Motor unit firing rate patterns during voluntary muscle force generation: a simulation study

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Received 28 August 2013, revised 13 January 2014
Accepted for publication 4 February 2014
Published 24 March 2014

Abstract

Objective. Muscle force is generated by a combination of motor unit (MU) recruitment and changes in the discharge rate of active MUs. There have been two basic MU recruitment and firing rate paradigms reported in the literature, which describe the control of the MUs during force generation. The first (termed the reverse ‘onion skin’ profile), exhibits lower firing rates for lower threshold units, with higher firing rates occurring in higher threshold units. The second (termed the ‘onion skin’ profile), exhibits an inverse arrangement, with lower threshold units reaching higher firing rates. Approach. Using a simulation of the MU activity in a hand muscle, this study examined the force generation capacity and the variability of the muscle force magnitude at different excitation levels of the MU pool under these two different MU control paradigms. We sought to determine which rate/recruitment scheme was more efficient for force generation, and which scheme gave rise to the lowest force variability.

Main results. We found that the force output of both firing patterns leads to graded force output at low excitation levels, and that the force generation capacity of the two different paradigms diverged around 50% excitation. In the reverse ‘onion skin’ pattern, at 100% excitation, the force output reached up to 88% of maximum force, whereas for the ‘onion skin’ pattern, the force output only reached up to 54% of maximum force at 100% excitation. The force variability was lower at the low to moderate force levels under the ‘onion skin’ paradigm than with the reverse ‘onion skin’ firing patterns, but this effect was reversed at high force levels. Significance. This study captures the influence of MU recruitment and firing rate organization on muscle force properties, and our results suggest that the different firing organizations can be beneficial at different levels of voluntary muscle force generation and perhaps for different tasks.

Keywords: motor unit, discharge rate, recruitment, muscle force

(Some figures may appear in colour only in the online journal)
that there be a higher MU discharge rate for effective fusion of successive MU force twitches. Thus, if the later recruited larger MUs discharge at higher rates, the discharge rates would be well-matched to the contractile properties of the MUs, and force output would be maximized for a given set of activated MUs. This strategy would maximize the muscle force output of a given muscle and also lead to a stable force output.

In contrast, other studies have reported that the later recruited MUs tend to discharge at lower rates than the earlier recruited MUs, generating the so-called ‘onion skin’ property of the superimposed force-firing rate trajectories. This scheme has also been reported in both animal [8] and human muscles [9–11] during voluntary contractions. One functional interpretation regarding this type of recruitment–rate organization is that later recruited MUs are more fatigable [12]; thus a lower firing rate for larger MUs can limit MU fatigue to maintain a sustained muscle contraction and could also help fine control the muscle force, by increasing muscle force in smaller quanta. In addition, it has been suggested that the lower firing rate in later recruited larger MUs would allow for force reserves such that these MUs can still generate higher forces in emergency situations or substitute the twitch force variability.

Using a mathematical model of the human first dorsal interosseous muscle (FDI), the objective of the current study was to examine the muscle force generation capacity and the variability of the muscle force at different excitation levels, under these two organization schemes. We simulated these two recruitment–firing paradigms by modifying the model originally developed by Fuglevand and colleagues [14], and compared the generated force amplitudes as well as muscle force variability.

We found that the ‘onion skin’ scheme led to a smaller net force generation than the reverse ‘onion skin’ scheme starting from 50% to 100% of the maximum excitation drive. Conversely, the ‘onion skin’ scheme revealed a more stable force output at low and moderate force levels (20%–40% of maximum excitation) but a less stable force output at high force levels (80%–100% of maximum excitation).

This study captures the impact of different MU recruitment and rate coding schemes on muscle force-generating properties. Further studies are required to systematically examine the rate-recruitment organizations of simultaneously active MUs, using different task protocols involving different muscles.

**Materials and methods**

**Motor unit pool model**

We simulated the MU recruitment and firing rate, as well as the muscle force output using an established model of MU recruitment and rate coding [14]. The original model is comprised of a motoneuron pool model, a force generation model, and a surface electromyogram (EMG) model. We used only the portions of the model for the motoneuron pool and force output.

