



Physiological validation of the decomposition of surface EMG signals

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ABSTRACT

Advances in technology have ushered in a new era in the measurement and interpretation of surface-recorded electromyographic (EMG) signals. These developments have included improvements in detection systems, the algorithms used to decompose the interference signals, and the strategies used to edit the identified waveforms. To evaluate the validity of the results obtained with this new technology, the purpose of this review was to compare the results achieved by decomposing surface-recorded EMG signals into the discharge times of single motor units with what is known about the rate coding characteristics of single motor units based on recordings obtained with intramuscular electrodes. The characteristics compared were peak discharge rate, saturation of discharge rate during submaximal contractions, rate coding during fast contractions, the association between oscillations in force and discharge rate, and adjustments during fatiguing contractions. The comparison indicates that some decomposition methods are able to replicate many of the findings derived from intramuscular recordings, but additional improvements in the methods are required. Critically, more effort needs to be focused on editing the waveforms identified by the decomposition algorithms. With adequate attention to detail, this technology has the potential to augment our knowledge on motor unit physiology and to provide useful approaches that are being translated into clinical practice.

1. Introduction

By virtue of its capacity to transmit an activation signal and transform it into contractile activity, the motor unit is known as the basic functional unit of the neuromuscular system (Lidell and Sherrington, 1925). The force exerted by a muscle during a voluntary action is controlled by varying motor unit recruitment and rate coding (Duchateau and Enoka, 2011; Enoka and Duchateau, 2017). As first demonstrated by Adrian and Bronk (1928), the action potentials discharged by single motor units can be recorded with intramuscular electrodes. Despite the elegance of these methods, however, they provide limited information about activity at the whole-muscle level (Farina and Negro, 2015; Thompson et al., 2018).

Alternatively, multi-unit recordings provide a more global measure of muscle activation, but the signals are difficult to interpret (Blok et al., 2002; Denny-Brown, 1949; Enoka and Duchateau, 2015; Farina et al., 2004; Farina et al., 2014; Merletti et al., 2008). Critically, there is a non-linear relation between the number of muscle fiber action potentials (muscle activation) and the number of motor unit action potentials (neural drive to muscle) (Dideriksen et al., 2011; Martinez-Valdes et al., 2018) due to the exponential distribution of innervation number within a motor unit population (Enoka and Fuglevand, 2000). Moreover,

variation in the size of motor unit action potentials can contribute to differences in EMG amplitude between muscles (Farina et al., 2004). Consequently, adjustments in the amplitude of a multi-unit signal, such as a surface-recorded electromyogram (EMG), are not directly related to changes in the neural drive to muscle (Del Vecchio et al., 2017; Dideriksen et al., 2011; Martinez-Valdes et al., 2018).

One solution to the dilemma between methods that provide too little (single motor unit recordings) and too much (multi-unit recordings) information is to resolve the global measurement into its constituent elements. This can be accomplished with decomposition methods that separate an interference EMG signal—overlapping motor unit action potentials—into the times at which individual motor units discharge action potentials (Merletti et al., 2008). LeFever and De Luca (1982) developed such an approach for signals recorded with intramuscular electrodes and this method has been expanded and adopted by a number of different research groups (McGill et al., 2005; Muceli et al., 2015; Schomacher et al., 2012; Thompson et al., 2018; Vieira et al., 2012). In contrast, there has been much more controversy over the capacity of different approaches to decompose surface-recorded EMG signals into the discharge times of multiple motor units (De Luca et al., 2015; Farina et al., 2015).

From a signal-processing perspective, it is a daunting challenge to

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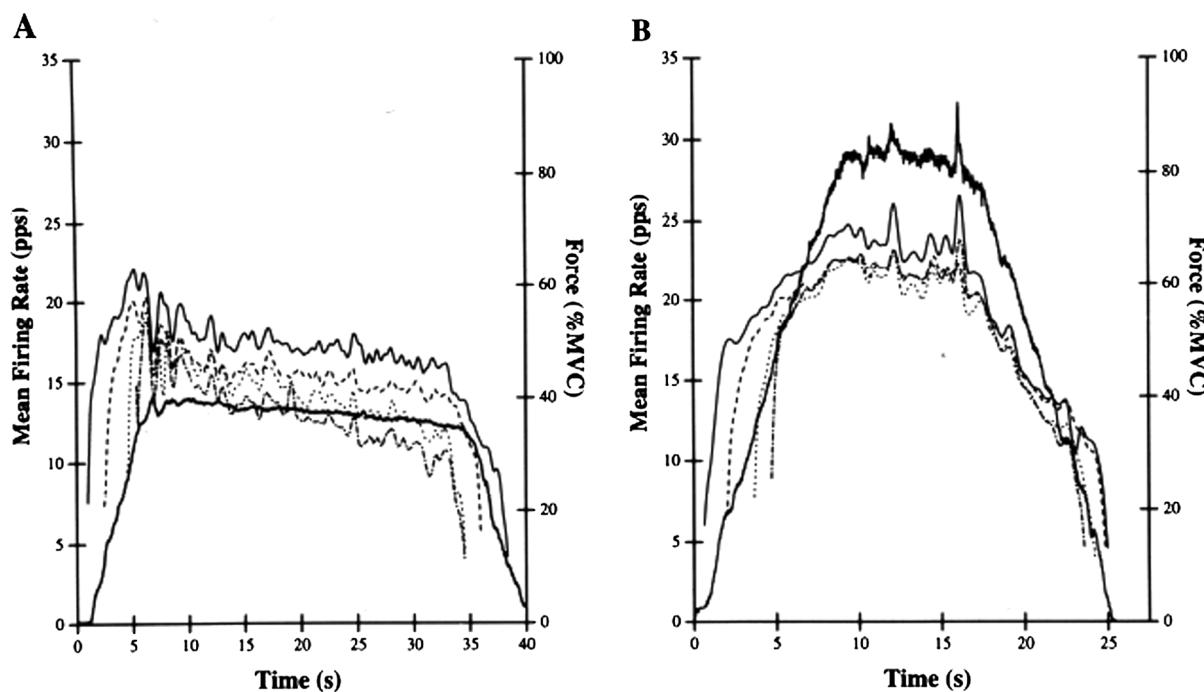


