Roles of Motor-Unit Recruitment in Producing Force Variability of Simulated Muscle Contractions

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The purpose of this study was to examine the effect of motor-unit recruitment on force variability by using computer simulated isometric contractions of a hand muscle (i.e., first dorsal interosseus). The force was simulated at 10 levels of excitation, ranging from 10 to 100% of maximum. Two recruitment conditions were simulated to compare the relative effect of motor-unit recruitment (MUR) on the relationship of force variability and level of force. One condition (40%MUR) recruited all motor units at 40% of the maximum excitation level, and the other (50%MUR) recruited all motor units at 50% of the maximum. The 40%MUR condition had a greater number of motor units than the 50%MUR group before the excitation level reached 50% of the maximum. The results showed that force variability increased at a faster rate before the completion of motor-unit recruitment and, thereafter, increased at a slower rate. In addition, the 40%MUR group showed greater force variability than the 50%MUR group. These data suggest that motor-unit recruitment is an important factor in causing force variability.

Key Words: motor unit, motor-unit recruitment, discharge rate, force variability

Introduction

Force variability has been observed in many studies when people attempt to produce a target level of force (Carlton & Newell, 1988; Christou, Grossman, & Carlton, 2002; Newell & Carlton, 1985, 1988; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979; Sherwood & Schmidt, 1980; Sherwood, Schmidt, & Walter, 1988; Slifkin & Newell, 1999, 2000). Most recently, Christou et al. (2002) reported an interesting study in which they modeled variability of force during continuous isometric contractions of the quadriceps femoris. They observed that force variability increased almost linearly as the level of force increased up to 60% MVC, and then continued to increase, but at a slower rate. Similar findings were also reported in both a...
study with isometric hand-grip tasks (Loscher & Gallasch, 1993) when force was bandpass filtered with a frequency range of 5–30 Hz, and with simulated isometric contractions of a hand muscle (Yao, Fuglevand, & Enoka, 2000). Based on these results, Christou et al. (2002) suggested that variability for continuous isometric contractions was best described by a sigmoidal function. Furthermore, Christou et al. (2002) hypothesized that the sigmoidal relationship between force variability and %MVC is related to motor-unit recruitment and discharge rate. Slifkin and Newell (2000) had proposed a similar hypothesis that also suggested a possible role of motor-unit recruitment and discharge rate in the relationship between force and force variability.

It has been known for a number of years that muscle force is gradated by two mechanisms, namely motor-unit recruitment and discharge rate. Several studies have found that motor-unit recruitment is completed at about 40% of the MVC for small muscle groups such as hand muscles or at about 80% of the MVC for large muscle groups (De Luca, LeFever, McCue, & Zenakis, 1982; Enoka, 1994; Milner-Brown, Stein, & Yemm, 1973b; Rothwell, 1994). It was interesting to note that the maximum force variability observed in Christou et al.’s (2002) study was at approximately 60% MVC, which was close to the range at which motor-unit recruitment is completed in large muscles. As to why motor-unit recruitment played an important role in determining force variability, Christou et al. (2002) assumed when new motor units were recruited, the magnitude of motor-unit synchronization would become larger. This, in turn, caused the fast increasing rate of force variability. Motor-unit synchronization is a measure of the correlated discharge of action potentials among motor units. The magnitude of synchronization depends on the number and rate of shared inputs and the size of the unitary excitatory postsynaptic potentials evoked in the motor neurons (Nordstrom, Fuglevand, & Enoka, 1992). In a study with simulated isometric contractions of a hand muscle, Yao et al. (2000) found that force variability increased when motor-unit synchronization index increased.

Although Christou et al.’s (2002) hypothesis regarding the cause of the relationship between force variability and level of force may ultimately prove to be correct, it seems to be premature at this point. This is because motor-unit behavior in a pool was not measured directly in their study (Christou et al., 2002). The primary purpose of this study was to investigate the roles of motor-unit recruitment in producing force variability during simulated isometric hand muscle (i.e., first dorsal interosseus) contractions. A computer-simulation approach was used in the study because it was impossible to experimentally observe the behavior of all motor units in a motor neuron pool. This approach made it possible to evaluate the influence of motor-unit recruitment and discharge rate on force variability and level of force.

**Method**

This study involved computer simulations of muscle force based on models developed by Fuglevand and colleagues (Fuglevand, Winter, & Patla, 1993; Fuglevand, Winter, Patla, & Stashuk, 1992). The force during isometric muscle contractions was
simulated with the sampling frequency of 500 Hz for 10 s. The advantages of using isometric contractions were that the effect of temporal parameters was eliminated (Enoka, 1996), and the force variability is related directly to the excitation level and to the associated neuromuscular noise (Christou et al., 2002).

