

A new muscle model

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This is a paper that proposes a new muscle model to replace the one that has been used in the literature for many years. The old model uses linear spring elements and a signal-driven force generator with the force being independent of muscle length. This model fails to reproduce the basic observations of muscle behavior such as the Hill curve found in quick-release experiments. The new model makes the length of contractile elements depend (negatively) on the driving signal and also uses springs with the exponential force-length characteristic that is observed for passive stretch in most real muscles. All the main observations of muscle characteristics are reproduced by this model with one set of parameters. A C-language function is provided that can be used in computational models.

Introduction

In 1992, Shadmehr and Arbib presented a mathematical analysis of muscle behavior in a single-joint system. The present authors, engaged in constructing a simulation of limb control based on biomechanical control systems and physical dynamics, used this article as a basis for making a previous model of arm control (Powers 1999) more realistic. It soon became evident, however, that the accepted muscle model (Fig. 1) needed some modifications to account for basic observations.

One problem with several analyses using the series/parallel spring model (McMahon 1984 p. 24, Shadmehr & Arbib 1992 p.471) is that they use linear springs, while the actual spring elements are known to show an exponential relationship between force and stretch. More important, the diagram can't explain the results of quick-release experiments which are used to determine force-velocity curves. In a quick-release experiment, a muscle is excited to produce tension while held at a fixed length equal to its resting length in the body, then is released to contract while a smaller constant force acts to stretch it. Assume that the springs in Fig. 1 start at their relaxed lengths. Activating the force generator will stretch the upper spring and shorten the lower one. Releasing the upper end of the muscle can then only make the parallel spring shorter still. McMahon says specifically that the parallel spring exerts no force in compression (op. cit., p. 17). With a position-independent upward force (F_t) less than the downward force (the condition of the quick-release experiment), the muscle can only shorten to its lower limit – it will not shorten to a new intermediate length, as is observed to happen.

In McMahon's worked problem 2, the lower (parallel) spring element is actually required to work in compression, the only way the contraction could be limited after release if the forces are both independent of position. This oversight makes the analysis of the quick-release experiment questionable.

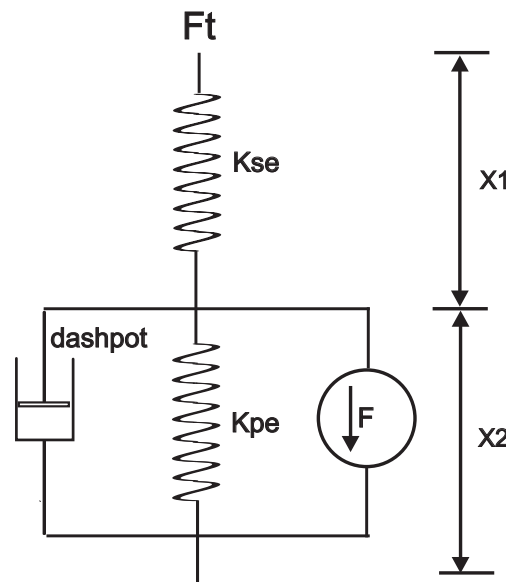


Figure 1: A widely-used muscle model, redrawn from McMahon (1984) Fig. 1.11. According to McMahon, the two springs, representing the lengths of muscle elastic components, are in their fully relaxed states in the body when no driving signal is present. This means that the lower spring does nothing at all when the muscle contracts unless it operates in compression.

Shadmehr and Arbib (1992) used a linear muscle model, yet were able to arrive at the required exponential muscle behavior by approximating the twitch response with the difference between two exponentials. Integrating this response led to an exponential form for the relationship between driving signal frequency and steady-state force generated by a muscle (their fig. 9). That nonlinear relationship rather than nonlinear elastic elements was the source of the ultimate exponential force-stretch law that was derived in their paper. Their model also employed the parallel spring in compression.

In this paper we propose a different muscle model that will fit the quick-release behavior and other observed phenomena while still using the observed exponential-law elastic properties of muscle and connective tissue.

A New Muscle Model

The basic unit of organization of a muscle fiber is a sarcomere, a cylindrical structure with thin filaments extending inward from the ends, interleaving with thick filaments suspended in the center. When neural signals activate the sarcomere, crossbridges form between the thick and thin filaments, attaching in an extended state and then contracting. The action has been likened to the movements of an inchworm.

