Factors Governing the Form of the Relation Between Muscle Force and the EMG: A Simulation Study

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Zhou, Ping and William Zev Rymer. Factors governing the form of the relation between muscle force and the EMG: a simulation study. J Neurophysiol 92: 2878–2886, 2004. First published June 16, 2004; 10.1152/jn.00367.2004. The dependence of the form of the EMG-force relation on key motoneuron and muscle properties was explored using a simulation approach. Surface EMG signals and isometric forces were simulated using existing motoneuron pool, muscle force, and surface EMG models, based primarily on reported properties of the first dorsal interosseous (FDI) muscle in humans. Our simulation results indicate that the relation between electrical and mechanical properties of the individual motor unit level plays the dominant role in determining the overall EMG amplitude-force relation of the muscle, while the underlying motor unit firing rate strategy appears to be a less important factor. However, different motor unit firing rate strategies result in substantially different relations between counts of the numbers of motoneuron discharges and the isometric force. Our simulation results also show that EMG amplitude (estimated as the average rectified value) increases as a result of synchronous discharges of different motor units within the pool, but the magnitude of this increase is determined primarily by the action potential duration of the synchronized motor units. Furthermore, when the EMG effects are normalized to their maximum levels, motor unit synchrony does not exert significant effects on the form of the EMG-force relation, provided that the synchrony level is held similar at different excitation levels.

INTRODUCTION

The relation between isometric force and surface EMG amplitude has been the subject of extensive investigation in the past. Two broadly different characteristic forms of the surface EMG amplitude-isometric force relation have been described. For small muscles with narrow motor unit recruitment force ranges, such as the first dorsal interosseous (FDI) muscle, the observed relation between force and the average rectified value (ARV) of surface EMG is reported as being approximately linear. For larger muscles with wide motor unit recruitment force ranges, such as proximal leg or arm muscles, the observed relation is reported to be nonlinear, with the ARV of surface EMG increasing faster than force (Basmajian and DeLuca 1985; Lawrence and De Luca 1983; Milner-Brown and Stein 1975; Moritani and deVries 1978; Solomonow et al. 1990; Woods and Bigland-Ritchie 1983).

In this report, we describe an attempt to better understand the mechanisms that underlie the observed relations between surface EMG amplitude and muscle force. Specifically, we implemented a model to quantitatively evaluate factors governing these relations, focusing on the relation between single motor unit electrical and mechanical outputs, and on motor unit firing rate strategies. Furthermore, in light of findings about the occurrence of motor unit synchrony, which has been reported to occur frequently during voluntary contractions in several different limb muscles (Datta and Stephens 1990; De Luca et al. 1993; Nordstrom et al. 1992; Sears and Stagg 1976), the effects of motor unit synchrony on the form of the EMG-force relation were also investigated.

Our primary aim was to determine the effects of these parameters on the overall EMG-force relations of the muscle, with the view toward better interpretation of experimentally derived EMG-force relations.

METHODS

Isometric whole muscle force and surface EMG signals were simulated using a motoneuron pool model, a muscle force model, and a surface EMG model. For the motoneuron pool and the muscle force simulations, we implemented models developed by Fuglevand et al. (1993). Some properties of the models were modified according to recent experimental findings, and the parameters were assigned based on the reported properties of the FDI muscle. To promote simplicity of the surface EMG simulations, we used Hermite Rodriguez (HR) functions to represent the basic shapes of the surface motor unit action potentials (MUAPs) (Lo Conte et al. 1994).