Fig. 1. Mean discharge rate (firing rate) of motor units in tibialis anterior during an isometric contraction in which the net force exerted by the dorsiflexor muscle increased linearly to a target force of either 40% MVC (A) or 80% MVC (B). The thicker solid line represents the applied force and the four other lines each indicate the average discharge rate of single motor units as recorded with an intramuscular electrode. (Reproduced with permission from Erim et al., 1996).

decompose an interference signal that contains hundreds of overlapping motor unit action potentials into the discharge times of single motor units (Blok et al., 2002; Farina et al., 2008; Holobar et al., 2009; Merletti et al., 2008). Once this has been done, however, the key issue is how to validate the results. One approach is to use the two-sensor method in which the discharge times identified by the decomposition of a surface-recorded signal are compared with those detected with an intramuscular electrode (Farina and Enoka, 2011). As an example of this approach, Farina et al. (Farina et al., 2010) compared the discharge times of motor units recorded with surface and intramuscular electrodes in a hand muscle during a low-force isometric contraction. The comparison assessed: (1) sensitivity - the number of discharge times identified in both decomposed signals divided by the number of discharge times detected in the intramuscular recording; and (2) false positives - the number of discharge times found in the surface recording but not in the intramuscular recording divided by the total number of discharge times detected in the intramuscular recording. The data for four motor units shown in their Fig. 5 indicate that sensitivity ranged from 92% to 100% and the number of false positives ranged from 4% to 11% for this specific protocol.

The findings reported by Farina et al. (2010) demonstrate that it is possible to decompose surface-recorded EMG signals into the discharge times of single motor units provided the shapes and locations of the action potentials are sufficiently unique (Farina et al., 2008; Holobar et al., 2009). However, the question remains as to how well these results generalize to other experimental conditions and decomposition approaches? To address this question, the purpose of my review is to compare the results achieved by decomposing surface-recorded EMG signals into the discharge times of single motor units with what is known about the rate-coding characteristics of single motor units based on recordings obtained with intramuscular electrodes. The characteristics compared are peak discharge rate, saturation of discharge rate during submaximal contractions, rate coding during fast contractions, the association between oscillations in force and discharge rate, and adjustments during fatiguing contractions.

The comparison focuses on those decomposition studies that have been able to replicate the findings on single motor unit activity

recorded with intramuscular electrodes. The comparison has two limitations, however: (1) it presumes that our current knowledge on motor unit physiology (Duchateau and Enoka, 2011; Heckman and Enoka, 2012) as derived from single motor unit recordings is correct; and (2) the results produced by the two approaches can only be compared when similar experimental protocols were used.

2. Peak discharge rate

In a seminal study on the modulation of discharge rate during force-varying isometric contractions, Person and Kudina (1972) recorded the discharge rate of motor units in rectus femoris while subjects linearly increased the net force exerted by the knee extensor muscles to a submaximal target force (~40% of maximal voluntary contraction [MVC] force) and then linearly decreased it back to zero. They found that the peak discharge rate achieved by the motor unit with the lowest recruitment threshold was greater than that for later recruited motor units. Subsequent studies have found that this association is stronger in some muscles (e.g., first dorsal interosseous) than in other muscles (e.g., deltoid and tibialis anterior) (De Luca et al., 1982; Duchateau and Hainaut, 1990; Van Cutsem et al., 1997). This behavior was subsequently referred to as the “onion-skin phenomenon” (De Luca and Erim, 1994).

Although others have also reported a similar distribution of peak discharge rates during these types of contractions (Carpentier et al., 2001; Masakado et al., 1995; Westgaard and De Luca, 2001), the evidence suggests that the inverse association between recruitment-threshold force and peak discharge rate is not observed during stronger contractions. For example, when Erim et al. (1996) recorded the discharge rate of single motor units in tibialis anterior with a 4-channel intramuscular electrode (quadrifilar needle) during linear increases and decreases in the net force (10 MVC/s) exerted by the dorsiflexors during an isometric contraction, they found that “...the firing rates of motor units converged to the same maximal value as the targeted force level reached the maximal voluntary contraction level.” (Fig. 1). Similarly, Oya et al. (2009) found that the peak discharge rates for motor units in soleus when recorded with an intramuscular electrode during a linear

increase in net plantar flexor force up to 100% MVC were greatest for later recruited motor units (see their Fig. 3).

The results are mixed on the capacity of decomposition approaches to reduce surface-recorded EMG signals into profiles that match the rate-coding behavior shown in Fig. 1B. An example of a successful approach comes from the work of Del Vecchio et al. (2017). The surface EMG signals were detected with a grid of 64 electrodes that were arranged in 5 columns and 13 rows. Each of the gold-coated electrodes was 1 mm in diameter with 8 mm between adjacent electrodes. The signals recorded with the grid electrodes—known as high-density EMG recordings (Blok et al., 2002)—were decomposed into the action potentials of single motor units with the method of convulsive blind source separation (Negro et al., 2016). Briefly, this method uses the sparseness of the discharge times (usually < 50 pps) relative to the sampling rate (~2 kHz) to identify a set of filters (action potential shapes) that can distinguish between different motor units. Decomposition accuracy is assessed with a silhouette measurement that quantifies the amplitude of the deconvolved motor unit spikes relative to the background noise; the threshold for acceptance of a waveform as a motor unit action potential is often set at a silhouette value of > 0.9 (Negro et al., 2016). Instantaneous discharge rate is calculated as the reciprocal of the time between consecutive action potentials and then low-pass filtered with a first-order Butterworth filter and a cut-off frequency set at 0.5 Hz.

