A Nonlinear Model of the Phasic Dynamics of Muscle Activation

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Abstract—This paper presents a phasic excitation-activation (PEXA) model of the process of motoneuron excitation and the resultant activation and force development of a motor unit. The model input is an amount of depolarizing current (as when injected with an intracellular electrode) and the model output is muscle force. The model includes dynamics and nonlinearities similar to phenomena discovered experimentally by others: the firing rate response of motoneurons to steps of depolarizing current and the “catch-like enhancement” of force produced by overlapping motor neuron action potentials. The parameter values used in this model are derived from experimentally measured data and expressed in physical units, and model predictions extend to published data beyond those used in generating the model parameter values.

INTRODUCTION

Each of the thousands of fibers composing a skeletal muscle is associated with others and a single motoneuron in the ventral horn of the spinal segment to form a “motor unit.” This paper reports a quantitative model of the process by which depolarization of the motoneuron results in force measured at the muscle. By varying model parameters, the model can simulate both “fast” and “slow” motor units.

A primary motivation for this work is to prepare for extension of previous study of the control of fast voluntary movements [1]-[7]. Thus, this model focuses on events which are significant at the time scale relevant to fast movements, e.g., the first 200 ms of a sudden muscle activation.

The model is based on published experimental in vivo investigations in which current was injected into cat motoneurons and output action potentials were observed on the efferent nerve [8]-[11] and later work in which bursts of action potentials were delivered to the motor unit fibers through axonal stimulation, and resultant force observed isometrically [12], [13]. The next logical step is the concatenation of these two experiments which was performed [14], [15] by stimulation of the motoneuron and the recording of force. Based on these experiments and previous muscle modeling work, the model could then be constructed in three sections: motoneuron excitation, activation dynamics, and muscle force generation.

Motoneuron excitation is the process through which injected current depolarizes the axon hillock and results in a stereotyped wave of depolarization down the axon. Activation dynamics represent the process by which depolarization of the neuromuscular junction results in the so-called “active state,” and muscle force generation describes the transfer from “active state” to output muscle force.

Experimental Data

Excellent experimental data exist describing the short time dynamics of these processes. These basic experiments measured responses of motoneurons when driven intracellularly by steps of transmembrane depolarizing current [8], [11], the force output of motor units when their axons were stimulated with different patterns of pulses [13], and the concatenation of these two paradigms, the force response of motor units in vivo to a step or ramp of depolarizing current injected into the controlling motoneuron [14], [16], [17], [15].

Kernell and Granit [8], [11] found with intracellular stimulation that when a step of depolarizing current was applied to motoneurons in the cat spinal cord, the rate of output firing was not constant but actually decreased from a very high phasic rate (measured by the reciprocal of the first time interval between pulses after stimulation) to a lower tonic firing rate. They measured this behavior as a function of the amplitude of the current step.

Later, Burke, Rudomin and Zajac, following earlier work in the crayfish [18], examined the next step in the sequence of events. They stimulated motor units through pulsatile intracellular stimulation of the motoneuron (again in vivo in the cat) and measured the force response of the gastrocnemius muscle [12], [13]. From these records, they computed the integrated area of the force record per action potential (units: gram second) which was a highly nonlinear function of the interstimulus interval. A striking demonstration of this nonlinearity was what they dubbed the “catch-like” effect (after the “catch effect” of invertebrate muscle) in which a single brief (10 ms) interval before a train of longer (25 ms) intervals results in a significant increase in output force lasting as long as one second.

In an elegant experimental study, Zajac and Young [19], [20] found that, presumably because of the “catch-
like effect,' a sequence of stimulation containing a brief (≈ 10 ms) firing interval followed by a lower rate sustained firing produced a maximum value of tension-time area [19]. They further found that firing patterns of motoneurones in the cat hindlimb during locomotion evoked by constant stimulation of the mesencephalic locomotor region were similar to this optimal pattern [20]. This work suggests that this type of optimal stimulation may be quite common in the routine operation of motor units as well as in fast movements.