Motoneuron pool model

To assess the impact of different motor unit recruitment and firing rate strategies, we simulated input output-properties of the motoneuron pool. We included 120 motoneurons, which is the estimated number of motor units contained in the FDI muscle (Feinstein et al. 1955). The motoneuron threshold distribution was modeled as an exponential of the form (Fuglevand et al. 1993)

\[ RTE(i) = e^{ai} \]  
\[ a = (\ln RR)/n \]

where \( RTE \) was recruitment threshold excitation, \( i \) was an index identifying the motoneuron, and \( a \) was a coefficient used to establish a range of threshold values, \( R \) was the natural algorithm, \( RR \) was the range of recruitment thresholds desired, which was set to be 40% of the maximum excitation according to the properties of the FDI muscle (De Luca et al. 1982), and \( n \) was the total number of neurons. By this means, many neurons were assigned low thresholds, whereas relatively few neurons were assigned high thresholds. A motoneuron
remained inactive as long as the excitatory drive was less than the neuron’s assigned recruitment threshold value.

The firing rate of a motor neuron was modeled to increase linearly with increased excitatory drive above the recruitment threshold excitation. The minimum firing rate was set at 8 Hz for every motoneuron. The interspike interval of the motor unit firing was modeled as a random process with a Gaussian probability distribution function. The SD of the interspike interval was fixed for all motor units at 15% of the mean interspike interval.

The precise motor unit firing rate distribution that occurs for different motor units in vivo is still unknown. The most common observation during voluntary contraction has been that low-threshold motor units attain higher peak firing rates than do later recruited motor units, which gives rise to an “onion-skin” appearance of the rate traces of simultaneously recorded motor units (De Luca et al. 1982, 1996; Freund et al. 1975; Masakado et al. 1995; Tanji and Kato 1973). Recent experimental studies of voluntary contraction, relying on advanced intramuscular EMG decomposition techniques, indicate that all the motor units finally reach the similar peak firing rate (Erim et al. 1996). At the other extreme, we examined a model that predicts that high-threshold units will reach much higher peak firing rates than initially recruited units. This is because higher threshold motoneurons display shorter afterhyperpolarization (AHP) potentials and can ultimately discharge repetitively at higher rates than will cells with longer AHPs. Furthermore, motoneurons innervating fast twitch muscle fibers display shorter AHPs than those innervating slow muscles. In this model, the peak firing rates of high-threshold motor units should eventually surpass those of low-threshold motor units (Kernell 1965). This firing strategy is intuitively appealing, because it avoids potential overdriving and saturation of small slow-twitch motor units. However, it currently lacks strong experimental support. Since it is very difficult to track motor unit firing rates at high contraction levels (due to the tremendous MUAP superposition contained in EMG signal), it seems that this limitation may be a result of recording constraints, and it is possible that higher threshold units will ultimately be shown to achieve higher firing rates than will low-threshold units.

Accordingly, three types of motor unit firing rate strategies were used in the simulation. The first type (FR1; Fig. 1A) modeled the “onion-skin” phenomenon of the motor unit firing rates observed from the voluntary contractions. To facilitate this, the slope of the excitatory drive-firing rate relation was set to be the same for all motoneurons. The peak firing rate of a motor unit was inversely proportional to its recruitment threshold according to

$$PFR_i = PFR_1 - PFRD \times \frac{RTE_i}{RTE_{120}} \quad i = 2:120$$

where $PFR_1$ was the assigned peak firing rate of the first recruited unit, $PFRD$ was the desired difference in peak firing rates between the first and the last recruited units, $RTE_i$ was the recruitment threshold of the studied motor unit, and $RTE_{120}$ was the recruitment threshold of the last recruited motor unit (Fuglevand et al. 1993). In the simulation, $PFR_1$ was set at 50 Hz, $PFRD$ was set at 12 Hz, and $RTE_{120}$ was set at 40% maximum excitation.

For the second type of motor unit firing rate strategy (FR2; Fig. 1B), the slope of the excitatory drive-firing rate relation of the motoneuron increased with the recruitment threshold, i.e., the firing rate of later recruited motor units increased faster than early recruited ones. All the motor units finally reached the same peak firing rate at maximum excitation, which was set at 50 Hz.