Briefly, the model consists of a pool of 120 MUs with systematic variations in recruitment threshold (RT) and firing rate patterns of the MUs. A prescribed excitatory drive in the arbitrary unit (au) was used as the model input to simulate the MU recruitment and discharge patterns, and the excitatory drive was assumed to have uniform distribution across the motoneurons.

**Recruitment.** The RT rules across the MU pool were the same as in the original model [14]. Specifically, the recruitment variation was modeled as an exponential such that most of the MUs were recruited at relatively low threshold:

\[ RT(i) = e^{(\text{ln}(RR)-i)/n} \] (1)

where RT(i) was the RT of i-th MU, ln was the natural logarithm, RR was the range of RT, and n was the total number of MU in the pool.

For this model, different recruitment ranges can result in different number of active MU at particular force levels, which can, therefore, influence the overall force production capacity and force variability. The recruitment range was calculated in excitatory drive units. For example, when the range of recruitment (RR) was set at 20 fold, the first MU was recruited at an excitation drive of 1 au and the last MU was recruited at an excitation drive of 20 au.

To examine the effect of the recruitment range on the force output, a series of recruitment ranges were selected, varying from narrow to wide. The narrow RR was set at 10 fold compared with a moderate range of 20 fold and a wide range of 30 fold. Earlier studies have reported that the MU recruitment of the FDI muscle is observed up to 50% maximum force [15, 16], which corresponds to a 10-fold RR in the current simulation.

In contrast, studies have shown that MUs recruit around 70% of the maximum force, which leads to a wide recruitment range of 30 fold [13]. In the current simulation, the recruitment ranged from 1 to 10 au in the narrow range, from 1 to 20 au in the moderate range, and from 1 to 30 in the wide recruitment range. Based on the firing rate organization (see next section), the recruitment ranged from 4% to 40% of excitation drive, given a maximum excitation of 25 au in the narrow recruitment range; the recruitment ranged from 3.5% to 70% of excitation, given a maximum excitation of 28.5 au in the moderate range; and the recruitment ranged from 2.9% to 87% of excitation, given a maximum excitation of 34.5 au in the wide recruitment range.

**Peak firing rate.** Studies have shown that the peak firing rate (PFR) varies from as low as 10 Hz up to as high as 35 Hz depending on the MU recorded and the force level produced [10, 13, 16, 17]. In addition, based on the twitch parameters (described below), the firing rates that lead to the tetanic MU force range from 11 Hz to 33 Hz. In effect, the minimum inter-spike interval (ISI) approximates the rise time of the MU twitch, which is also close to the range of shortest intervals recorded in the experimental studies. In the current simulation, intervals ranged from 91 to 30 ms (with PFR ranging from 11 to 33 Hz).

For the reverse ‘onion skin’ firing pattern, the PFR of the MUs was also set at values, such that the mean ISIs
equal the time-to-peak of the MU twitch. In this setting, the 
PFR of the first recruited MU was again 11 Hz and the last 
recruited MU was 33 Hz. The relation between the excitation 
drive and the mean firing rate every 10th MUs (10, 20, . . . , 
120) is shown in figure 1(B).

For the ‘onion skin’ firing pattern, the PFR of MU \( i \) was 
set based on equation (2):

\[
PFR_i = PFR_1 - PFRD \cdot \frac{RTE_i}{RTE_{ref}}, \tag{2}
\]
where PFR\(_1\) was the PFR of the first recruited MU and was set as 33 Hz, PFRD was the difference in PFR between the first and last recruited MUs and was set at 22 Hz, and RTE\(_i\)/RTE\(_n\) represents the RT of MU \(i\) normalized by the RT of the highest threshold MU (\(n = 120\)).

During the simulation, the minimum firing rate of all the MUs was set at 5 Hz, a steady firing rate that has been observed in multiple recent studies using both intramuscular EMG recordings and skin surface EMG recording utilizing advanced decomposition techniques [13, 18, 19].