During continuous neural excitation, crossbridges are continually being formed and releasing, pulling one end of the crossbridge along the thin filament and stretching its elastic component on each cycle. On the average, the population of all the crossbridge attachments is moved by an average amount that depends on the rate at which neural impulses are arriving throughout the whole muscle. The average movement of the crossbridge attachment creates an average stretch in the crossbridge itself, producing an internal contractile force. The resulting force and contraction stretches connective tissue and tendons in series with the sarcomeres, producing the force the muscle exerts externally. This general picture was obtained from a review in McMahon (op. cit.), particularly chapters 3 and 4. We have left out some details which may or may not prove important.

We assume that all the springs have an exponential dependence of force on stretch (McMahon 1984, p 8).

In our revision of the muscle model, we assume a representative crossbridge, one end of which is moved by an amount that depends on the composite neural signal reaching the muscle. At low rates of excitation only a small fraction of the attachments is moved at a given instant, or alternatively, the end of the representative crossbridge moves by only a small amount. As the signal level increases, the average movement reaches an asymptote when all the attachments have moved as much as possible. Since we do not know the details, we assume a simple negative-exponential relationship. The contractile part is shown as x_1 in Fig. 2. The length x_1 is expressed by

$$x_1 = kc \cdot \exp(-s/ks),$$

where kc is the unshortened length, and ks defines the signal level at which $1/e$ or 37% of the ultimate shortening occurs. Programming, rather than algebraic, notation is used.

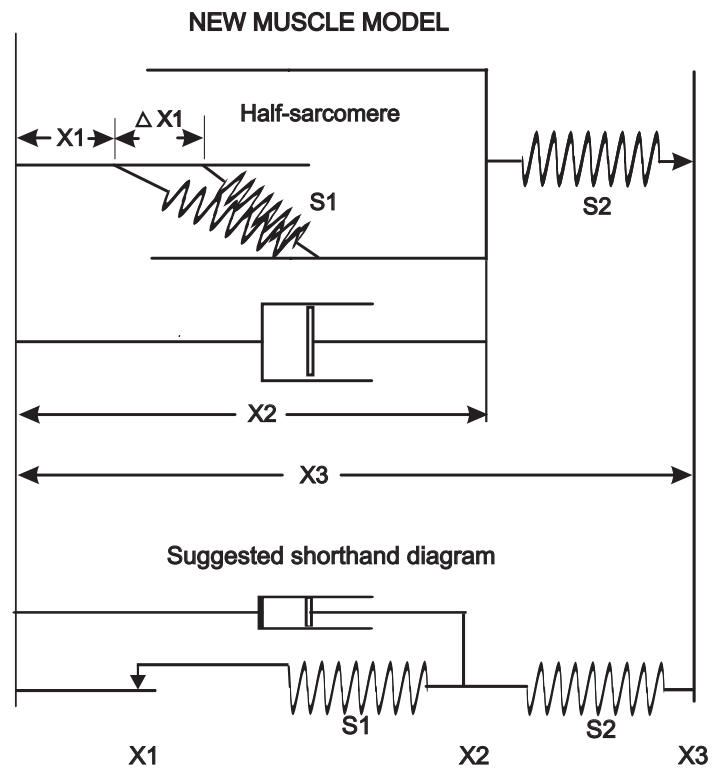


Figure 2: New muscle model using a true contractile component shown as a schematic half-sarcomere rather than a force generator in parallel with a spring. Springs S1 and S2 are identical and nonlinear, imposing an exponential dependency of force on length. The dashpot is nonlinear. Contraction shortens the length x_1 .

This exponential form has nothing to do with the nonlinear springs. It is a way of creating a contraction function that starts out linear at low values of the signal s , and then approaches an asymptote (of zero length) as the muscle approaches complete tetanus, where as many of the contractile sarcomeres as possible are simultaneously in the shortened state.

Forces due to springs S1 and S2 are calculated from the lengths of the springs, as

$$f_1 = \exp(kf^*(x_2 - x_1)) - 1.0$$

$$f_2 = \exp(kf^*(x_3 - x_2)) - 1.0$$

following the form used by McMahon (1984, p. 8) and Feldman (1966). It is assumed (from Shadmehr and Arbib's Fig. 3A – C) that the contractile unit for the biceps shortens by at most 6 cm, stretching each spring in the steady state by 3 cm. We assume that the resting lengths of springs S1 and S2 are both 12 cm, leading to a maximum total relaxed muscle length of 30 cm, about right for the human biceps.