For the third type of motor unit firing rate strategy (FR3; Fig. 1C), the slope of the excitatory drive-firing rate relation was also set to be the same for all motoneurons. However, peak firing rates were linked to the mechanical properties of motor units, i.e., large rapidly contracting units were assigned higher peak firing rates than were those with lower force recruitment thresholds and with small twitches and slow contraction times. For example, for the slowest motor unit, the force output was maximum at the firing rate of ~20 Hz, whereas for the fastest unit, a peak firing rate of ~50 Hz was required to attain full force output (see Muscle force generation model).

To investigate the effects of motor unit synchrony on the EMG-force relation, synchrony was simulated following the approach proposed by Yao et al. (2000). Two steps were involved in the selection of

![FIG. 1. Simulation of motoneuron firing rate strategies. A: motor unit firing rate strategy. FR1: slope of the excitatory drive-firing rate relation was set to be the same for all motoneurons. Peak firing rate of a motor neuron was inversely proportional to its recruitment threshold. B: motor unit firing rate strategy. FR2: slope of the excitatory drive-firing rate relation of a motoneuron increased with increasing recruitment threshold. All motor units finally reached the same peak firing rate at maximum excitation. C: motor unit firing rate strategy. FR3: slope of the excitatory drive-firing rate relation was set to be the same for all motoneurons. Peak firing rates were linked to mechanical properties of motor units, i.e., large rapidly contracting units were assigned higher peak firing rates than those with lower force recruitment thresholds and with small twitches and slow contraction times.](image-url)
of MUAPs to be synchronized. First, 10% of the MUAPs discharged by reference motor unit were randomly selected, and then, for each selected MUAP of the reference motor unit, 10% of the other active motor units were randomly selected to have the timing of the nearest MUAP adjusted so that it was coincident with the reference MUAP. Variable synchrony was used, and the time separation between the synchronized MUAPs had a Gaussian distribution with a mean of 0 ms and an SD of 2 ms. The process was repeated until each of the active motor units was selected as a reference unit.

Muscle force generation model

The muscle force simulation uses a previously published model (Fuglevand et al. 1993). Twitch force was modeled as the impulse response of a critically damped, second-order system. Figure 2A shows the simulated twitch forces of a few motor units with different recruitment thresholds. Peak twitch force was varied over a wide range (100-fold) and was linked to the motor unit recruitment thresholds. Figure 2B shows the simulated twitch forces of a few motor units with different twitch-MUAP relation. Figure 2C shows the simulated twitch forces of a few motor units with different twitch-MUAP relation.

Surface EMG simulation

The surface EMG signal is comprised of the sum of MUAPs from different motor units within the recording range of the electrode. In general, the waveform of a MUAP is determined by the relative position of the recording electrode and the muscle fiber distribution within the motor unit. For different motor units, the muscle fiber distributions within the muscle are potentially different. However, for surface EMG recordings, the detection surface is large and relatively distant from the motor unit current sources. Consequently, differences in detailed muscle fiber arrangements of motor units are less important. This feature (i.e., consistent shapes of motor units in surface recordings) is also quite characteristic for the FDI muscle because of its small size and the wide distribution of the muscle fibers from the individual motor units (Milner-Brown and Stein 1975). In addition, because of the low-pass filter effects of skin and subcutaneous tissues, the spatial integrating effects provided by the surface electrode, the differences in the shapes of surface MUAPs from different motor units will be further obscured. It follows that the waveforms of the surface MUAPs are routinely much less complex than those recorded using intramuscular electrodes.