Baldissera and Parmiggiani [14] stimulated the motoneuron with current steps and recorded muscle force directly, asserting that the rapid decline of firing rate was due to changes in potassium conductance of the motoneuron. This they reasoned served as a compensation network for slow muscle properties. More recently Baldissera et al. [15] measured the relationship between rate of increase of depolarizing current and rate of motor unit force development.

There can be no doubt that these nonlinear dynamic effects are potentially important to the understanding of the control of fast movements. Fast, single degree of freedom voluntary movements are accomplished in as little as 200 ms [5], [21]. Furthermore, because these movements are driven by the so-called triphasic pattern in the electromyogram (EMG), muscle activation dynamics on an even shorter scale are involved (the EMG bursts take between 50 and 100 ms) [22].

**METHODS**

**Phasic Excitation-Activation (PEXA) Model**

In building a model from the three sets of experimental studies reviewed above we can anatomically divide the motor unit system into three subsystems, the motoneuron, muscle activation, and muscle unit mechanics (Fig. 1). In this case then we have data which give us the behavior of the individual components [11], [12] as well as of their concatenation [14].

The first model block, the motoneuron, consists of a transresistance amplifier (an amplifier with current input and voltage output), high-pass filter, and spike generation implemented as a voltage to pulse rate converter. Its output is a series of unit value impulses which exhibit a decline in firing rate (adaptation) with constant current input. The next block, labeled “activation dynamics” consists of a pulse rate to voltage converter, piecewise linear relation, nonlinear RC circuit, and multiplier. This block produces a multiplication of the effects of the action potential impulses to simulate the nonlinear enhancement found by Burke et al. [12].

Finally, the muscle is described by a second-order nonlinear model obtained by removing a single muscle from the sixth-order nonlinear full joint model used by Stark and his students [1]-[4].

The motoneuron model is designed to approximately reproduce current-step to pulse-rate responses. The basic form of the response to a step of current is a quick rise to an initial firing rate, followed by an exponential decline in firing rate, having time constant $\tau$, to a steady-state rate $\theta$. Because of the motoneuron’s nonlinear response, the dynamic parameters of the step response $\tau$, $\tau$, and $\theta$ are functions of the current step amplitude $I$. The firing rate step response [expressed in pulses per second (pps)] is modeled by the exponential form

$$f_r(t, I) = \theta(I) + [(I - \theta(I))e^{-(t-\theta(I))/\tau}]. \quad (1)$$

The computer simulation of this behavior was performed by numerical integration of the differential equations describing the equivalent circuit model in Fig. 1. The neuron model was implemented by the following algorithm:

**Current to voltage transduction (transconductance):**

$$V \leftarrow 2.0 \text{pps} \left( i - 15 \text{na} \right) + 75 \text{pps} \quad (A1:1)$$

$$V \leftarrow \frac{V_i - V_{i-1}}{\delta t} \quad (A1:2)$$

where $V$ is membrane voltage, $i$ is input current, and $\delta t$ is the integration time step ($0.0005$ s).

**Motoneuron dynamics:**

$$f_r \leftarrow f + \frac{V_f}{R_C} + \frac{f}{R_C} \quad (A1:3)$$

$$f \leftarrow f + f \delta t \quad (A1:4)$$

where $f$ is a voltage encoding rate of firing.
Spike generation:

\[ t_{\text{next}} \leftarrow t_{\text{last}} + \frac{1}{f} \]  

(A1:5)

if \((f < 0.0001)\) then \(t_{\text{last}} \leftarrow t\)  

(A1:6)

if \((t = t_{\text{next}})\) then output \(-1\), \(t_{\text{last}} \leftarrow t\)  

(A1:7)

It can be shown through analysis of the equivalent circuit of Fig. 1 that

\[ R_I C = \frac{\tau(I)}{\theta(I)} \]  

(A1:8)

\[ R_C C = \frac{\tau(I)}{\theta(I)} \]  

(A1:9)

To identify the parameter values, I made two assumptions:

1) the parameter values are instantaneous functions of the input current \(I\) and
2) the parameter values are linear functions of the input current amplitude.

