed over the bellies of the flexor (one-third of the distance from the medial humeral epicondyle on a line joining the medial humeral epicondyle and the styloid process of the radius) and extensor (one-third of the distance from the lateral humeral epicondyle on a line joining the lateral humeral epicondyle and the styloid process of the ulna) carpi radialis muscles approximately parallel to the direction of the muscle actions. A reference electrode was placed over the bellies of the flexor of the other arm. EMG signals were preamplified (model 301, Biocommunication Electronics, Madison, WI, input impedance 1010 Ω, common mode rejection ratio = 140 dB) before further amplification.

The tension of the steel cable and the angular position of the handle were measured by the load cell and potentiometer, respectively. The analog signals were filtered (20- to 1,000-Hz band pass for EMG and 1,000-Hz low pass for force and angle) and amplified by using a general-purpose amplifier (model 205, Biocommunication Electronics) before being digitized (12-bit resolution) at a sampling rate of 500 Hz by using the Wattscope data-collection system (Northern Digital, Waterloo, ON).

The force measured by the load cell was displayed to the subject by using a storage oscilloscope (model 5111, Tektronix, Beaverton, OR) stationed on the tabletop next to the apparatus. The signal from the load cell was branched off to the oscilloscope and displayed as a horizontal line on the cathode ray tube screen. Considering a free body diagram of the hand and summing the moments about the transverse axis of the wrist joint, the total moments due to forces of the wrist flexors must be equal to the moment due to the contact force acting through the handle. Assuming the wrist flexors act as a single equivalent muscle (3, 24), we obtain

\[ F_R d_2 = F_{mus} d_1 \]

where \( F_R \) is the force measured by the load cell, \( d_2 \) is the distance between the line of action of the steel cable and the AOR, \( F_{mus} \) is the muscle force, and \( d_1 \) is the moment arm of the wrist flexors. Because \( d_2 \) and \( d_1 \) are constants, the position of the force line (load cell force \( F_R \)) was linearly related to the muscle force (i.e., \( F_R = F_{mus} (d_1/d_2) \)). When there was no load attached to the load cell, the "0% force line" was positioned to the top of the screen. It should be pointed out that it is impossible to mimic a "zero-load" condition because, even if the load cell and weight plate holder were removed from the setup, the resistance due to the masses of the pulley, handle, and hand cannot be avoided. Because the inertial resistance at the instant of release was the same in all trials and the absolute muscle shortening velocity values were not the main focus of this study, the inertial resistance should not affect the main results obtained in this study.

Data collection. Before the experimental trials, the subject was asked to perform 3 sets of 10 repetitions of wrist flexion against a load of 55.7 N as warm-up. To align the wrist joint with the AOR, the positions of the forearm, hand, and handle were adjusted such that the tip of the styloid process of the ulna (1) was directly above the AOR. The data-collection session started with three trials of maximum isometric contractions against a very large resistance provided by the active electromagnet. In each trial, the operator triggered the data collection once the maximum deflection of the force line was attained. The average maximum deflection (100% force line) was used to construct a template. The template was a small card (2 × 8 cm) fixed on the left-hand side of the cathode ray tube screen. Along the right edge of the card, the space between the 0 and 100% force lines, as it appeared on the screen, was divided into five equal spaces, and the divisions became force lines at 20% intervals. \( F_{max} \) was computed as the average of the maximum forces recorded in the first three trials.

The next three trials were maximum isometric extension contractions. The operator applied a force to the back of the subject's hand, and the subject was encouraged to extend the hand with maximum effort. The purpose of these three trials was to obtain the maximum EMG level of the wrist extensors.

QR trials followed isometric trials. In each trial, the load (weight plates and holder) was initially held down by the active electromagnet, and the subject was asked to apply force on the handle and maintain the effort at a particular force level. In other words, the subject contracted the wrist flexors such that the force line remained at a specific position indicated on the template. Once the force line stayed at a specific position, the operator triggered the data collection and followed with the release of the load by switching off the electrical supply to the electromagnet. In each trial, the digital data were collected for 1.5 s and stored on the hard disk.