The basic parameters and simulation procedures in the current study were similar to those used by Fuglevand et al. (1993) and Yao et al. (2000). Briefly, simulations in the current study first determined the recruitment and discharge times of a population of 120 motor neurons in response to different levels of excitatory drive. Excitatory drive is defined as the net synaptic input to motor neurons during a voluntary muscle contraction (Heckman & Binder, 1991). The recruitment of motor neurons was determined by two parameters: excitatory drive and recruitment threshold (the minimum level of excitatory drive required to initiate repetitive discharge in a motor neuron). It was assumed that the input was uniformly distributed across the pool such that all neurons received the same level of excitatory drive. The recruitment thresholds of the 120 motor neurons in the pool were determined from an exponential function that assigned many neurons to have relatively low thresholds and progressively fewer neurons to have higher thresholds (Fuglevand et al., 1993). The units of measurement for recruitment threshold and excitatory drive were arbitrary excitation units. A motor neuron was recruited when the excitatory drive \( \geq \) recruitment threshold for the motor neuron.

In order to compare the relative effect of motor-unit recruitment and discharge rate on the relationship of force variability and level of force, two recruitment conditions were simulated, each consisting of 10 excitation levels. One recruitment condition had an upper limit of recruitment at 40% of maximal excitation (40%MUR). The other recruitment condition had an upper limit of recruitment at 50% of maximal excitation (50%MUR).

Once a motor neuron was recruited, the discharge rate of the neuron was defined by the following parameters: its minimum and maximum discharge rates, the relationship between excitatory drive and discharge rate, and the variability in the interspike intervals (ISIs) between successive action potentials discharged by a recruited motor neuron.

Several studies have demonstrated that during voluntary muscle activity in humans, minimum discharge rate is similar for all motor units in a muscle, regardless of recruitment threshold (De Luca et al., 1982; Freund, Budingen, & Dietz, 1975; Monster & Chan, 1977; Tanji, & Kato, 1973). Therefore, the minimum rate in the simulations was the same for all motor neurons: 8 impulses/s (imp/s). The maximum discharge rate, however, varied across the pool such that the low-threshold units achieved higher rates at maximum activation (De Luca et al., 1982; Monster & Chan, 1977; Tanji, & Kato, 1973). The maximum rate of motor neuron 1 was 35 imp/s and for motor neuron 120 was 25 imp/s for both simulated recruitment conditions (i.e., 40%MUR and 50%MUR).

The ISIs were characterized as a random process distributed with a Gaussian probability function (Andreassen & Rosenfalck, 1978). These intervals were normally distributed about the predicted mean discharge interval with a coefficient of variation equal to 0.2 (Nordstrom et al., 1992). This variability was introduced into the timing of all action potentials discharged by each active motor neuron at the
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Various levels of excitatory drive (Fuglevand et al., 1993). The minimum acceptable interval between successive action potentials was 20 ms.

The second major step in the current simulation was to determine motor-unit force.

The time course of the twitch response of a motor unit was modeled as the impulse response of a critically damped second-order system (Milner-Brown, Stein, & Yemm, 1973a). The distribution of twitch force magnitudes across the pool of motor units was modeled as an increasing exponential function with the lowest threshold motor unit assigned to have the smallest force and the highest threshold unit to have the greatest force. The range of twitch forces used in the simulations was set at 100 fold. One unit of force was equivalent to the twitch force of the first recruited motor unit, and the last unit recruited had the highest twitch force, 100 force units.

The distribution of contraction times was based on experimental observations that showed low-force units to have contraction times spanning most of the range of observed values, whereas the strongest units tended to have briefer contraction times (Burke, 1981). The relationship between twitch force and contraction time, therefore, was approximated as an inverse power function (Fuglevand et al., 1993). The contraction time for the lowest threshold, the weakest motor unit, was 90 ms and for the highest threshold, strongest unit, was 29 ms.

The nonlinear relationship between discharge rate and force was simulated by varying the impulse response magnitude as a function of the instantaneous discharge rate and contraction time of the motor unit (Fuglevand et al., 1993). The general form of the relationship between steady-state force and activation frequency was sigmoidal, but the specific shape varied depending on the contraction time of the unit. Motor units with longer duration contraction times required lower activation rates to attain half-maximal or maximal force compared to motor units with briefer contraction times. Muscle force was calculated as the sum of the forces exerted by the active motor units.

Statistics and Dependent Variables

Although levels of motor-unit synchronization were not directly imposed in the simulations, they were altered by the change in motor-unit recruitment and discharge rate. The magnitude of motor-unit synchronization within the pool was quantified with the Population Synchrony Index, which was calculated by using a Binomial-Poisson method (Yao et al., 2000). This method indicated the total number of coincident action potentials for all active motor units in excess of that expected due to chance for independently activated units (Taylor, Steege, & Enoka, 2002).