The validity of the first assumption cannot be proved or disproved using data from the experiments considered here because current is held constant during the step inputs. Ramp current stimuli as used by Baldissera [15] will be considered below. The second assumption can be eliminated in future work by using nonlinear fits to the experimental data in place of the linear analysis used below.

Because the model component values have been expressed in terms of the step response parameters [see (A1:8, 9)] it is sufficient to find the model parameters by calculating the dependence of \(\rho_1, \rho_2, \tau, \Theta, \) and \(\Theta\) on \(I\). For an interval of time \(dt\) during which \(f(t)\) declines from \(P_1\) to \(P_2\),

\[ \rho_2 = \theta(I) + [\rho_1 - \theta(I)] e^{-dt/\tau(I)} \]  

(2)

\[ \tau(I) = \frac{-dt}{\ln \left( \frac{\rho_2 - \theta(I)}{\rho_1 - \theta(I)} \right)} \]  

(3)

\(\tau(I)\) can thus be estimated from the experimental current step to firing rate data. These values have been measured directly from the experimental data of Granit and Kernell [8], [11], [23] and are reproduced in Table I.

Fitting a straight line to the two average values gives

\[ \tau(I) = 0.014 s - \left( \frac{0.000825}{s} \right) (I - i_{\text{min}}) \]  

(4)

where \(i_{\text{min}}\) is the firing threshold observed in the experimental data (13 na). Using similar derivations from the experimental data, one can obtain

\[ \tau(I) = 75.0 \text{pps} + 15.4 \text{pps} (I - i_{\text{min}}) \]  

(5)

\[ \theta(I) = 20 \text{pps} + 2 \text{pps} (I - i_{\text{min}}) \]  

(6)

### Activation Dynamics

This section of the model represents the interval-dependent increase in the active state generated by each action potential in a sequence. Burke et al. [13] quantified this effect by plotting the enhancement of integral area \((gm sec)\) as a function of interstimulus interval (isi) (Fig. 2).

A similar nonlinear enhancement effect was simulated using the piecewise linear, Area Enhancement Map shown in Fig. 2. In the experimental data [13] the enhancement function has a relatively fixed maximal value for intervals around the "contraction time" (the time to peak twitch tension) \(tc\) of the motor unit. For intervals greater than \(tc\), the enhancement declines to unity as the effect is "forgotten." The enhancement due to intervals less than \(tc\), is reduced according to the sequence in the pulse train, declining rapidly after the first few intervals.

To model this effect, I have assumed that for intervals shorter than the "contraction time" the phenomenon depends on the degree of muscle activation. In the piecewise linear approximation (Fig. 2: solid line), the decline in enhancement due to repeated stimulation is controlled by the amount of muscle activation: a state variable in the nonlinear muscle model.

The piecewise linear approximation is described by four parameters, indicated graphically on the axes of Fig. 2. \(A_{\text{max}}\), the enhancement axis intercept, shows the maximum possible enhancement of twitch activation, corresponding to zero interstimulus interval for the first interval. \(S_1\), the slope of the initial interval enhancement line, is derived from \(A_{\text{max}}\) and \(tc\), the interval beyond which there is no enhancement. For intervals below \(tc\), enhancement declines with muscle activation. This is achieved by defining the intercept to be:

\[ A_{\text{int}} = A_{\text{max}} - (A_{\text{max}} - A_{\text{min}}) \frac{HT}{HT_{\text{max}}} \]  

(7)

where \(HT\) is the muscle active tension state, and \(HT_{\text{max}}\) is a normalizing constant.

Parameter identification of the enhancement model nonlinearity is then simply a matter of deriving a piecewise linear fit to twitch tension enhancement experiments such as those of Fig. 2.

The enhancement effect of small isi's occurs instantaneously but persists for a time on the order of a second. The nonlinear circuit used in the model has this asymmetrical dynamical property. Since the persistence time

### Table I

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represented by two state equations:

\[ x = \frac{1}{b} (-K(x - HT)) \]  

where scale relates enhanced spike amplitude (the neural input signal) to force generation, and \( N_{in} \) is the neural input signal.