For the purpose of this study, an AL was defined as a fraction of the \( F_{max} \) (21). Five ALs, ranging from 20 to 100% at intervals of 20%, were employed in this study. Except for 20% AL, six different loads were used for each AL. For all ALs, the
lightest load used was the weight of the weight plate holder plus load cell, which was 11.15 N. In this study, the smallest increment in the load was 5.6 N, which was not small enough to provide six different loads for 20% AL trials. Trials of the same AL were conducted as a group from heavy to light loads. Trials progressed in the order of 100–20–80–40–60%. The order was designed to minimize the effect of fatigue. The 20 and 40% AL trials served as recovery periods after periods of intense muscle contractions (i.e., 100 and 80% AL trials). Rest intervals between consecutive trials ranged from 1 to 5 min, depended on the AL. The data-collection session ended with a maximum isometric flexion trial to test for the presence of fatigue.

Data reduction. Before the F-V data were computed, the forces attained immediately before QR were examined first, and it was found that these deviated from the expected forces by 7.17 ± 8.74 (SD) % of F_max on average in one subject. The average deviations were 1.97 ± 2.42, 2.06 ± 2.86, 2.29 ± 2.70, and 3.13 ± 3.63% for the remaining four subjects, respectively. Only data of these four subjects were used in subsequent analyses.

To compute the angular velocity, the time instant when the handle was 5° away from the release position (5° instant) was identified. The angular positions of the handle at the instants 4 ms before and after the 5° instant were then identified. The angular velocity was obtained by dividing the change in angular position by 8 ms. Angular velocities of the handle at the instants of 2.5, 5, and 10° away from the release location were also computed in one subject, and it was found that the normalized F-V curves for these three positions were qualitatively similar. The normalized F-V data obtained by using these three handle locations could be fitted well with the Hill equation, and each set of F-V curves exhibited similar trends (e.g., decrease in V_max with decreasing activation).

It was assumed that the shortening velocity of the wrist flexors was linearly related to the angular velocity of the hand. This assumption is considered acceptable because an arc segment of a circle can be approximated as a straight line if the angle defining the segment is small. Because the highest angular velocity recorded was 491.2°/s, the largest angular distance used for the calculation of angular velocity in this study was 3.9° (i.e., 491.2°/s × 0.008 s). The tendon compliance was not considered because wrist flexors are relatively small muscles and cannot generate sufficient force to stretch the tendons appreciably. Lehman and Calhoun (16) estimated the tendon stiffness of the flexor carpi radialis to be 8 × 10^4 N/m.

Hill’s characteristic equation (Eq. 1) was fitted to each set of F-V data by using the least squares technique (minimizing the sum of the squared force residuals; see Appendix A). By setting F in Eq. 1 equal to 0, the V_max was obtained by the following equation

\[ V_{\text{max}} = \frac{(F_{\text{max}} b)}{a} \]  

The force and velocity data were then normalized as fractions of the F_max and V_max for the 100% AL, respectively. The normalized data were pooled, and Hill’s hyperbolic curves were fitted to the data of the same AL. The coefficient of determination (r^2) for each fitted curve was also computed (see Appendix A).

For the QR trials, the average time elapsed from triggering the data collection to the moment of releasing the load (average delay time) was found to be 330 ± 155 ms. The EMG level was computed as the average rectified integrated value during the delay, i.e., by dividing the area under the rectified EMG curve by the respective delay time. For each subject, the EMG values for the wrist flexors and extensors obtained for each trial were expressed as percentages of the corresponding average EMG values in maximum activation trials.

RESULTS AND DISCUSSION

In the last trials of the data-collection sessions, the four subjects could produce, on average, 96.4% of their own F_max (SD = ±1.95%). Thus fatigue was minimal. It was observed in most low load-high activation QR trials that, very soon after the load was released (e.g., 46 ms in Fig. 2), the activity of the wrist flexors diminished for a short period of time (e.g., 54 ms in Fig. 2) and at the same time there was a burst of activity in the extensors. The diminution in muscle activity in the flexors and the burst of activity in the extensors are typical examples of unloading and stretch reflexes, respectively (17). The reflex responses produced no effects on the results of this study because they occurred after the instant when the angular velocity was measured. Because the angular velocity of the hand was measured before voluntary or reflex intervention to the unloading, we assumed that there was a high degree of repeatability of responses even if there was only one trial for each load-activation condition. Such repeatability was observed in preliminary tests of the apparatus.