The HR functions were selected to represent surface MUAPs as described by earlier investigators (Farina et al. 2000; Laterza and Olmo 1997; Lo Conte et al. 1994; Olmo et al. 2000). We have also shown earlier that, by simultaneously recording surface EMG and intramuscular EMG from the FDI muscles, using the spike triggered averaging technique, we can obtain surface MUAPs from different motor units. We determined that the basic shapes of the recorded MUAPs can be well represented by the second-order HR (HR2) function or its modifications (Zhou and Rymer 2004). The nth order HR function is proportional to the nth derivative of a normal function. Accordingly, in the simulation, the HR2 function was routinely used to represent the basic shape of surface MUAPs. Due to the wide distribution of the motor unit muscle fibers throughout the FDI muscle, all the motor units may be viewed as being at similar depth, which results in similar duration of the recorded surface MUAPs (Milner-Brown and Stein 1975). Therefore, in our surface EMG simulation, the MUAPs from different motor units were assigned the same duration (11.72 ms) based on the experimental observations for the FDI muscles (Zhou and Rymer 2004).

Many factors contribute to the amplitude of the MUAPs recorded at the surface, such as motor unit size, motor unit location, motor unit muscle fiber arrangement, electrode position, and the thickness of the subcutaneous tissue. As a result, it has been frequently reported that MUAP amplitudes are quite scattered with respect to motor unit twitch forces. Nonetheless, using a scatter plot, a positive relation between the MUAP amplitude and the twitch force of motor units can still be obtained (Clamann and Robinson 1985; Gielen et al. 1991;

Although many different relations between motor unit electrical and mechanical properties have been reported experimentally, in our current simulation, MUAP amplitude assignment was based on one of two relations. This choice was made because these relations are supported both by theoretical and experimental observations and also because these two relations have been recorded experimentally from the FDI muscles (Herdman et al. 1986; Milner-Brown and Stein 1975) (see DISCUSSION).

1) MUAP peak-to-peak amplitude is linearly proportional to twitch force; therefore the smallest motor unit has the action potential peak-to-peak amplitude of 1 au and the largest one has the action potential amplitude of 100 au.

2) MUAP peak-to-peak amplitude is linearly proportional to the square root of twitch force; therefore the amplitude of the smallest and largest motor unit is 1 and 10 au, respectively.

The simulated MUAPs of a few motor units with different recruitment thresholds are shown in Fig. 2, B and C, based on each of the above relations, respectively.

**Simulation procedures**

Two MUAP-twitch relations (linear or square root relation), three motor unit firing rate strategies (FR1, FR2, or FR3), and two motor unit synchrony conditions (absence or presence of synchrony) were tested in the simulations. For each combination of these conditions, muscle force and surface EMG were simulated at 10 levels of steady-state excitation: for FR1, the 10 levels were set at 8, 16, 26, 34, 42, 50, 60, 70, 80, and 100% maximum excitation; for FR2, 17, 27, 34, 41, 47, 53, 58, 67, 77, and 100% maximum excitation, and for FR3, 8, 16, 24, 30, 36, 42, 48, 56, 65, and 100% maximum excitation. In addition, for comparison purposes, the same excitation level (60% maximum excitation) was also used to simulate surface EMG and force signals for different combinations of motor unit firing rate strategy and synchrony conditions.

The duration of each simulation period for each level of excitation was 3 s. The EMG was simulated at a sampling rate of 5,120 Hz and force at 1,024 Hz. At each level of excitation, the average force and the ARV of EMG were determined over the steady-state (0.5–3 s) simulation period. For each combination of the conditions, 10 trials of muscle force and surface EMG signals were simulated.

**RESULTS**

The output of the simulation comprised the surface EMG and the muscle force at a given steady-state level of excitation. We found little variation for the repeated simulation trials. Here, for each combination of conditions examined, we report only the results from one simulation trial, which was representative of the rest.

Examples of the outputs of the model are shown in Fig. 3. In this figure, comparisons are drawn between simulated surface EMG and force signals derived using the three different motor unit firing rate strategies described in METHODS, each with and without motor unit synchrony. For each case, the level of excitation was set to be the same (60% maximum excitation), and the same MUAP-twitch relation (linear) was used.