Regarding the gain of the excitation-firing rate relation, earlier studies have reported that the gain is independent of the RT in cats [20, 21]. However, an increasing gain with RT in the reverse ‘onion skin’ firing pattern has been described recently in humans [5, 10]; namely, the firing rate rises faster in the later recruited MUs than in earlier MUs with increasing excitation. In contrast, a decreasing gain with RT in the ‘onion skin’ firing pattern has also been reported [11, 13, 22], such that the firing rate rises more slowly in the later recruited MUs than the earlier ones. In the current simulation, the gain was specified from equation (3):

\[
G_i = \frac{PFR_i}{PFR_n - RR}.
\]

where \(G_i\) was the excitation-rate gain of MU \(i\), PFR\(_i\) was the PFR of MU \(i\), PFR\(_n\) was the highest PFR of the MU in the pool, which was 33 Hz in this case and RR was the RR.

In this setting, the gain decreases with the RT in the ‘onion skin’ firing pattern, and increases with the RT in the reverse ‘onion skin’ firing pattern.

The firing rate of a MU was expressed as

\[
FR_i(t) = G_i \cdot [E(t) - RT] + MFR \quad E(t) \geq RT,
\]

\(\)where FR\(_i\) was the firing rate of \(i\)th MU, \(E\) was the excitation drive, and MFR was the minimum firing rate. The firing rate as a function of excitation of every tenth MU is illustrated in figure 1.

Firing rate variability and synchronization. During the simulation, variability of the firing rate was implemented, and the CV of 20% in the ISI was adopted from the original Fuglevand model [14]. Previous studies have shown that different motoneurones within a pool receive common drive [23–25]; as a result, some timing synchrony of firings has been observed, and this synchronization leads to an increased force variability [26]. Accordingly, a moderate firing synchronization between MUs was also implemented (i.e. 10% of the action potentials of other active MUs were synchronized with 10% of the action potentials of the reference MU). The synchronization was simulated using the method of [26, 27]. Specifically, one MU was designated as the reference unit, and a portion of the firing events was randomly selected as reference action potentials. A certain portion of the remaining units was then selected as the synchrony MUs, and the timing of the firing events of these MUs was adjusted to be aligned with the reference action potentials. Only the firing events within ±15 ms of the reference firing events were adjusted. The adjusted firing time followed a Gaussian distribution with the mean at the reference firing time and standard deviation of 1.67 ms [27]. The adjustment was recursive such that each MU was served as the reference unit and all others were synchrony units.

Twitch. The twitch follows a second-order critically damped impulse response, again adopted from the original Fuglevand model. The range of twitch amplitudes across the MU pool was set at 100 fold. MU 1 is the first recruited smallest MU and has a peak twitch force of 1 au and a time-to-peak of 90 ms. MU 120 is the largest and has a peak twitch force of 100 au and a time-to-peak of 30 ms. The half-relaxation time ranges from 80 ms for MU 120 to 238 ms for MU 1, with an approximately 3-fold difference between the first and last MUs. The nonlinear force-stimulates rate relation was set to be the same as the original model, and this gain was used to amplify the MU impulse response. During the simulation, the twitches of all the MUs were summed linearly to generate the total muscle force. In the reversed ‘onion skin’ pattern, the PFR was derived from the maximum observed force-rate gain of 1 in cats [28, 29], which led to approximately 85% of the maximum force output.

Procedure

Ten repetitions at each contraction level were simulated to take into account the stochastic properties of the model. During each repetition, the excitation drive increased linearly and then held at a prescribed steady state level from 1 s till the end of simulation. Ten steady state levels were simulated, ranging from 10% to 100% of maximum excitation with 10% increments. With this excitation setting, the force output plateaus before 4 s for all the force levels. The duration of the simulation was 20 s, and the force was simulated at a sampling interval of 10 ms. Optimal firing rates of MUs were also simulated to test the maximum force generation capacity. In particular, the optimal firing rate was set at values such that the ratio between time-to-peak of twitch and ISI was 1.2, where the MU force reaches 98% of the maximum.