In QR experiments using isolated muscle preparation (8, 12), a typical displacement (length change)-time curve rose sharply immediately after the release of the load and was followed by a steady increase. The initial slope, indicating rapid shortening, was attributable to the series elastic component of the muscle. However, this was not observed in the present study.

The EMG of the wrist extensors at different ALs indicated that the degree of cocontraction increased with the activation of the agonist. On average, the

![Fig. 2. Plot of raw data of a quick-release trial, maximum activation and 11.15-N load. Top to bottom: load cell, potentiometer, and EMG activity of flexors and extensors, respectively.](image-url)
EMG of the wrist extensors at 20 and 100% ALs of the flexors were 1 and 7%, respectively. It was assumed that the effects of the wrist extensors were negligible because of the low EMG and because the maximal extension torque is usually much smaller than the maximal flexion torque for the wrist joint.

The F-V curves at different ALs for subject KR (Table 1) are considered atypical compared with the results of the other subjects because the maximal velocities were similar for the 40, 80, and 100% ALs. The cause of such atypical results is not known. However, a more homogeneous muscle fiber population in wrist flexors of subject KR is a possible explanation. It may also be due to the single-trial protocol used in this study, and the data collected from this subject were not reliable. The very large value (2,912°/s) predicted from regression analysis for the 20% AL was due to an outlier, indicated by an arrow in Fig. 3. (Note: To avoid confusion, \( f_{\text{max}} \) and \( v_{\text{max}} \), expressed as a fraction of \( F_{\text{max}} \) and \( V_{\text{max}} \) respectively, denote the isometric force and estimated maximum shortening velocity for submaximal ALs.)

As indicated by the coefficient of determination \( r^2 \) values, the F-V data at different ALs can be fitted remarkably well with Hill's characteristic equation (Table 1). In general, the velocity of shortening decreases with activation for a given load. For example, when a horizontal line is drawn for a given normalized force in Fig. 3, the shortening velocity decreased with the activation. These findings are in agreement with results obtained in isolated muscle (21) but contrary to results obtained in individual muscle fibers in which maximum unloaded velocity is independent of AL (5, 23). The property of constant \( v_{\text{max}} \) is not found in the whole muscle because of the different fiber and motor unit types in a whole muscle and motor unit recruitment order. Because type S motor units are slow contracting because they contain type I fibers and are recruited at low force output according to the size principle (7), the wrist flexors, which have an even distribution of fast- and slow-twitch fibers (13), are expected to contract more slowly as the activation decreases.

Although individual differences are apparent in most of the characteristic parameters (Table 1), it is notewor-

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**Table 1. Characteristics parameters of the force-velocity curves at different activation levels of all subjects**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Activation Level, %</th>
<th>( F_{\text{max}}^* ) or ( f_{\text{max}}, N )</th>
<th>( V_{\text{max}}^† ) or ( v_{\text{max}}, °/s )</th>
<th>Hill Constants</th>
<th>( a/F_{\text{max}} ) or ( a/f_{\text{max}} )</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>KS</td>
<td>100</td>
<td>192.0</td>
<td>468.9</td>
<td>104</td>
<td>0.52</td>
<td>0.987</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>154.0</td>
<td>465.8</td>
<td>82</td>
<td>248</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>60</td>
<td>117.0</td>
<td>401.0</td>
<td>103</td>
<td>353</td>
<td>0.88</td>
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<tr>
<td></td>
<td>40</td>
<td>76.0</td>
<td>386.3</td>
<td>76</td>
<td>183</td>
<td>0.47</td>
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<tr>
<td></td>
<td>20</td>
<td>38.0</td>
<td>290.7</td>
<td>20</td>
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<tr>
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<td>67</td>
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<td></td>
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<td>428.5</td>
<td>61</td>
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<td>0.62</td>
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<td></td>
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<tr>
<td></td>
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<td>25.0</td>
<td>450.0</td>
<td>7</td>
<td>126</td>
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<td>134.0</td>
<td>403.4</td>
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<tr>
<td></td>
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<td>105.0</td>
<td>418.3</td>
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<td>239</td>
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<tr>
<td></td>
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<tr>
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<td>227.9</td>
<td>222</td>
<td>1,150</td>
<td>5.05</td>
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</table>

\( F_{\text{max}} \) and \( V_{\text{max}} \), maximal force and velocity, respectively; \( f_{\text{max}} \) and \( v_{\text{max}} \), isometric force and estimated \( V_{\text{max}} \) for submaximal activation levels.