Program 1, below, is the simulation of the muscle proper. At a given instant, the length of the dashpot x_2 is fixed, providing a beginning point for calculating the forces in the two springs. Once the spring forces f_1 and f_2 have been calculated, they are used to determine the new length of the dashpot, x_2 , for the next iteration: x_2 changes at a rate that depends on the net force $f_2 - f_1$ applied to the dashpot.

```
double muscle(double s)
{
double x1, k, el;
x1 = kc*exp(-s/ks); // contractile segment
if(x2 < x1) x2 = x1; // x2 must be between
if(x2 > x3) x2 = x3; // x1 and x3
el = x2 - x1; // elongation of spring 1
if(el > 4.0) el = 4.0; // limit elongation to 4 cm
f1 = exp(kf*el) - 1.0; // compute internal force
el = x3 - x2; // elongation of spring 2
if(el > 4.0) el = 4.0; // limit elongation to 4 cm
f2 = exp(kf*el) - 1.0; // compute external force
k = kd/(1.0 + kh*f2); // nonlinear dashpot coeff
x2 += k*(f2 - f1)*dt; // net force moves dashpot
return f2; // returns external force
}
```

Program 1: C program segment containing the muscle model. The function receives the magnitude (frequency) of the driving signal s and returns the force exerted by the muscle between its attachments. Named constants and undeclared variables are defined outside this function. Limits on elongation prevent very large forces from appearing as startup transients.

The dashpot must be nonlinear to make the muscle's force-velocity curve fit the Hill curve shown in McMahon (1984, Fig. 1.10, p. 15). The dashpot constant k is an empirical function of the external force f_2 . The expression $kd/(1 + kh*f_2)$ adjusts the curvature of the force-velocity curve. If kh is set to zero the Hill curve becomes linear. The value of kh can be chosen for best fit to the curve that Hill represented as an hyperbola.

The force-velocity curve is shown later (Fig. 6) and is discussed along with the quick-release experiment in which it is measured.

Performance of the model

In this section, the simulated muscle is used in a series of "experiments" like those done with real muscles. The results are compared with either data or other models. Throughout the rest of the paper, the model parameters are set as follows: $kd = 0.005$, $kh = 0.0023$, $kf = 2.67$, $kc = 6.0$, $ks = 9.0$, and $dt = 0.0001$ sec.

Fig. 3 shows the dynamic response of the model to a sudden driving input under isometric conditions (x_3 held constant).

This performance is reasonably close to that of the Shadmehr and Arbib model shown in Fig. 4.

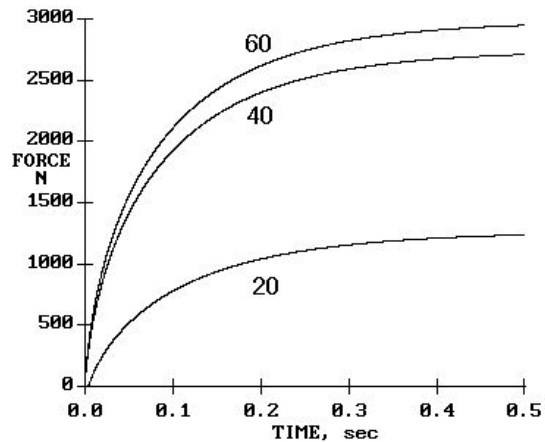


Figure 3: Dynamic behavior of model under isometric conditions. Curves show how tension develops with time given a step input rising instantly from 0 at time zero to a steady 20, 40, or 60 impulses per second. Note: all performance curves in this paper are computed directly from the nonlinear muscle model and automatically plotted as the simulation runs

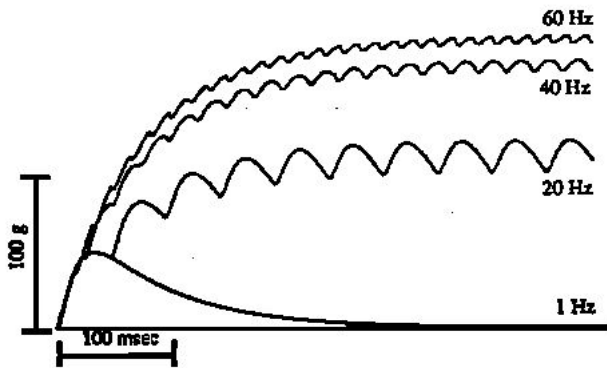


Figure 4. Shadmehr and Arbib Fig. 9, showing step response for various input signal frequencies. Vertical = force, horizontal = time. Derived by summing successive twitches.