Fig. 2 shows the instantaneous discharge rate (upper panel) for the

first and last three recruited motor units in tibialis anterior during gradual (5% MVC/s) increases and decreases in the net force exerted by the dorsiflexors during an isometric contraction. The target force was 70% MVC. The bottom panel in Fig. 2 shows the average discharge rates for the 28 motor units that were identified during the contraction. The left-most end of each colored line denotes the moment in time when the motor unit began discharging action potentials; that is, the recruitment threshold of the motor unit. The brown and red lines represent motor units with relatively low recruitment thresholds, whereas the blue lines correspond to motor units with higher recruitment thresholds. The oscillations in average discharge rate are similar to those observed for motor units in medial gastrocnemius discriminated from an intramuscular recording with fine-wire electrodes (see Fig. 7 in McGill et al. (2005)). The key feature of the figure is that there was less of a difference in the average discharge rates for low- and high-threshold motor units during the force plateau (70% MVC), as observed with intramuscular recordings (Fig. 1B).

Although not evident in Fig. 2, the decomposition method used by Del Vecchio et al. (2017) was also able to discriminate the discharge times of single motor in the tibialis anterior muscle of all 13 subjects over the full range of the ramp contraction (see Fig. 2 in Del Vecchio et al., 2017). Notably, the recruitment thresholds of some motor units in all subjects were close to the minimal recorded force, which contrasts with the results found in other studies that have used different approaches to decompose surface-EMG signals (De Luca and Contessa,

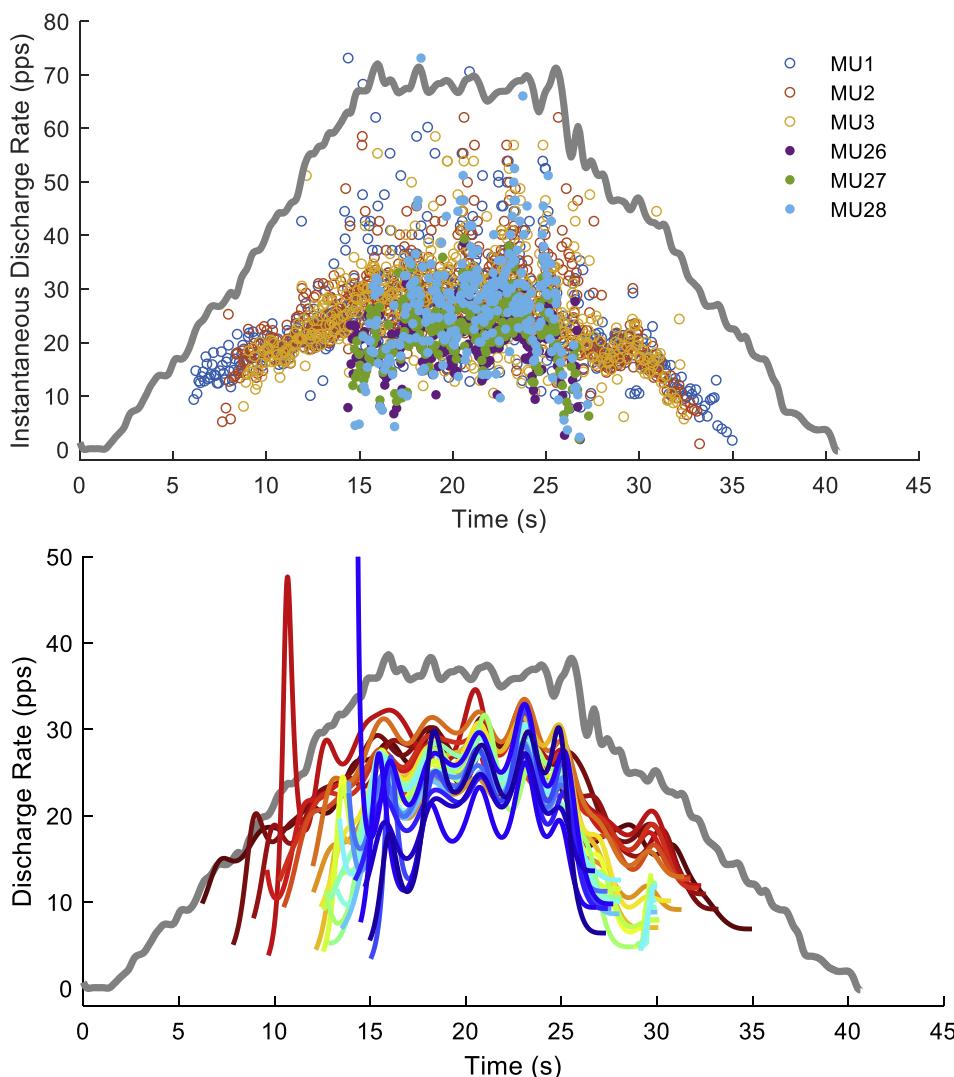


Fig. 2. Modulation of discharge rate by 28 motor units in tibialis anterior during gradual increases and decreases in the net force (5% MVC/s) exerted by the dorsiflexor muscles during an isometric contraction (Del Vecchio et al., 2018, in press). The upper panel indicates the instantaneous discharge rate for the first three (open circles) and last three (filled circles) motor units detected in the high-density EMG recordings during this task. The bottom panel shows the average discharge rate for the 28 motor units, which was obtained by filtering the instantaneous rates with a low-pass filter that had a cut-off frequency of 0.5 Hz. Unpublished data provided by Alessandro Del Vecchio, Ph.D.

2012; Miller et al., 2018; Sterczala et al., 2018).