*Force recorded by the load cell immediately before the quick release. †Maximum shortening velocity estimated by the curve fitting (see APPENDIX A). ‡A data point from this subject (an outliner) was excluded from subsequent analysis.

**Fig. 3. Normalized force-velocity data from all subjects (n = 4). Curves were obtained by fitting Hill's hyperbolic curves to data of same activation level by using least squares technique (best-fit curves in Table 2). Each symbol on abscissa represents 4 data points, 1 from each subject.**
thy that, for all subjects, almost all of the \(a/F_{\text{max}}\) and \(a/f_{\text{max}}\) values at 100 and 80% ALs are in the neighborhood of 0.5 and 0.6. These values are greater than those obtained from isolated muscles (25) and muscle fibers (6). (Note: the \(a/F_{\text{max}}\) value, a ratio that has no units, indicates the curvature of the hyperbolic curve. The smaller the \(a/F_{\text{max}}\) value, the greater the curvature of the curve.) The only exception is that Phillips and Petrofsky (21) reported \(a/F_{\text{max}}\) values of 0.5 or above in three different cat muscles, lateral and medial gastrocnemius and soleus. Interestingly, in another study (19) the same authors reported values of ~0.25 in cat medial gastrocnemius.

When a curve is fitted to the normalized F-V data of each AL (Fig. 3), the data point that was responsible for the huge 20% AL \(v_{\text{max}}\) for subject KR (indicated by an arrow in Fig. 3) accounted for more than one-half of the sum of the squared force residuals (SSR; see Appendix A) of the 20% AL curve. It was decided to exclude this data point from the determination of best-fit curves and mathematical models. Despite the fluctuations in the 60 and 80% ALs, both Hill constants of the best-fit curves (Table 2) show a trend of decrease with decreasing activation. Both linear and nonlinear relationships between Hill constants and activation have been reported in the literature (20, 21).

With the assumption of nonlinear relationships (2nd-order polynomials) between Hill constants and AL, the following equations were obtained if the shape of the normalized curve at 100% AL was retained (i.e., both curves relating the Hill constants to AL will pass through the data point: \(a = b = 59\%\), AL = 100% curves in Fig. 4 and Appendix B)

\[
a = (59 - y_1)(A - x_1)/(100 - x_1)^2 + y_1 \quad (4)
\]

\[
b = (59 - y_2)(A - x_2)/(100 - x_2)^2 + y_2 \quad (5)
\]

where \(x_1\), \(y_1\), \(x_2\), and \(y_2\) are constants and \(A\) is the AL expressed as a percentage. The scaled \(V_{\text{max}}\) model is obtained by substituting Eqs. 4 and 5 into Eq. 1. By using all normalized data, the constants were estimated by employing “carpet search” and least squares criteria. The values \(x_1\), \(y_1\), \(x_2\), and \(y_2\) were found to be 94.2, 59.3, 70.3, and 72.0, respectively. The F-V curves at different ALs generated by the scaled \(V_{\text{max}}\) model are presented as solid lines in Fig. 5.

By setting the Hill constant \(a = F_{\text{max}}\) or \(f_{\text{max}}\) (see Eq. 3) in the parameter-searching process described in Table 2. Characteristics parameters of the force-velocity curves at different activation levels obtained by best-fit, scaled maximum-velocity model, and when constant maximum velocity is assumed