A frequency analysis was performed on the simulated force output signal using Welch’s averaged periodogram method, with a window size of 1024 and 50% overlap. The mean force was subtracted from each signal before the frequency analysis was performed. The maximal power and frequency at maximal power were determined during the analysis.

The dependent variables of the study were the mean and variability of the simulated force as a function of excitation. The force variability was determined by
calculating the standard deviation of force productions. The average force and the force variability were determined over the interval from 1.0 to 9.0 s of simulations at each level of excitation.

Results

Motor-Unit Discharge Rate and Recruitment

The average discharge rate for 50%MUR was faster than for 40%MUR at each of the excitation levels, although the difference was small (Figure 1A).

The 40%MUR group recruited 51 motor units at 10% of maximum excitation and recruited all motor units in the pool at 40% of maximum excitation. The 50%MUR group also started with 51 motor units at 10% of the maximum but finished recruiting all motor units at 50% of maximum excitation. That is, the 40%MUR group recruited more motor units than the 50%MUR group at 20%, 30%, and 40% of the maximum, but had the same number of motor units at the rest of the excitation levels (Figure 1B).

Motor-Unit Synchronization

Figure 1C compares the Population Synchrony Index (PSI) between the two groups of simulations. There was little difference in PSI between the two groups at lower excitation levels. After 50% of the maximum excitation level was reached, the 50%MUR then showed relatively larger magnitude of PSI than the 40%MUR group.

Force and Force Variability

Figure 1D shows the mean outputs of the simulated hand muscle forces in response to 10 steady-state levels of excitation at 10–100% of maximum in 10% increments. Figure 2 presents the examples of simulated force at excitation levels of 20%, 40%, and 60% maximum for 40%MUR and 50%MUR recruitment conditions. At the excitation levels beyond 50% maximum, the 50%MUR showed greater force production than the 40%MUR, but the difference was very small. No visible difference in force between the two simulated groups was seen at any other excitation levels.

The power spectrum of the simulated force was similar for the two recruitment conditions (Figure 3). The total power increased with the level of excitation, and peak powers were located at low frequencies (e.g., <4 Hz). These results were consistent with experimental data (Slifkin & Newell, 1999; Vaillancourt, Slifkin, & Newell, 2001). However, while the experimental study (Slifkin & Newell, 1999) showed little change of the frequency at which the peak power was located across the force range, the current study illustrated a small shift of the peak power to the higher frequency when the level of excitation increased. For example, the peak power was located at 0.98 Hz and 1.95 Hz for the 40%MUR and 50%MUR at the excitation level of 20% maximum, respectively. In contrast, the peak power was located at 3.4 Hz and 2.9 Hz for the 40%MUR and 50%MUR at the excitation level of 60% maximum, respectively.
Figure 1 — Simulated relationships between excitation level and mean discharge rate of all recruited motor units (A), excitation level and number of motor units recruited (B), excitation level and population synchronization index (PSI) (C), excitation level and mean force (D), and excitation level and force variability (E) for 40%MUR (●) and 50%MUR (○). The arrows represent the excitation levels where motor-unit recruitment was completed for 40%MUR (□ or □) and 50%MUR (□ or □).

Figure 1E demonstrates the variability of the hand muscle forces at excitation levels of 10–100% of maximum excitation. The marked differences in force variability can be seen between the 40%MUR group and the 50%MUR group at 30% and 40% of the maximum excitation level. The 40%MUR had greater variability than the 50%MUR group at these two excitation levels. The 50%MUR group had greater variability than the 40%MUR group at excitation levels beyond the 50% maximum, but the differences were very small. In addition, Figure 1E also
Figure 2 — Simulated isometric force (from top to bottom) at 20%, 40%, and 60% of maximum excitation.

shows that the slope of excitation level versus standard deviation of force curve changed dramatically at the level of excitation associated with the completion of recruitment for both motor-unit recruitment conditions. The slope of the linear regression before the completion of motor-unit recruitment was 6.76 and 5.47 for the 40%MUR and 50%MUR conditions, respectively. In contrast, the slope after the completion of motor-unit recruitment was 1.02 and 0.89 for the 40%MUR and 50%MUR conditions, respectively.
Figure 3 — Power spectra of simulated isometric force (from top to bottom) at 20%, 40%, and 60% of maximum excitation.