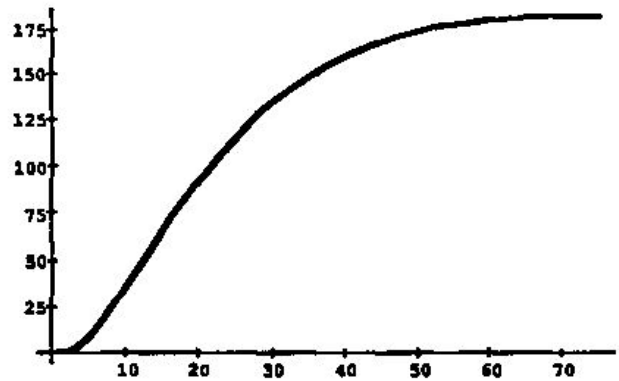


Figure 6. Shadmehr and Arbib plot of force (vertical, grams) versus motor signal frequency, impulses per sec.

A plot of steady-state force versus driving signal frequency approximately matches the Shadmehr and Arbib model's behavior: Fig. 5 is the present model's response; Fig. 6 is that of the Shadmehr and Arbib model.

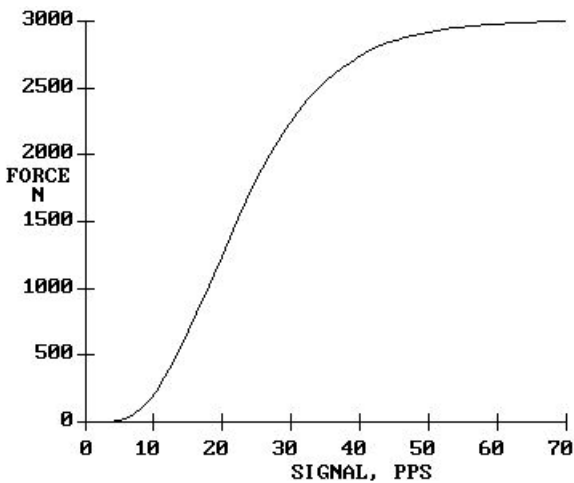


Figure 5: Steady-state force versus average motor signal frequency. Frequency scale is arbitrary.

The basic observation that leads to giving muscles an exponential force-stretch property is that muscle stiffness grows linearly with the force being actively produced by the muscle (Hoffer and Andreassen 1978). When the new muscle model is set up in an "experiment" similar to the real one, the muscle is activated with a constant signal to produce a force, and then it is stretched by a small amount (here 1%)

to measure the change of force with respect to length. The change of force divided by the change in length is the stiffness. The result is the force-stiffness curve shown in Fig. 7. McMahon's Fig. 1.5 in Fig. 8 shows data for rabbit heart muscle indicating the wide range and accuracy of this relationship.

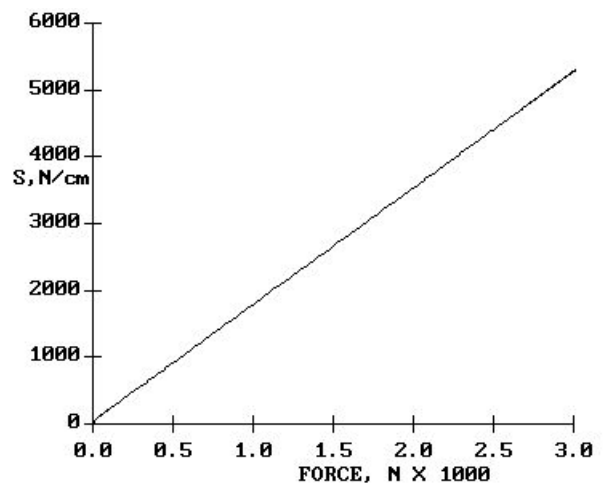


Figure 7: Stiffness as a function of muscle force. The muscle is held at a length equal to its resting length. A signal is applied to create a tension. Then the muscle is stretched by one percent and the tension is measured again. Stiffness S is the change in tension divided by the change in length. The above plot is obtained for several hundred different steady-state tensions.