Data analysis

The first 5 s of the transient force record was removed from the subsequent analysis and only the steady state forces were analyzed. The mean force at each excitation level was then calculated and was normalized by the maximum force when all the MUs discharge at their optimal rates. The CV of force was calculated to estimate the force variability. To examine the effect of the recruitment–firing rate organization, a two-tailed two-sample t-test was performed on the mean forces and CV of forces at each force level.

Results

Actual firing rate at specified excitation levels

The plateau MU firing rates, calculated over different recruitment range at the ten specified excitation levels are shown in figure 2. At low excitation levels, few MUs reached their PFR, and both firing paradigms overlap or resemble ‘onion skin’. As the excitation level increases, the earlier recruited MUs in the reverse ‘onion skin’ condition reached
Figure 2. Actual plateau firing rate of MUs at the ten specified excitation levels. (A) With a RR of 10, firing rates plateau at particular levels when a specified excitation drive is reached. Black circles represent the optimal firing rate, solid lines represent the actual firing rates in the ‘onion skin’ firing pattern, and dash lines represent the actual firing rates in the reverse ‘onion skin’ firing pattern. Lines get thicker with increasing excitation levels. (B) Plateau firing rate at different levels of excitation drive with a RR of 20. (C) Plateau firing rate at different levels of excitation drive with a RR of 30.

their PFR, whereas the firing rate of these MUs continues to rise in the ‘onion skin’ condition until the PFR is reached.

The muscle forces achieved at the specified excitations are shown in figure 3. The muscle force levels were comparable between the two firing patterns at low force levels (10%–40% excitation). The force generation in the reverse onion firing pattern became stronger than in the ‘onion skin’ firing pattern from 50% excitation up, and this difference became more evident as the force level increased.

**Force generation capacity and force variability**

The average force outputs and force variability over ten repetitions at each excitation level are illustrated in figure 4. In the narrow RR (RR = 10) condition as in figure 3(A), the force levels were not different at the low to moderate (10%–40%) excitations ($p > 0.05$, t-test); however, the force levels at the moderate to high (50%–100%) excitations were significantly higher under the reverse onion firing pattern compared with the ‘onion skin’ firing pattern ($p < 0.05$). At 100% excitation, the force output under the reverse onion firing pattern reached 88% of the maximum force generation capacity (MUs discharge at optimal rate), and the force only reached 54.2% of the maximum force under the ‘onion skin’ firing pattern.

Regarding the force variability (right panel in figure 4(A)), the CV of the output force initially decreased substantially with increasing force in both conditions. However, the CV tended to plateau at moderate to high forces under the ‘onion skin’ condition, whereas the CV continued to decrease with increasing force under the reverse ‘onion skin’ condition. The end of the MU recruitment is marked by a vertical arrow on the plot. The CV of force at 20%–40% excitation was lower under the ‘onion skin’ firing pattern than under the reverse ‘onion skin’ firing pattern ($p < 0.05$). In contrast, the CV at 80%–100% excitation was higher under the ‘onion skin’ than under the reverse ‘onion skin’ firing pattern ($p > 0.05$). No difference in CV was found at other excitation levels.

In the moderate (RR = 20, figure 4(B)) and wide (RR = 30, figure 4(C)) recruitment range conditions, the force level differences between the two different firing patterns followed the same trend as in the narrow recruitment range; namely, the force production diverged at 50% of excitation. The CV of force also followed similar patterns with lower CV at low to moderate forces but higher CV at high forces under the ‘onion skin’ pattern in comparison with the reverse ‘onion skin’ firing pattern.

**Discussion**

This study examined the muscle force generation capacity and the variability of the muscle force at different excitation levels of the FDI muscle under two different firing rate organization patterns (‘onion skin’ versus reverse ‘onion skin’). We found that the force output of both firing patterns leads to graded force output with increasing excitation of the motoneuron pool, but that the force generation capacity of the two different paradigms started to diverge at around 50% excitation, regardless of the RR. In the reverse ‘onion skin’ firing pattern, at 100% excitation, the force output reached close to (88%) theoretical maximum force production of the muscle. Conversely, in the ‘onion skin’ firing pattern, the force reached only up to 54% of maximum force. Under ‘onion skin’ firing, the CV of force was lower at the low to moderate force
levels but was higher at high force levels than under reverse ‘onion skin’ firing patterns. The benefits and limitations of each firing organization are discussed in the following sections.