Moreover, the average discharge rates of the motor units discriminated by Del Vecchio et al. (2017) extended over a similar range from minimal values at recruitment (~ 5 pps) up to peak values of 30 pps during the plateau phase of the task (Fig. 2) as found in recordings obtained with intramuscular electrodes for 83 motor units in tibialis anterior during isometric ramp contractions (minimum: 8.4 ± 3.0 pps; peak: 33.2 ± 14.7 pps (Van Cutsem et al., 1997). Similarly, the initial discharge rate at recruitment of the motor units shown in Fig. 2 does not appear to vary with recruitment threshold, which is consistent with the results of Van Cutsem et al. (1997) but contrasts with the results reported in other decomposition studies (De Luca and Contessa, 2012; Trevino et al., 2016). Thus, these results demonstrate that the decomposition approach used by Del Vecchio et al. (2017) was able to replicate the range of rate coding and recruitment thresholds observed in intramuscular recordings during moderately strong ramp isometric contractions with leg muscles.

3. Saturation of discharge rate during slow increases in muscle force

In some instances, such as slow increases in muscle force, low-threshold motor units fail to increase discharge rate during progressive increases in net excitatory input onto the motor neurons; that is, the action-potential generating processes become saturated (Baldissara et al., 1984; Cushing et al., 2005; Powers et al., 2005; Powers et al., 2012). Gydkov and Kosarow (1974) were among the first to report this phenomenon when they found that some motor units in biceps brachii continued to increase discharge rate with progressive increases in contraction strength, whereas other motor units did not (their Fig. 4). They found that saturation of discharge rate was more prominent among low-threshold motor units. Subsequently, Duchateau and Hainaut (1990) reported that saturation appears to be an adaptable property as it was observed to increase in hand muscles after several weeks of limb immobilization.

Discharge-rate saturation has been characterized most thoroughly by Fuglevand et al. (2015) during slow ramp isometric contractions. Fig. 3 shows an example of discharge-rate saturation; the identified motor unit in biceps brachii achieved a peak discharge rate of 15 pps

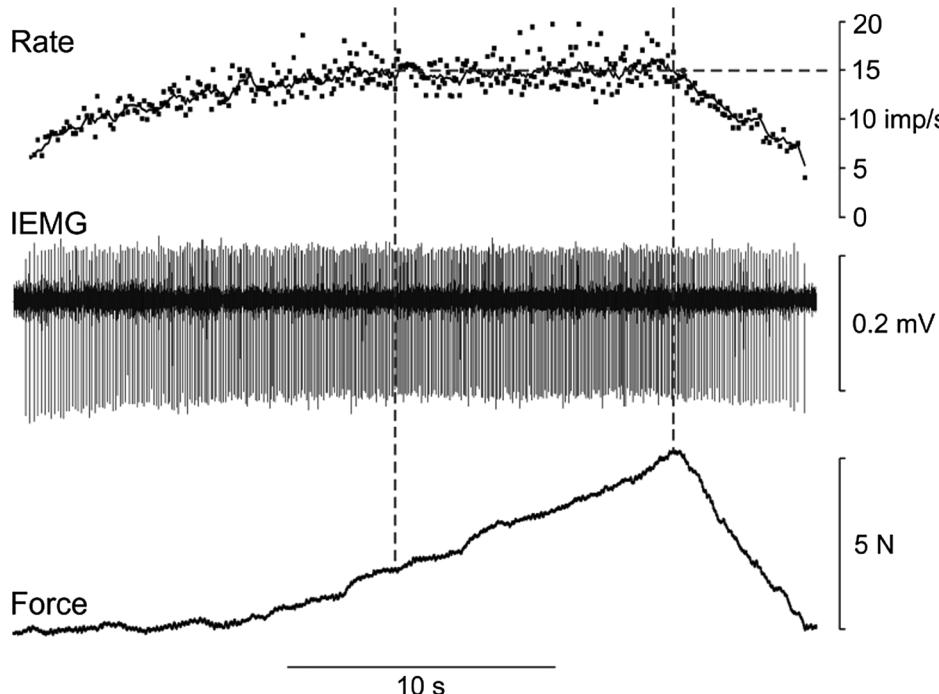


Fig. 3. The train of action potentials and associated instantaneous discharge rate (imp/s) of a single motor unit in biceps brachii recorded with an intramuscular fine-wire electrode during a slow increase in the force exerted by the elbow flexors during an isometric contraction. The motor unit had a low recruitment threshold and the peak force was $\sim 5\%$ MVC. (Reproduced with permission from Fuglevand et al., 2015).

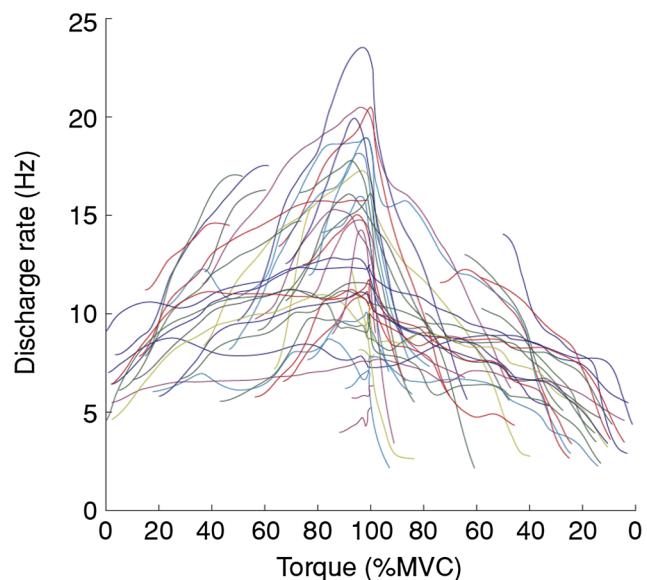


Fig. 4. Average discharge rate (low-pass filtered at 0.5 Hz) for 42 motor units in soleus from four different subjects during a ramp isometric contraction up to 100% MVC force with the plantar flexor muscles. Each motor unit is indicated by a different color line. The recruitment range of the motor units went from 0.2% to 96.4% of MVC force. (Reproduced with permission from Oya et al., 2009).

that then remained constant while the net elbow-flexor force continued to increase. The saturation of instantaneous discharge rate was characterized for each motor unit with a rising-exponential function ($1 - e^{-f/\tau_{\text{au}}}$) relative to the applied force. They recorded the discharge rate of 136 motor units during the slow ramp contractions ($0.40 \pm 0.36\%$ MVC/s) and found that the rate coding for 90% of them ($n = 123$) was best fit with an exponential function, whereas a linear function was better for 10 of them (see their Fig. 3). Average recruitment threshold for the 136 motor units was $2.1 \pm 2.2\%$ MVC force with initial discharge rates of 6.7 ± 2.3 pps. Steady-state discharge rate for the units that exhibited saturation was 14.8 ± 2.0 pps, which enabled these motor units to generate $\sim 63\%$ of their maximal force.