It is evident that motor unit synchrony had a substantial influence on the output of the motor unit pool. For both motor unit firing rate strategies, adjusting the relative timing of MUAPs substantially increased surface EMG amplitude (Fig. 3, A, C, and E) and decreased force steadiness but had little effect on average force magnitude (Fig. 3, B, D, and F). This
was consistent with previously published findings (Yao et al. 2000).

However, in our simulation, in which we set the MUAP duration at 11.72 ms, with synchrony, the EMG was only increased by 18.3% for FR1, 13.9% for FR2, and 15.6% for FR3. These EMG values are much less than the 65% increase reported by Yao et al. (2000) using the same synchrony level. This is presumably attributable to the difference in the duration of the synchronized MUAPs used in the two simulations.

To further explore this postulate, we systematically changed the duration of the surface MUAPs to different values and simulated the resulting surface EMG signals.

A comparison of the results using different MUAP durations is shown in Table 1. It is evident that the longer the MUAP duration, the larger the percentage of the increased EMG amplitude caused by motor unit synchrony. It is worth noting that, if the MUAP duration was very short (5.47 ms), synchrony decreased mean rectified EMG (relative to the control state without synchrony), and the amplitude of the surface EMG was then less than the EMG amplitude under the condition of no synchrony.

Figure 4 shows the resultant EMG amplitude-force relations from different simulation inputs. EMG amplitude-force relations were constructed based on the relation between the excitation level and the isometric contraction force and the relation between the excitation level and the ARV of the surface EMG signal simulated in response to 10 steady-state excitation levels.

Figure 4, A and B, is the EMG amplitude-force relations obtained using motor unit firing rate strategy FR1, with the later recruited motor units having lower peak firing rates than earlier recruited units. If the MUAP amplitude is set to be proportional to the square root of the motor unit twitch force, the ARV of the surface EMG increases more slowly than the force (Fig. 4A). However, if the MUAP amplitude is set as being linearly proportional to the twitch force, the ARV of the surface EMG increases more linearly with the isometric force (Fig. 4B).

This result held true both for simulation conditions with no synchrony and with synchrony. Although action potential synchrony increased the EMG amplitude, it did not have discernible effects on the form of the normalized EMG amplitude-force relation, since the relative increased amount of EMG was similar at different excitation levels (Table 1).

Similarly, Fig. 4, C and D, presents the simulation results from motor unit firing rate strategy FR2, in which all the motor units ultimately reach the same peak firing rate. Figure 4, E and F, presents the simulation results from motor unit firing rate strategy FR3, in which the later recruited motor units reach higher peak firing rates than earlier recruited motor units. For both motor unit firing rate strategies, the simulation indicates that the relation between the electrical and mechanical outputs at motor unit level played a dominant role in determining the force-EMG amplitude-force relation. If the MUAP amplitude is set to be proportional to the square root of the twitch force, the ARV of the surface EMG increases more slowly than does muscle force (Fig. 4, C and E). If the MUAP amplitude is set to be linearly proportional to the twitch force, the ARV of the surface EMG increases more linearly with the isometric force (Fig. 4, D and F). Again, this result held true for simulation conditions of no synchrony and with synchrony.

A comparison of Fig. 4, A, C, and E, or Fig. 4, B, D, and F, using the same motor unit electrical and mechanical relations, but different firing rate strategies, also indicates that the force-EMG amplitude relation varied somewhat with the underlying motor unit firing rate strategies. We quantitatively compared the variations of the force-EMG amplitude relations induced by different motor unit electrical and mechanical output relations, and by different motor unit firing rate strategies. We used the area between the two relation curves as an index of the variation of the two normalized force-EMG amplitude relations. The area was calculated for each pair of the relations simulated from different motor unit firing rate strategies when the MUAP-twitch relation was held the constant, and from different MUAP-twitch relations when motor unit firing rate strategy was held constant. The average variation index of the normalized force-EMG amplitude relations induced by the three different motor unit firing rate strategies was 0.051 (for the condition of no synchrony), a value much less than the average variation index of 0.092 induced by the two different MUAP-twitch relations.