**RESULTS**

The PEXA model can be tested and calibrated against experimental data in sections. The first section to be tested is the current-step to firing rate relation of the motoneuron.

In the real motoneuron, the firing rate in response to current steps is characterized by an initially high rate (short interspike intervals) followed by adaptation in which the firing rate decreases to a steady state value. The effective firing rate corresponding to an interspike interval is the inverse of the time spanned by the interval. The adaptation process is illustrated by plotting the interval firing rate as a function of depolarization current for sequential intervals (Fig. 3). In a given experiment, a fixed current step is applied to the neuron and output spike arrivals are recorded. The firing rates given by the first-, second-, and steady-state intervals are plotted along a vertical line specified by the current step amplitude. The points can be connected in groups to illustrate the dependence of interval firing rate on interval number and step amplitude.

In the cat motoneurons studied by Kernell [11] and Baldiesser and Parmigiani [14] the first interval firing rate (first group, solid lines) increased dramatically with depolarizing current step size, ranging from 10 pps to over 250 pps as current increased from 7 to 24 na. In the second interspike interval following the current step (second group, dotted lines) the firing rate rises more slowly with current, and the steady state firing rate ("infinity" group, dashed lines) rises gently to a maximum value of about 80 pps. The dynamics of adaptation are such that steady-state firing rate is essentially reached after only two to four intervals: a time of less than 100 ms.

When steps of current were applied to the simulated motoneuron, the firing rate of the model for the first, second, and steady-state intervals closely matched the experimental data (Fig. 3). The frequency represented by the first firing interval rose sharply as step current exceeded the input threshold from 77 pps at 13 na to 250 pps at 23 na. Rates for the second firing interval increased more slowly to reach 203 pps at 32 na, and steady state firing rates increased from 20 pps to 58 pps as current increased from 23 to 32 na.

The next section of the model, firing rate to muscle force, can be tested in a simulation experiment analogous to those performed in vivo by Burke et al. [12] in which force output was recorded in response to pulse train inputs of varying frequencies. For each frequency, two pulse train stimuli were generated. One consisted of a simple train of pulses at that frequency. The second was the same but for the addition of an extra pulse 10 ms after the first
of the train. In each force record (Fig. 4, inserts), the higher amplitude signal came from the pulse train input containing the extra pulse, and the “catch-like enhancement” persisted over approximately a full second.

The experiment was repeated using the PEXA model for basic pulse train periods of 900, 120, 82, and 45 ms. Force output was recorded in response to pulse train input to the “muscle activation” and muscle mechanics models (Fig. 4, main traces). These compare well with the experimental data [12], which are reproduced for comparison as inserts to Fig. 4.

Three model parameters for the area enhancement map (originally obtained from the twitch tension enhancement piecewise linear fit, Fig. 2) [12] were changed slightly to fit the nonlinear enhancement data: the motor unit contraction time, $t_c$, was changed to 57 ms to match the reported contraction time of the motor unit from which this particular data was obtained, and the amplitude parameters, $A_{\text{max}}$ and $A_{\text{min}}$ (see Fig. 2), were altered to obtain the same amount of nonlinear enhancement as observed in the data. Resulting values were 3.0 and 1.0 for $A_{\text{max}}$ and $A_{\text{min}}$, respectively. The motor unit used to obtain the catch effect data thus exhibited less area enhancement than that from which the effect was initially quantified.

The 900 ms interval (Fig. 4, upper left) is used for comparison with the impulse-pair experiments of Burke et al. [12]. The difference in force between the high and low traces reflects the area enhancement due to the 10 ms interval of the added pulse and compares well with experimental data in their Fig. 2(a).

The force traces resulting from the simulations are very consistent with the data in peak force, steady-state force, and transient decline of “area enhancement.” However, the simulations appear to have slightly slower dynamics in the initial rise of force.

Finally, we can simulate the complete experiment in which we inject current steps of varying amplitude into the model motoneuron and observe peak force development at the muscle tendon (Fig. 5). The peak of force increased from 16.6 to 51.4 g for a simulated motor-unit driven by current steps between 10 and 40 na, respectively. Experimental data [14] are plotted for comparison. Although the model peak force is approximately 10-15 g higher than the experimental data, note that the model parameter values were obtained from data described above on the individual system blocks [11]-[13] and independently of the current to force data [14].