**Force generation capacity**

At low (10%–20%) excitation levels, most of the MUs have yet to reach their PFR (figure 2), and the ‘onion skin’ property is observed in both types of firing patterns. As a result, the force outputs are similar in the two firing patterns. In contrast, in the reverse ‘onion skin’ firing pattern, as the force level increases and when the MU discharge and muscle fiber twitch properties are matched, most of the MU forces are close to fusion, and more muscle force is produced with a prescribed level of excitation drive. In the ‘onion skin’ firing pattern, the larger MUs with larger but briefer twitches discharge well below their fusion frequency, which leads to less individual MU force and, therefore, less total muscle force output.

One key constraint in this simulation is that the MU fatigue is not considered; namely, in our simulation, fast and fatigable MUs are set to discharge at sustained high rates and generate unchanged MU twitches. In more realistic situations, these MUs would likely show declining firing rates and reduced twitch amplitudes [30–32]; thus, the simulated high force levels cannot realistically be sustained for long periods in the reverse ‘onion skin’ firing pattern.

In contrast, the low firing rates of the fatigable MUs in the ‘onion skin’ firing pattern can potentially be sustained for extended contractions [13], and thus can maintain a stable muscle force output during sustained muscle contractions. Furthermore, the ‘onion skin’ firing rate pattern can provide force reserves so that additional forces can be produced to increase the total muscle force output or to compensate for reduced forces of other MUs. Indeed there are several published examples [4, 5, 33] where strong voluntary contractions do drive high threshold MUs to reach high (potentially near fusion) firing frequencies, although these studies involved other muscles, and unitary data was collected piecemeal, not concurrently active MUs. Furthermore, these studies are intrinsically very difficult to perform, so the lack of extensive data is not unexpected.

**Force variability**

When examined at different excitation drive levels, the normalized force variability exhibits an exponential decay with increasing excitation level, and the CV tends to plateau at moderate contraction levels, especially in the ‘onion skin’ firing pattern. This trend of plateaued CV at moderate contraction levels is consistent with the experimental findings in the human hand muscles [4, 34]. At low force levels, a small portion of the MU pool is recruited, and these units discharge at relatively low rates, which lead to substantial ripple in the MU forces that cannot be cancelled sufficiently, presumably due to the small number of active MUs. As the force level increases, more MUs are recruited and MU firing rates also increase.

In the ‘onion skin’ firing pattern, firing rates of the small MUs can theoretically exceed their optimal firing rates, and lead to a tetanic MU force with minimal force fluctuations. The high firing rate in these MUs may potentially reduce the variability in the muscle force as observed in the 20% to 40% excitation levels.

In the reverse ‘onion skin’ firing pattern, as the muscle force increases further, the CV tends to decline. This is likely due to the fact that the later recruited MUs discharge at rates
Figure 4. Force level and force variability at different excitation levels. (A) Narrow RR = 10. Muscle force in the two different onion and reverse ‘onion skin’ patterns at different excitation levels (left panel). Normalized force variability of force output (right panel). The vertical array represents the end of the MU recruitment. (B) Moderate RR = 20. (C) Wide RR = 30. Error bars represent the standard error over the ten repetitions.

close to their fusion frequency. This increases the muscle force but has minimum contribution to the force variability. Therefore, the normalized force variability is further reduced. We acknowledge that the low force variability at high force levels under the reverse onion firing pattern may be an artifact of the model simplification; namely, the effect of fatigue on force variability is not considered in the reverse ‘onion skin’ firing pattern. Studies have shown that the variability of force increases substantially after sustained muscle contraction, partly due to a reduced firing rate and to greater synchronized firing between MUs [35]. This fatigue associated changes in MU firing can increase the force fluctuations and lead to higher rather than lower force variability.

In the ‘onion skin’ firing pattern, the later recruited MUs discharge at rates far from their fusion frequency, and make little contribution to the muscle force level. In addition, the MU force ripples can be compensated across different MUs to some extent, given that a large portion of the MUs pool is active at high muscle contraction levels. Thus, little change in the CV of force is observed at high force levels.