Figure 5 presents the normalized relation between the number of motoneuron discharges (or the number of MUAPs in EMG signal) and the isometric force, based on motor unit firing rate strategies FR1, FR2, and FR3. For each motor unit firing rate strategy, with or without synchrony, the relations were almost the same, since motor unit synchrony had little effect on the average force.

It is worth noting that, for different motor unit firing rate strategies, the difference in the simulated EMG amplitude-force relations was not very significant, whereas there was a

| Table 1. Effects of the MUAP duration on the amount of EMG amplitude changes caused by motor unit synchrony at different excitation levels for motor unit firing rate strategies FR1, FR2, and FR3 |

<table>
<thead>
<tr>
<th>MUAP Duration, ms</th>
<th>FR1</th>
<th>FR2</th>
<th>FR3</th>
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<tr>
<td></td>
<td>34% E</td>
<td>60% E</td>
<td>100% E</td>
</tr>
<tr>
<td>5.47</td>
<td>−7.5%</td>
<td>−4.2%</td>
<td>−3.7%</td>
</tr>
<tr>
<td>10.94</td>
<td>1.0%</td>
<td>5.2%</td>
<td>4.3%</td>
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<tr>
<td>16.60</td>
<td>21.5%</td>
<td>29.6%</td>
<td>33.9%</td>
</tr>
<tr>
<td>21.88</td>
<td>47.1%</td>
<td>49.6%</td>
<td>38.9%</td>
</tr>
<tr>
<td>26.95</td>
<td>64.9%</td>
<td>71.1%</td>
<td>78.5%</td>
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MUAP, motor unit action potential. Each value of the percentage of the EMG amplitude change is the mean from 10 trials of simulations.
more substantial difference in the form of the relation between the number of motoneuron discharges and the isometric force.

**DISCUSSION**

Many studies (e.g., Jones et al. 2002; Taylor et al. 2003; Yao et al. 2000) have attempted to investigate the impact of firing characteristics of motor units on force and EMG output of the whole muscle. These studies usually rely on motor unit recruitment and rate coding models, such as the one developed by Fuglevand et al. (1993). In this study, the latter model has been used to investigate the factors governing the form of EMG-force relations. We explored in detail the effects of several key parameters, such as single motor unit electrical and mechanical output relations, motor unit firing rate strategies, and motor unit synchrony, on the overall EMG-force relation of the muscle, using the human FDI muscle as a test case.

In contrast to the well-documented EMG amplitude-force relations for isometric contractions of whole muscle, several different relations have been reported between motor unit electrical and mechanical properties:

1) MUAP amplitude is linearly proportional to twitch force (Gielen et al. 1991; Herdmann et al. 1986; Lemon et al. 1990);

2) MUAP amplitude is linearly proportional to the square root of twitch force (Milner-Brown and Stein 1975; Totosy de Zepetnek et al. 1991);

3) MUAP amplitude increases faster than twitch force (Clamann and Robinson 1985; Goldberg and Derfler 1977);

4) Twitch force increases exponentially with MUAP amplitude (Vogt et al. 1990);

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**FIG. 4.** Normalized force-EMG amplitude relations using different simulations. A reference line (dotted line) from (0, 0) to (1, 1) was plotted for easy comparison. Both conditions of no and with synchrony are shown in each panel. A, C, and E: simulated force-EMG amplitude relation when MUAP amplitude (A) is proportional to square root of twitch force (f). A: simulated force-EMG amplitude relation derived from motor unit firing rate strategy FR1. C: simulated force-EMG amplitude relation derived from motor unit firing rate strategy FR2. E: simulated force-EMG amplitude relation derived from motor unit firing rate strategy FR3. B, D, and F: simulated force-EMG amplitude relation when MUAP amplitude (A) is linearly proportional to twitch force (f). B: simulated force-EMG amplitude relation derived from motor unit firing rate strategy FR1. D: simulated force-EMG amplitude relation derived from motor unit firing rate strategy FR2. F: simulated force-EMG amplitude relation derived from motor unit firing rate strategy FR3.
5) There is no correlation between MUAP amplitude and twitch force (Hulliger et al. 2001).