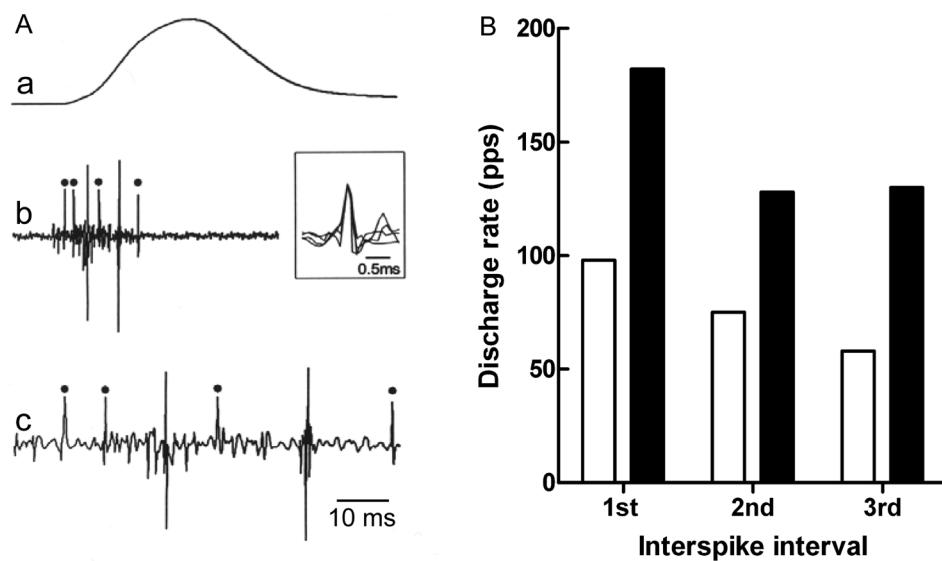


Fig. 5. Discharge rates for motor units in tibialis anterior during ballistic contractions performed with the dorsiflexor muscles. (A) Action potentials discharged by a single motor unit during a ballistic contraction performed before the training program. The peak force during the ballistic contraction was ~40% MVC force. Traces indicate dorsiflexor force (a) and action potentials detected by an intramuscular electrode at slow (b) and fast (c) display speeds. As indicated in trace c, there was a progressive increase in the duration of the interspike interval between the first four action potentials. The dots indicate action potentials from the same motor unit, as shown by the superimposed waveforms to the right of trace b. (B). Average instantaneous discharge rates for the first three interspike intervals before (white bars) and after (black bars) 12 weeks of training with dynamic contractions. Data from Van Cutsem et al. (1998).

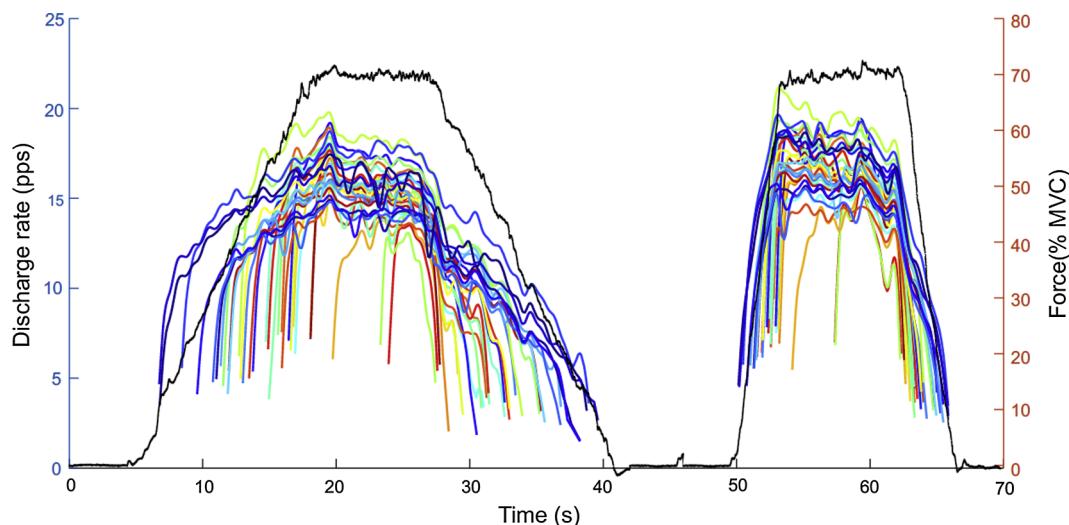


Fig. 6. Rate coding by multiple motor units in tibialis anterior during two isometric contractions performed with the dorsiflexor muscles. The target force was 70% MVC for both contractions, but the rate of increase in force was 5% MVC/s for the contraction on the left and 20% MVC/s for the one on the right. Each colored line represents the average discharge rate for a single motor unit as derived from high-density recordings of surface EMG. The grid electrodes comprised 5 rows by 13 columns of electrodes that were each 1 mm in diameter with 5 mm between electrodes. (Data provided by Negro et al. (2018), Psek and Cafarelli (1993)).