In a similar experiment Baldissera et al. [17] injected ramps of depolarizing current into the motoneuron and observed instantaneous firing rate and tension development. The PEXA model was driven by current ramps whose slopes $(\frac{\text{d}t}{\text{d}t})$ varied from 4.0 na · ms$^{-1}$ to 0.4 na · ms$^{-1}$. The ramps began at $t = 0.01$ s and terminated at a maximum depolarizing current of 60 na. These values match those used Baldissera et al. [17]. Note that model parameter values now vary with time in accordance with assumption 1. The resulting current, pulse rate, and force outputs (Fig. 6) show initial phasic responses in the motoneuron firing rate (circles) whose peak output rate depends strongly on the current slope and ranges from 308 pps at 4.0 na · ms$^{-1}$ to 135 pps at 0.4 na · ms$^{-1}$ with the occurrence of the maximum firing rate ranging from the second interval at $t = 0.21$ (dtdt = 4.0 na · ms$^{-1}$) to the ninth interval at $t = 0.152$ (dtdt = 0.4 na · ms$^{-1}$).

The force output slope was estimated by fitting a straight line to the force record up to the time of the decline in
Fig. 5. Current to motor unit peak force. Simulation versus experimental data of Baldiserra and Parmiggiani illustrate relationship between step amplitude of motoneuron depolarizing current and peak force measured at intact muscle tendon.

Fig. 6. Response of PEXA model to current ramps. Plotted are simulations of the complete model driven by current ramps of six decreasing rates of change of current. Shown are current ramps and resulting muscle force (straight and curved solid lines, respectively) and instantaneous firing rate of the motoneuron (circles).

firing rate to its tonic level (there is no nerve conduction delay in the model). The slopes ranged from 1.11 gf · ms⁻¹ (di/dt = 4.0 nA · ms⁻¹) to 0.76 gf · ms⁻¹ (di/dt = 0.4 nA · ms⁻¹). The slopes however saturated at about 1.1 gf · ms⁻¹ for the current slopes above 1.0 nA · ms⁻¹. Fitting a line to the force slopes below saturation gives a “dynamic gain” of 0.61 gf · nA⁻¹ for the simulated motor unit, a value quite typical of the experimentally measured units [17].

An interesting feature of the simulation output not seen in the data is a transient rise in output force which is inversely related to ramp slope (note higher force level at t = 0.25 s for slowest ramp). This slope dependence disappears by the time the simulations were stopped: 2.5 s.

Muscles contain a population of motor units having a distribution of twitch-speed/fatigue properties which is commonly approximated with a bimodal one having “fast” and “slow” peaks. Although fatigue properties
PARAMETER VALUES USED TO SIMULATE FAST (LEFT COLUMN) AND SLOW (RIGHT COLUMN) TWITCH MUSCLES. LINES BEGINNING IN "#" ARE COMMENTS

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are not modeled, parameter values relating to the muscle activation block and the muscle mechanics block change the twitch behavior of the PEXA model. It is initially assumed that motoneuron dynamical properties are invariant between fast and slow units. Thus, the only changes were to the values of activation time constant, the "twitch time" parameter of the catch effect, tc, and the muscle equivalent viscosity b. Two parameter vectors (Table II) were chosen to simulate "fast twitch" and "slow twitch" fibers. Responses were plotted when the motoneuron model was driven by a depolarizing current of 20 na. The resulting adapted discharge rate was 33.33 pps (period = 30 ms) (Fig. 7). The complete response of the two models consists of a train of action potentials (weighted with the catch-like enhancement), muscle activation ("active state"), and isometric muscle force. The longer activation time constant in the "slow" unit model is evident in the smaller excursions of activation (20-40 gf, steady state versus 10-45 gf). Force output rises beyond 12.5 gf (50% of its final value of 25 gf) in 21 ms for the fast unit versus 87 ms for the slow unit.