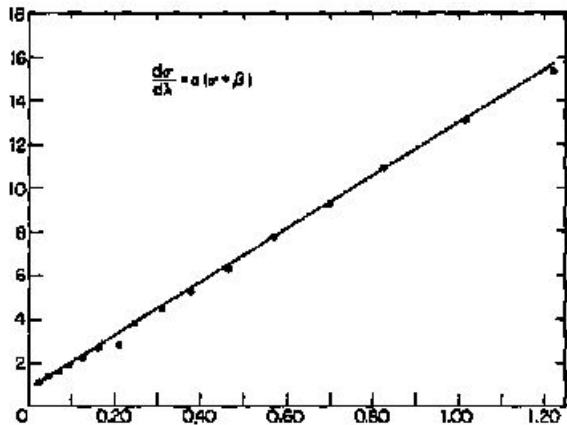


Figure 8: McMahan's Fig. 1.5. Stiffness as a function of muscle force in the papillary muscle of rabbit heart. Vertical: stiffness; horizontal: force.

We turn now to the quick-release experiment. The new muscle model is supposed to explain the quick-release experiment where the linear series-parallel spring model cannot. To reproduce this experiment, we start with the model muscle held at its resting length by fixed attachments. Then a specific amount of tension is generated by a signal that sets the contractile element x_1 to a length less than its maximum length. Finally, the end of the muscle is released and a constant force (less than the initial force) is applied to the right-hand spring, to reproduce the conditions shown in McMahan's Fig. 1.8.

The results are shown in Fig. 9. To make them look like McMahan's Fig. 1.8 shown in Fig. 10, it was necessary to subtract out the resting lengths of the springs, making the changes more evident (the actual length changes are at most 20% of the total muscle length). The new model shows the correct general form of muscle response in the quick-release experiment.

The quick-release experiment was used by Hill to determine the force-velocity relationship (represented by an hyperbolic equation as shown in McMahan's Fig. 1.10). Simulating the experiment, we vary the post-release force in repeated runs of the experiment and plot the initial post-release slope (shortening velocity) against the post-release force, normalizing both axes to the initial values. The result is shown in Fig. 11.

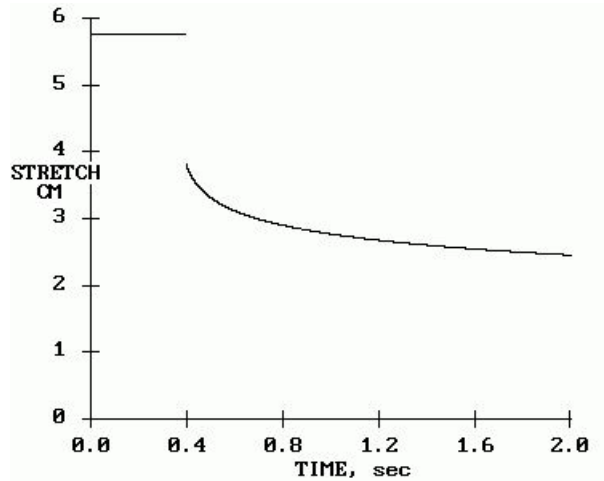


Figure 9. Quick-release experiment. An initial force of about 2500 N is generated by a signal that contracts the muscle isometrically. At $t = 0.4$ seconds, the muscle is released and a constant stretching force of 10 N is applied (note that these numbers are appropriate for a whole muscle like the biceps; they would be scaled down greatly for a single fiber). The muscle length changes initially by about 2 cm as the spring S2 instantly shortens to a new (constant) length. Then the muscle contracts further as the spring S1 shortens to a new length set by the length of the contractile element and the new applied force. The transition is slowed by the dashpot.