Saturation of discharge rate can also be observed during ramp contractions performed at more typical speeds (10% MVC force/s). Fig. 4 shows the low-pass filtered (0.5 Hz) discharge rates of 42 motor units in soleus when four subjects performed ramp isometric contractions with the plantar flexor muscles (Oya et al., 2009). The average rate of change in force was $9.7 \pm 0.7\%$ MVC/s during the ramp-up phase and $9.8 \pm 0.3\%$ MVC/s during the ramp-down phase. The motor unit signals were recorded with a fine-wire electrode (Enoka et al., 1988) that was inserted into the muscle. A key feature of these data is the saturation of discharge rate for many of the low-threshold motor units despite the progressive increase in synaptic input to the motor neuron pool to achieve the maximal force.

Although Fuglevand et al. (2015) suggested that the saturation phenomenon should be studied with methods that decompose surface EMG recordings due to the limitations of their intramuscular recordings, this remains to be done with the protocol used by Fuglevand and colleagues (very slow increases in muscle force). However, even in decomposition studies that produce results similar to those obtained with intramuscular electrodes and with rates of increase in force (5% MVC/s) similar to that used by Oya et al. (2009), there is no evidence of

saturation in discharge rate for low-threshold motor units (Fig. 2). Decomposition methods can clearly detect the discharge times of low-threshold motor units (Del Vecchio et al., 2017), but no study has yet been able to reproduce the findings shown in either Fig. 3 or Fig. 4. Such a study would add to the weight of evidence underscoring the validity of the methodology.

4. Rate coding during rapid submaximal contractions

Intramuscular recordings have consistently found that the rate of increase in force during a submaximal voluntary contraction depends on the rate at which the activated motor units discharge action potentials (Bawa and Galancie, 1983; Büdingen and Freund, 1976; Desmedt and Godaux, 1977; Freund et al., 1975; Klass et al., 2008; Tanji and Kato, 1973; Van Cutsem and Duchateau, 2005). In a seminal study of this effect, Duchateau and colleagues compared the association between the discharge rates of motor units in tibialis anterior and rate of torque development during submaximal ballistic contractions with the dorsiflexor muscles before and after 12 weeks of dynamic training (Van Cutsem et al., 1998). A ballistic contraction involves a rapid

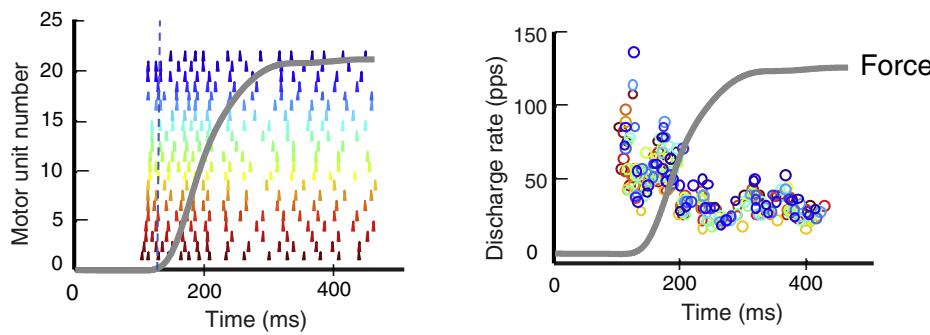


Fig. 7. Instantaneous discharge rate for 21 motor units in tibialis anterior during a rapid isometric contraction with the dorsiflexor muscles to a target force $\geq 80\%$ MVC. The applied force is indicated with a grey line. The discharge times of the motor units were obtained from high-density EMG recordings. Each motor unit is indicated by a unique color, with discharge times on the left and instantaneous discharge rates on the right. (Data provided by Del Vecchio et al., in press).

contraction followed by an immediate relaxation to produce a parabolic torque trajectory. The rate of torque development, which is measured as the average slope of the increase in torque, is greater during a

ballistic contraction than during a rapid contraction to reach and match a prescribed target force.

The training protocol used by Van Cutsem et al. (1998) increased MVC torque by 30% and the associated EMG amplitude by 19%, but there were no changes in the contractile properties of the twitch response evoked by electrical stimulation of the peripheral nerve. The mean rate of torque development during the five fastest ballistic contractions for each subject increased by 82% after training. The discharge rates of 475 motor units during the ballistic contractions were compared with 633 motor units after training. The representative data shown in Fig. 5 indicate that the identified motor units often discharged ~ 4 action potentials at the onset of each ballistic contraction. One of the main findings of this study was that the progressive increase in the time between successive action potentials observed before training (trace c in Fig. 5A) was reduced after training, which represented in an increase in discharge rate (Fig. 5B). On average, mean discharge for the first three interspike intervals was 75 ± 5 pps before training and 104 ± 10 pps after training. In addition, the proportion of motor units exhibiting double discharges (≤ 5 ms between action potentials) increased from 5.2% before training to 32.7% after training. These findings indicate that the increase in the rate of torque development during ballistic contractions after dynamic training was accompanied by a marked increase in instantaneous discharge rate.

Two decomposition studies have been able to replicate these results on the association between rate coding and rate of force development. Both studies used grid electrodes placed over tibialis anterior, convolutive blind-source separation to decompose the interference signals, and intensive manual editing of the identified spike trains. Representative findings from one study (Negro et al., 2018) are shown in Fig. 6. Subjects performed ramp contractions (linear increase in force) at two different speeds (5% MVC/s and 20% MVC/s) to submaximal target forces. Each target force was sustained for ten seconds and then the force was decreased linearly back to zero at the prescribed rate. As usually observed with intramuscular recordings—but not always (Fuglevand et al., 2015; Kiehn and Eken, 1997; Mottram et al., 2009; Oya et al., 2009)—when force increases continuously (Fig. 1), average discharge rate of the identified motor units increased at variable rates up to the target force (Fig. 6). The rate of increase in discharge rate was high initially and then declined, especially for the slower contraction (left panel in Fig. 6). Conversely, a similar adjustment was observed in the intramuscular recordings during the strong contraction (Fig. 1B), but not during the weaker contraction (Fig. 1A). Also note that the peak discharge rates in Fig. 6 were greatest for motor units recruited at intermediate forces during both contractions.