Discussion

The purpose of the current study was to determine the effect of motor-unit recruitment on force variability through simulating isometric contractions of a small hand muscle. The results of the current study showed small differences in force production...
between the two simulated groups beyond the 50% maximum, which could be caused by the differences in discharge rate. That is, at these high excitation levels, the 50%MUR had the same number of motor units as the 40%MUR (Figure 1B) but had faster discharge rates than the 40%MUR group (Figure 1A). It seemed surprising that no marked difference in force was found between the two simulated groups at lower excitation levels (e.g., <50%). The marked difference in force was expected because the 40%MUR had more motor units than the 50%MUR at the low excitation levels. This unexpected result, however, could be explained by the fact that the 50%MUR had a faster discharge rate than the 40%MUR. The effect of the faster discharge rate obtained by the 50%MUR might have counterbalanced the effect of the larger number of motor units obtained by the 40%MUR during the low excitation levels.

While the simulated force was increased proportionally with the increase in excitation levels (Figure 1D), the force variability was not. For both recruitment conditions, the increasing rates of force variability were different at lower excitation levels (e.g., <50% of maximum excitation) compared to the higher excitation levels. In general, the force variability increased at a faster rate at lower force levels, but at a much slower rate at the higher excitation levels. This result is predicted by the sigmoidal model (Christou et al., 2002) and is consistent with findings experimentally obtained from a number of previous studies (Christou et al., 2002; Loscher & Gallasch, 1993; Sherwood, Schmidt, & Walter, 1988; cf. Slifkin & Newell, 1999, 2000). Christou et al. (2002) attributed the sigmoidal relationship between force variability and level of force to the effect of motor-unit recruitment. They assumed that variability increased at an increasing rate to 60% MVC in their study because it was influenced by sequential motor-unit recruitment (from smallest to largest). Beyond the point where motor-unit recruitment was completed, variability increased at a decreasing rate because of a change in motor-unit discharge rate. This assumption was well supported in the current study. First, the simulated results clearly showed that the increasing rates of the force variability changed dramatically at the point where the completion of motor-unit recruitment occurred. That is, for both groups, the force variability increased at a much faster rate before the completion of the motor-unit recruitment than after. In addition, the results of the current study revealed that the 40%MUR group had much greater force variability than the 50%MUR group at 30% and 40% excitation levels. Recall that the 40%MUR group recruited more motor units at these two excitation levels than the 50%MUR.

Christou et al. (2002) did not only hypothesize the major role of motor-unit recruitment in affecting force variability, they also assumed that motor-unit recruitment affected force variability via the influence of motor-unit synchronization associated with the recruitment. However, this assumption was not fully supported in the current study. The current results show that, although there was no observable difference in motor-unit synchronization for the 40% MUR and 50% MUR (Figure 1C), force variability was markedly different at these two excitation levels (Figure 1E). This result seems to contradict Yao et al.’s (2000) finding that motor-unit synchronization had an effect on force variability. However, it should be noted that the findings from Yao et al. (2000) suggested that motor-unit synchronization had an effect on force variability but did not suggest that motor-unit synchroniza-
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Recruitment was the only factor causing force variability. Furthermore, in their study (Yao et al., 2000), motor-unit synchronization consisted of three different levels (i.e., no synchrony, moderate synchrony, and high synchrony), but the number of motor units and the average of discharge rate of each unit was constant across synchronization conditions for a given level of excitation. In the current study, the number of motor units and discharge rate were different for the two recruitment conditions at excitation levels less than 50% maximum. Therefore, although the current study did not show similar trends for force variability and motor-unit synchronization at low excitation levels, it might not indicate the absence of the effect of motor-unit synchronization on force variability. It only suggests that motor-synchronization was not the only factor to influence force variability. Recall that newly recruited motor units were larger than the previously recruited motor units. Thus, it is possible that the larger size of the newly recruited motor units might be a major factor in causing force variability (Chritakos, 1982; Semmler, Steege, Kornatz, & Enoka, 2000), which overshadowed the effect of motor-unit synchronization.

It should be pointed out that, while the current simulation study demonstrated the consistency in major findings with some experimental studies (Christou et al., 2002; Loscher & Gallasch, 1993; Sherwood, Schmidt, & Walter, 1988), it also showed discrepancy with others (Slifkin & Newell, 1999, 2000). For example, Slifkin and Newell (1999) found that the frequency at which the peak power was located was relatively constant across the force range. However, the current study indicated a shift of the peak power toward the higher frequency with the increase of the excitation level. Furthermore, Slifkin and Newell (1999, 2000) reported an exponential relationship between level of force and force variability, rather than a sigmoid relationship. These discrepancies may be due to the simulation-model-parameter setup and raise a question about what simulation-model parameters need to be changed to produce Slifkin and Newell’s (1999, 2000) findings. Answering this question is important and should be done in future studies.

In summary, the current study indicated that motor-unit recruitment had a large effect on the magnitude of force variability. The major role of motor-unit recruitment in affecting force variability may be mainly due to the involvement of larger motor-unit size of newly recruited motor units in contractions but not to motor-unit synchronization associated with motor-unit recruitment.

References


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