The relations 1) and 2), used in this simulation, were derived experimentally with accompanying theoretical support. The other relations were based solely on experimental reports.

Most of the studies cited above used voluntary contractions of different muscles and relied on the spike triggered averaging technique to extract data about unitary EMG and motor unit force characteristics. Even for units recorded from the same muscle (FDI), conflicting reports exist (Herdmann et al. 1986; Milner-Brown and Stein 1975). The diversity of the reported motor unit electrical and mechanical output relations may be due to the different experimental conditions, such as the placement of the EMG electrode and the thickness of skin and subcutaneous body tissues. Another possible reason for this diversity may be the limitations of the spike triggered averaging technique for estimating motor unit twitch force (Calancie and Bawa 1986; Kossev et al. 1994; Lim et al. 1995; Nordstrom et al. 1989; Thomas et al. 1990). The fusion of motor unit twitches that is routinely present during normal discharge limits the utility of this averaging technique as a means to extract the characteristics of the single motor unit twitch. Furthermore, synchronization of motor unit discharge can substantially influence estimates of twitch properties (Taylor et al. 2002). Therefore it is very difficult to accurately determine the motor unit electrical and mechanical relation experimentally in human muscles.

Similarly, the precise motor unit firing rate strategy that arises in vivo in human muscle is still not certain (see Methods). By varying the motor unit electrical-mechanical relation and firing rate strategies as inputs to the motor unit pool model, the resulting force-EMG amplitude relation can be used to evaluate the impact of a range of motor unit firing properties, using experimentally derived relations as the basis for comparison.

In our simulation, it is worth noting that, when we examined different motor unit firing rate strategies, we used a fixed pattern of motor unit recruitment, in which recruitment ceased at 40% of maximum excitation. It has been suggested that the relative contribution of rate coding and motor unit recruitment to force production is different in muscles of different fiber composition and function. In particular, rate coding appears to play a more important role in small muscles, such as FDI and aductor pollicis, while recruitment plays a more important role throughout the contractile force range in large muscles of mixed fiber composition such as biceps brachii (De Luca et al. 1982; Kukulka and Clamann 1981). Based on this, a narrow motor unit recruitment range (40% maximum excitation) was used in our simulation of the FDI muscle.

Actually, as was the case for firing rate data during strong muscle contractions, the motor unit recruitment range is also a relatively poorly described parameter, primarily because of limited experimental data. However, it is likely that variation in recruitment range will also influence the shape of the EMG-force relation in different muscles. This possibility was investigated in an earlier study (Fuglevand et al. 1993), where surface EMG amplitude-force relations were simulated using different motor unit recruitment and firing rate behaviors, based on a motor unit pool model. In this model, two motor unit recruitment conditions were tested: narrow (limit of recruitment 70% maximum excitation) and broad recruitment range (limit of recruitment > 70% maximum excitation). Three firing rate strategies were tested, two of which were similar to FR1 and FR3 used in this study. For the third firing rate strategy, all motor units were assigned the same peak firing rate, while the slope of excitatory drive-firing rate relation was also assigned the same value for all motoneurons, so the early recruited motor units reached peak firing rate and ceased to increase in firing before maximum excitation. In our current study, this strategy was modified (see FR2) according to recent
experimental findings from human voluntary contractions based on advanced intramuscular EMG decomposition technique (Erim et al. 1996). Each combination of two recruitment and three firing rate conditions was used to simulate the force-EMG amplitude relations. The simulation results indicated that a broad motor unit recruitment range (>70% maximum excitation) resulted in a more linear or parabolic shape of force-EMG amplitude relation (as reported in experimental observations) compared with the narrow recruitment range (<50% maximum excitation). This suggests that a broad recruitment range may be an optimal description of the motor unit behavior (Fuglevand et al. 1993).