In the other study, Del Vecchio et al. (in press) quantified rate coding when subjects performed strong isometric contractions with the dorsiflexor muscles as fast as possible and then sustained the target force for several seconds. Fig. 7 shows the discharge times and instantaneous discharge rates for 21 motor units in tibialis anterior during a rapid contraction. Subjects performed several trials of the rapid contraction to assess reliability and the action potentials of each motor unit were manually edited with a tool developed by Holobar and Zazula

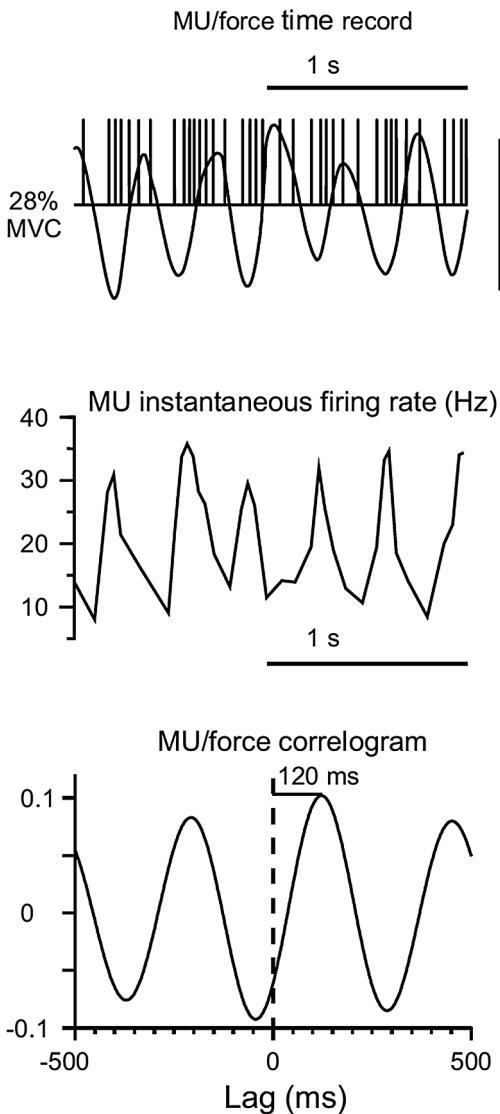


Fig. 8. Modulation of the discharge times recorded with an intramuscular electrode for a single motor unit in first dorsal interosseous that contributed to the controlled oscillation ($\pm 9\%$ MVC force) of the applied force about an average submaximal target force (28% MVC) during an isometric contraction. The discharge times, which are indicated as spikes in the upper panel, were converted into instantaneous discharge rate (middle panel) and compared in a cross-correlogram with the oscillations in force (bottom panel). The cross-correlogram indicates that the oscillations in force lagged those in discharge rate by 120 ms. (Reproduced with permission from Erimaki et al., 2013).

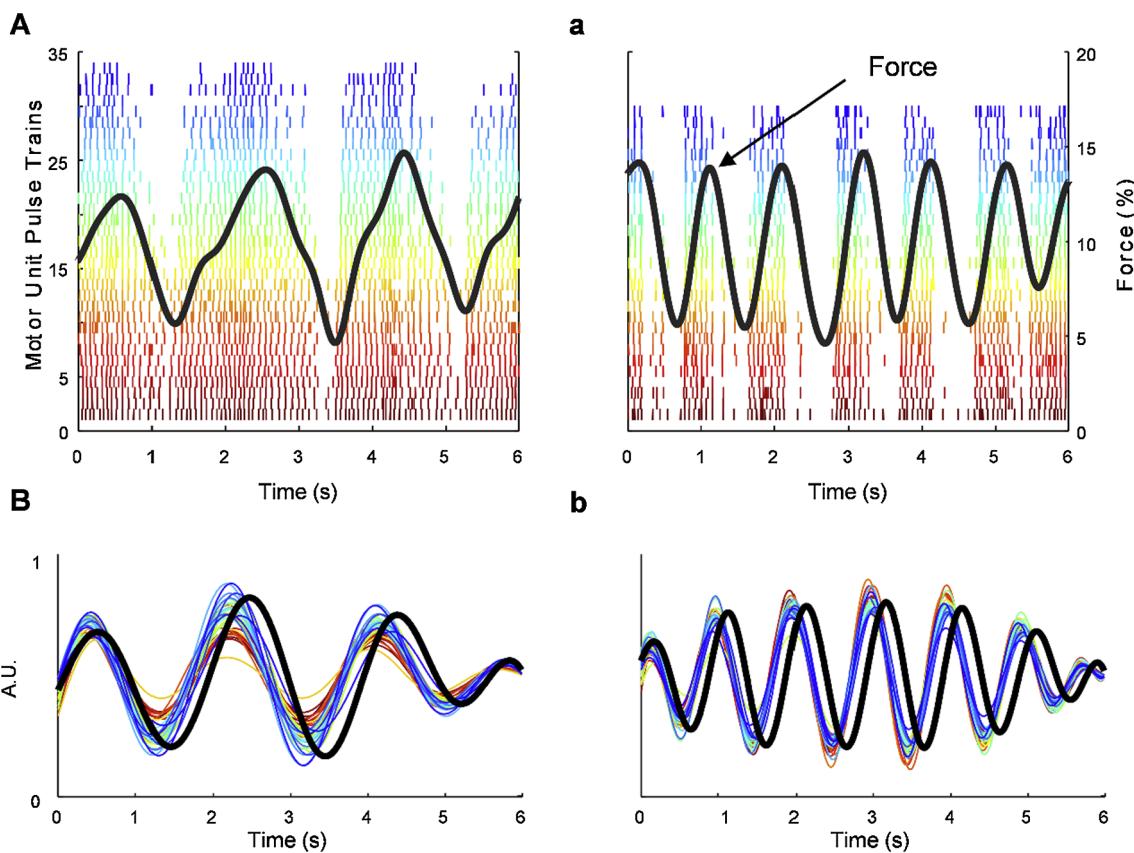


Fig. 9. Modulation of discharge times for motor units in tibialis anterior during two force-tracking tasks. In both tasks, the subject was asked to oscillate the force (black line) exerted during the isometric contraction at one of two rates (0.5 Hz or 1 Hz) with a peak-to-peak amplitude of 5% MVC force. The upper row indicates the discharge times for the identified motor units; each motor unit is indicated by a different color. The bottom row compares the fluctuations in the low-pass filtered (2 Hz) discharge rates of each motor unit relative to that for force. (Reproduced with permission from Del Vecchio et al. (2018).