Cross-MU force fusion

During voluntary contraction, most of the active MUs do not achieve complete MU fusion force as shown in figure 5. Instead, force variability is reduced because different units fire out of phase with each other, giving rise to relatively smooth force output overall. At low to moderate contraction levels (e.g., 30% excitation), this cross-MU fusion is more critical for reducing variability than within-MU twitch fusion for both firing patterns. Although the earlier active units discharge close to their fusion frequency, most of the later recruited MUs are far from fusion, giving rise to larger force variations for the individual unit force output. Despite these variations in individual MU force, the summed MU force evens out the fluctuations and produces relatively stable muscle force, provided that the MUs do not have closely synchronized discharges.

At high contraction levels (e.g., 100% excitation), this cross-MU fusion is still critical for generating sustained stable muscle forces in the ‘onion skin’ firing pattern, since the later recruited MUs with large and brief twitches discharge at lower rates and produce substantial MU force fluctuations. In the reverse ‘onion skin’ firing pattern, although most MUs produce unit forces close to fusion, the discharge variability can still lead to substantial force variations, especially in the later recruited MUs (e.g., the last recruited MU in bottom panel of figure 5), because these MUs have larger absolute firing variability (constant CV of ISI with lower ISI).

So which rate modulation scheme is best?

The determination of which scheme is best depends on the optimization criteria used to make this assessment. If efficiency of contraction is the key parameter, measured potentially by the amount of muscle force generated for a given amount of excitatory synaptic current, then the reverse ‘onion skin’ is superior, generating 84% of maximum force in our model (as compared with 54% in the ‘onion skin’ approach).

If the smoothness of contraction is the objective, then again reverse ‘onion skin’ is more effective, because fusion of high threshold units leads to smoother total force output than is recorded in the ‘onion skin’ strategy. However, the existing experimental data show plateau force variability at moderate to high contraction levels in the human hand muscles [4, 34], perhaps favoring the use of ‘onion skin’ as the basic pattern.
Figure 5. MU force of every tenth MU in the onion and reverse ‘onion skin’ firing patterns during 30% and 100% excitation drive levels.

that leads to relatively steady force variability starting from moderate force levels as shown in figure 4.

Can either rate profile strategy be selected according to task need?

We have no evidence currently to support the idea that different rate-recruitment strategies can be implemented according to task, but this is not really within the scope of this simulation, where we rely on the previously published data. None the less, the lack of clarity may be due potentially to the fact that most published MU studies utilized single intramuscular electrode recordings, and the MU pool behavior is assembled piece by piece, often across different sessions, and even different subjects. It is only with the advent of EMG grid surface recordings that multiple MU trains can be recorded simultaneously and a full picture of the behavior of many motoneurons in the pool can be derived. In the same vein, we have not been able to test many alternative force change protocols in experimental studies. In studies using one particular (multi-unit) recording system, the dEMG decomposition system is configured to use slowly rising isometric ramp forces, capped by a sustained plateau. There have not been any other force sequences tested with this system, and limited the use of different protocols using other surface arrays.

In short, it is not yet clear whether there is any degree of choice available to the neuromuscular system. Although a ‘choice’ MU strategy is plausible, it is difficult to see how such a strategy could be implemented practically, since a person will not know a priori what force profile will be needed to accomplish many natural tasks.

Conclusion

Using an MU pool model, we simulated the different firing patterns relative to MU recruitment to assess the influence of firing patterns on the force generation and force variability. The reverse ‘onion skin’ firing pattern can generate higher muscle forces than the ‘onion skin’ firing pattern. This firing organization is beneficial for tasks that are brief and require high force output. The ‘onion skin’ gives rise to more stable forces at moderate muscle contraction levels, and the force variability as a function of force resembles many experimental findings. This firing pattern is beneficial in tasks that involve fine motor control and sustained muscle contractions. Clearly, further experimental studies using the high yield MU recording techniques are necessary to investigate the rate-recruitment organizations in different task protocols using different muscles.

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