<table>
<thead>
<tr>
<th>Activation Level, %</th>
<th>(F_{\text{max}}^*) or (f_{\text{max}}^%)</th>
<th>(V_{\text{max}}^%)</th>
<th>Hill Constants</th>
<th>(a/F_{\text{max}}^*) or (a/f_{\text{max}}^%)</th>
<th>(r^2)</th>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>(a, %)</td>
<td>(b, %)</td>
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<td>Best-fit</td>
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<td>Scaled (V_{\text{max}}) model</td>
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<td></td>
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*Force expressed as a percentage of \(F_{\text{max}}\). †Velocity expressed as a percentage of \(V_{\text{max}}\).
APPENDIX A, the F-V curves were forced to converge at the $V_{\text{max}}$ (constant $V_{\text{max}}$ model). The F-V curves at different ALs generated by the constant $V_{\text{max}}$ model are presented as dashed lines in Fig. 5. The $r^2$ values for the constant $V_{\text{max}}$ curves are about the same as the corresponding values for the curves obtained by using the scaled $V_{\text{max}}$ model and slightly smaller than the corresponding values for the best-fit curves (Table 2). The $r^2$ values of these curves indicate that the SSR is not very sensitive to the changes in $a$ and $b$. However, by using $V_{\text{max}}$ as the dependent variable, a 5 (ALs) × 3 (models) ANOVA revealed significant differences in $V_{\text{max}}$ among the three models, best fit, scaled $V_{\text{max}}$, and constant $V_{\text{max}}$. The Duncan multiple-range test ($P < 0.05$) showed that $V_{\text{max}}$ values from the constant $V_{\text{max}}$ model were significantly different from the corresponding values from the other two models, and there was no significant difference in $V_{\text{max}}$ between the best-fit and scaled $V_{\text{max}}$ models.

The $V_{\text{max}}$ values of individual subjects and the comparison among models clearly suggested that the $V_{\text{max}}$ was not constant at different ALs. Although the limited samples available in this study do not provide much insight into the fine details of the F-V-A relationship, these results extend the findings of Zahalak et al. (29) concerning voluntary contractions of different velocities to contractions in which the subject voluntarily controlled only the AL. With reference to musculoskeletal modeling by using Hill’s characteristic equation, these results suggest that, unless the movement being modeled requires low velocity of shortening of the muscles, the $V_{\text{max}}$ should be scaled with activation. More data, especially from different muscles, are needed to further address the issues raised in this study.

APPENDIX A

Curve Fitting by Using Hill’s Characteristic Equation

With reference to Eq. 1, the SSR is given by

$$SSR = \sum_{i=1}^{n} \left( F_i - \frac{F_{\text{max}} b - av_i}{v_i + b} \right)^2$$

where $n$ is the number of data points in a set of F-V data. Curve fitting can be considered as searching for the combination of $F_{\text{max}}$, $a$, and $b$ that will give a minimal SSR.

To start a search, the input for $F_{\text{max}}$, $a$, and $b$ were 100–105% of $F_{\text{max}}$, at intervals of 1%, 50–200% at intervals of 4%, and 100–400% at intervals of 4%, respectively. These initial inputs for $a$ and $b$ were based on the results of the searches performed on several sets of data. In the subsequent rounds of search, the inputs for the $F_{\text{max}}$ remained the same. The inputs for $a$ and $b$ were plus and minus 50 of the respective values obtained in the previous round at intervals of 1%. A search would be terminated when the combinations obtained in two consecutive rounds of search were identical. In general, three to five rounds of search were required before the optimal combination was found.

Let $F$ be the sample mean of the forces

$$F = \frac{1}{n} \sum_{i=1}^{n} F_i$$

and SSY be the sum of the squares of deviation associated with $F$:

$$SSY = \sum_{i=1}^{n} (F_i - F)^2$$

The coefficient of determination ($r^2$) was obtained by

$$r^2 = \frac{\text{SSR}}{\text{SSY}}$$

APPENDIX B

Determination of the Relationship Between a Hill Constant and the Activation Level

Mathematically, a parabola (2nd-order polynomial) in a two-dimensional rectangular coordinate system (x-y plane) can be expressed as

$$(y - q) = (x - p)^2/f$$

where $(p, q)$ is the coordinate of the parabola’s vertex and $f$ is a constant related to the focus of the parabola. With reference to Fig. 4, a parabola passing through the data point for 100% AL (100, 59) is

$$(59 - q) = (100 - p)^2/f$$

Rearranging the terms, we get

$$f = (100 - p)^2/(59 - q)$$

Substituting Eq. 12 into Eq. 10, we have

$$y = (59 - q)(x - p)/(100 - p)^2 + q$$
Therefore, a second-order polynomial passing through (100, 59) will have the form of Eq. 13.

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