In this study, we used a similar simulation approach to study the overall EMG-force relation of the muscle by varying the motor unit electrical and mechanical output relations, motor unit firing rate strategies, and by adding or removing substantial motor unit synchrony. We found that the relation between electrical and mechanical properties at the single motor unit level plays a dominant role in determining the EMG amplitude-force relation of the whole muscle. In our simulation, MUAP amplitudes were linked to twitch forces based on a linear and a square root relation, respectively. We found (not surprisingly) that the overall EMG amplitude varied with the force in a similar manner that the MUAP varied with the twitch. For the case of the FDI muscle, the recorded relation between force and the ARV of surface EMG is reported to be approximately linear. From our simulation, this suggests that the choice of a linear relation between motor unit electrical and mechanical properties may reflect the actual relation in life.

It is further worth noting that, in the earlier model (Fuglevand et al. 1993), the diameter of muscle fibers of all motor units was assigned the same value, while bigger motor units contained more muscle fibers. This resulted in an approximately linear relation between MUAP peak-to-peak amplitude and twitch force. Therefore under analogous motor unit recruitment and firing rate conditions (narrow recruitment range, firing rate strategy FR1 or FR3), the resultant EMG amplitude-force relations were quite close to the ones derived using a linear MUAP-twitch relation in this study. The slight differences observed (relative to our own simulations) might have been a result of the choice of different surface EMG models used in two simulations.

Our simulations also indicate that the normalized surface EMG amplitude-force relations are not very sensitive to certain underlying motor unit firing rate strategies. This possibility was also suggested by the previous simulation results, e.g., the motor unit firing rate strategies similar to FR1 and FR3 both resulted in a linear force-EMG amplitude relation when motor unit recruitment operated over a broad range (Fuglevand et al. 1993).

In contrast, the simulated relations between the number of motoneuron discharges and muscle force show several different forms, according to different motor unit firing rate strategies. This suggests that the number of MUAPs in EMG signals may contain information about the properties of the neural command from CNS to control the muscle. However, the substantial MUAP superposition routinely existing in the standard surface EMG signal makes MUAP number estimation a rather difficult task, especially at high contraction levels.

It has been reported that motor unit synchrony increases EMG amplitude of simulated contractions (Yao et al. 2000). Our simulation study further indicates that the relative increase in EMG amplitude caused by synchrony is determined by the MUAP duration of the synchronized motor units. However, if the relative synchrony level is similar at different pool excitation levels, as assumed in this simulation, motor unit synchrony does not exert significant effects on the form of the normalized EMG-force relation. It is worth noting that the surface MUAP duration may range between 10 and 30 ms, which is determined by many factors including the location of motor units, the volume conductor effects of the interposed skin and subcutaneous body tissues, the conduction velocity of action potentials, and the properties of the recording electrode. To better understand the EMG-force relations over the full span of pool excitation, we would need to examine the effects of an increase in synchrony and of action potential duration changes with increasing motoneuron excitation. Currently we lack sufficient experimental data to guide such a simulation.

In summary, by systematically varying the input parameters to a motor unit pool model, we explored the impact of different factors on the EMG-force relations. We found MUAP-twitch relation plays a dominant role in shaping the relation between EMG amplitude and force, while motor unit firing rate strategy appears to be a less important factor. The relative increase in EMG amplitude caused by motor unit synchrony is governed by the MUAP duration of the synchronized motor units. However, motor unit synchrony will not have a significant impact on the form of the normalized EMG-force relation if the relative degree of synchrony is unchanged at different excitation levels. The results from our current simulations, when coupled together with the previous findings (Fuglevand et al. 1993), add new knowledge to our interpretation of the fundamental EMG-force relations and provide insights that may help drive future experimental protocols to study motor unit behaviors.

REFERENCES