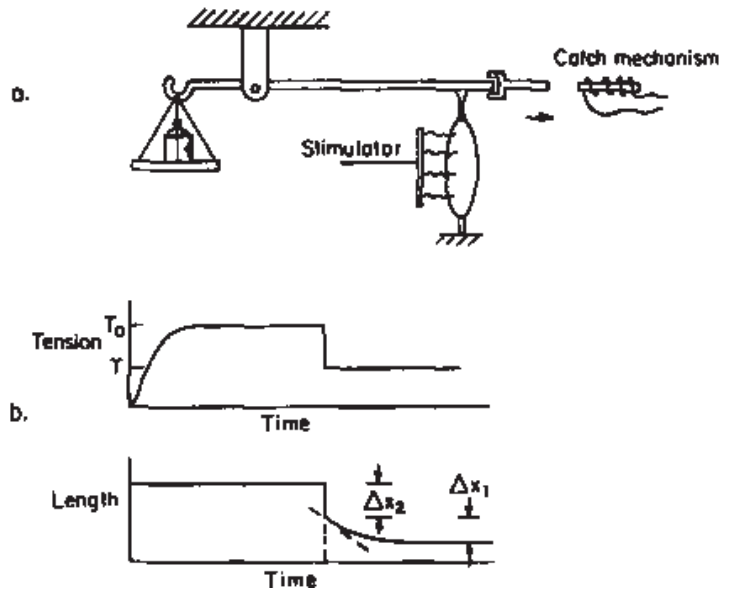


Figure 10. Quick-release experimental conditions and results. Excerpted from McMahan Fig. 1.8.

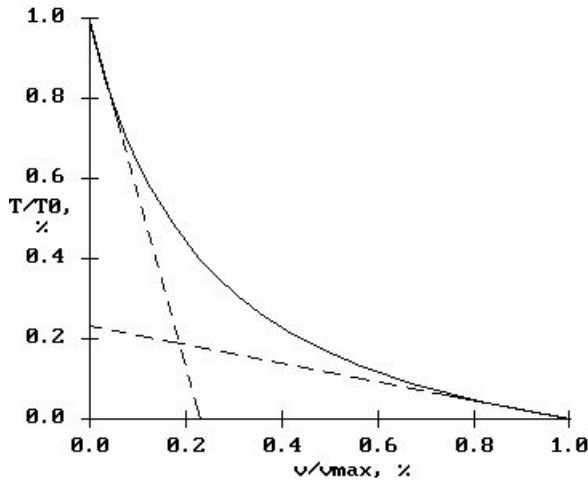


Figure 11. Force-velocity curve determined from many simulated quick-release experiments. With x_3 held at the resting length, the driving signal sent to the muscle is adjusted for an initial force T_0 of 2500 N. Then the length constraint is released and a post-release force T (position-independent) is applied to the free end of the muscle (see McMahon, Fig. 1.8). The above plot shows the result as the post-release force is held constant at values from T_0 down to zero during repeated experiments. A single constant adjusts the linearity (see Program 1 above).

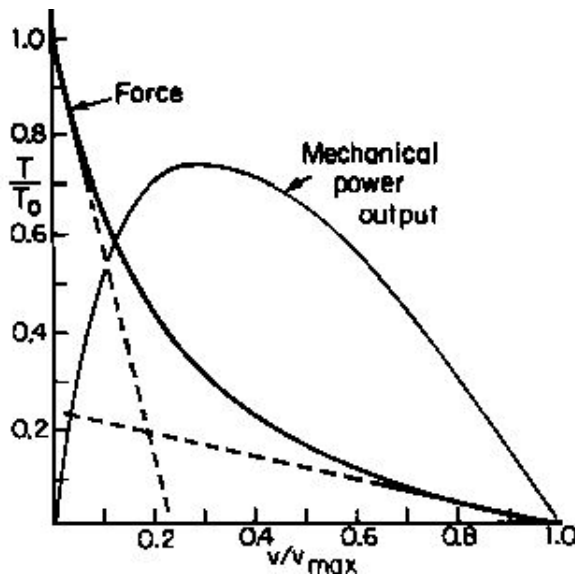


Figure 12: Hill's force-velocity curve plotted from Hill's hyperbolic equation by McMahon. Excerpted from McMahon's Fig. 1.10 to eliminate regions outside the range of interest (such as the force developed by hyperextensions of the muscle).

Compare Fig. 11 with Fig 12, which is Hill's force- (or tension-) velocity curve. Even though the two curves are derived from very different assumptions, they are nearly identical. This could mean that the new model would fit the original data just as well as would the hyperbolic curve.

Summary

Using a new muscle model in which there is a contractile element, two nonlinear series springs, and a nonlinear dashpot to simulate internal viscous friction, we have simulated the open-loop response to be expected from this model, and then tested the model in simulations of various experiments that are found in the literature. The new muscle model appears to have the right characteristics for use in modeling of motor control behavior.

References

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Note: Computer program notation is used in this paper. Multiplication is explicitly denoted by the asterisk. This permits multiple-character symbols to be used, as in "ks," which does not mean k times s ($k*s$) but is the unitary name of a constant.