DISCUSSION

A detailed model has been developed and tested which simulates important short term nonlinear dynamic effects in the muscle control and activation process. This model is ready to be used in a complete joint movement model with which the effects of these features can be judged on the control of fast movements.

Of further interest is the degree of homeomorphism of the individual components of the PEXA model.

The motoneuron model is a highly simplified one which reproduces the important short term dynamical phenomena. However, it's internal details are not homeomorphic to an individual motoneuron. More detailed homeomorphism can be achieved with a mathematically equivalent model (Fig. 8). In this neuron model, the three blocks correspond to the membrane conductance, after-hyperpolarization dynamics, and output spike generation.

Conversion of parameter values from the PEXA motoneuron model to this more homeomorphic model can be accomplished through straightforward application of network transformation and feedback laws.

More detailed motoneuron models based on diffusion and drift differential equations and voltage clamp data such as those of [25]-[28] point the way for further development of the motoneuron section of the model.

The experimental workers [8], [11] have found a roughly bilinear relationship between current and firing rate in which firing rate was found to vary approximately linearly in a "primary range" for firing rates up to approximately 40 Hz and with a higher slope in the "secondary range" above that. The PEXA model simplifies this to a linear relationship over the global range of firing rates. The resulting slope is close to that of the "secondary range" because of its greater extent in firing rate. In the control signals programming fast movements, we can readily expect large changes in currents and firing rates. In this context, although they could easily be added to the PEXA model, the differences between the primary and secondary ranges are not significant.
Simulation of the current ramp experiment tested assumption 1 that the model parameters were instantaneous functions of the depolarizing current. The spike train outputs produced (Fig. 6) were qualitatively and quantitatively an excellent match to the published data [17]. This gives support to the assumption. The small transient enhancement of contraction force for small current slopes, which was not observed by Baldiessera et al. arose from the catch-like property of the activation model and thus does not bear on assumption 1.

The muscle activation model block contains a non-linear integrator which generates a quickly acting "enhancement" signal which persists with a time constant of 500 ms. This time is long compared to the activation process and the control pulses used in fast movements. In the case of time optimal movements generated by the triphasic activation pattern, we have in the agonist two bursts of 50–150 ms duration separated by an interval of 50–150 ms. This model assumes that some "catch-like enhancement" would persist across the agonist inhibition period between the first (PA) burst and the third (PC) burst. Earlier work on the crayfish [18] suggests a more rapid resetting although the preparation is certainly not directly comparable. This suggests a need for further experimentation in which this effect could be tested in a mammalian muscle.

The muscle activation model is based phenomenologically on the "catch effect" data [12] and thus may not reflect the underlying physiology. For example, as suggested by Ebashi and Endo [29] enhancement of twitch tension may be due to slower uptake of Ca++ by the sarcoplasmic reticulum (i.e., slower relaxation of the contractile element) after closely repeated stimuli rather than the enhanced release of calcium (the process implied by the multiplication operator in the model, Fig. 2). Further homeomorphic detail for this model block can be developed using detailed models such as those [30]–[32]. The present simple model needs to be compared with these more detailed ones at the range of ISI's and under the phasic conditions reported here.

In previous incarnations of the muscle mechanics model [1], [2], [15], the input is taken to be a neurological signal often estimated by fitting a rectangular envelope to the EMG [7]. This assumes that the EMG, which typically has a roughly triangular envelope, reflects muscle activation which is a filtered version of this rectangular control signal. Others who have omitted the activation dynamics have achieved almost equivalent results by driving the model with triangular control signals [21] or Gaussian signals [33]. This illustrates that there is an important interaction between control signal models and system models: dynamics can be omitted from the system model if they are implicitly lumped into the control signal model and vice versa. Winters [3] added a pole to the sixth order nonlinear model to represent neural excitation dynamics.

The PEXA model attempts to explicitly extend a previously successful modeling strategy to these "early" dynamics. The addition of the motoneuron excitation and nonlinear enhancement models will hopefully play a role in understanding the control of the fastest voluntary movements in which these short time scales are significant.

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References


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