(2007). The key finding of the study was the demonstration that the decomposition approach was able to replicate the high discharge rates observed in intramuscular recordings of single motor units during ballistic contractions (Fig. 5).

5. Force oscillations

Classic studies on motor unit physiology have demonstrated that a single action potential will elicit a unitary contractile event—the twitch—and that many motor unit action potentials will produce spatial and temporal summation of the associated twitch responses (Burke et al., 1976; Milner-Brown et al., 1973; Powers and Binder, 1991). Conversely, a variable force profile produced by an activated muscle must be preceded by the appropriate modulation of motor unit discharge rates (Freund et al., 1975; Knight and Kamen, 2004; Martinez-Valdes et al., 2016; Person and Kudina, 1972; Sosnoff et al., 2005; van Bolhuis et al., 1997; Vieira et al., 2011). An example of the expected association is shown in Fig. 8. In this experiment, Erimaki et al. (2013) had participants modulate the force ($\pm 9\%$ MVC at 3 Hz) exerted by first dorsal interosseus about an average value of 28% MVC force during an isometric contraction (top panel in Fig. 8). The times at which an isolated motor unit discharged action potentials was detected with an intramuscular electrode and the instantaneous discharge rate was calculated (middle panel in Fig. 8). A cross-correlation between discharge rate and force indicated that the fluctuations in discharge rate preceded those in force by 120 ms (bottom panel in Fig. 8).

One decomposition study has been able to detect the expected modulation of motor unit discharge rate that produces oscillations in the net muscle force (Del Vecchio et al., 2018). The approach involved grid electrodes that were placed over tibialis anterior during isometric

contractions in which participants were asked to match an oscillating target force. The 64 monopolar signals were converted to 59 bipolar signals that were decomposed into motor unit discharge times with the convolutive blind-source separation algorithm. The output was examined to exclude waveforms with a pulse-to-noise ratio of < 30 dB or discharge times separated by more than 2 s. The purpose of the study was to measure the latency between an estimate of the neural drive to muscle and the force generated by the muscle. A central feature of the protocol was to match a target force that oscillated at one of three frequencies and one of three peak-to-peak amplitudes. Fig. 9 shows data obtained during two of these trials. The discharge times of each identified motor unit were converted to discharge rate and low-pass filtered (2 Hz) so that they could be compared with the oscillations in force. The lower row in Fig. 9 shows the strong correlation between the fluctuations in discharge rate for all motor units and the force exerted by the dorsiflexor muscles. As observed in intramuscular recordings (Fig. 8), all motor units in tibialis anterior exhibited the expected oscillations in discharge rate preceding the fluctuations in force. Moreover, the delay between the neural drive and muscle force decreased as the frequency of the oscillations (rate of force generation) increased. These findings demonstrate that at least one decomposition approach can detect the motor unit activity underlying intended force oscillations (Del Vecchio et al., 2018), but another approach failed to replicate this finding (De Luca et al., 2014).

6. Fatiguing contractions

One of the key themes in the substantial literature on fatiguing contractions is that the adjustments in motor unit activity vary with the details of the task being performed (Enoka and Stuart, 1992). In this

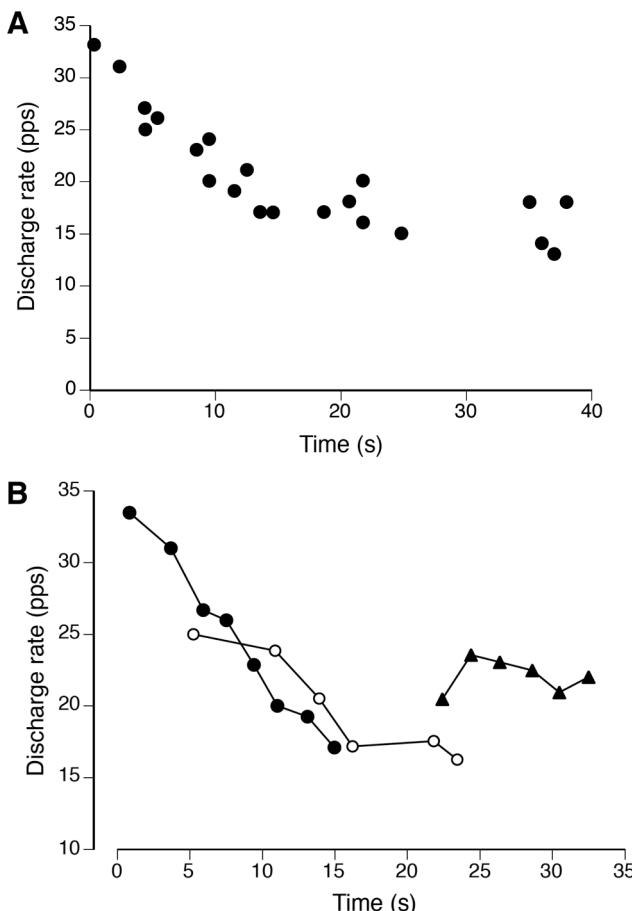


Fig. 10. Decline in discharge rates of motor units in adductor pollicis as measured with an intramuscular electrode during a sustained MVC. The upper panel shows the average discharge rate for 21 motor units at different times during a 40-s MVC. The lower panel shows the discharge rate for three single motor units; two were recruited early in the MVC (filled and open circles) and the third was recruited later (filled triangle). (Reproduced with permission from Bigland-Ritchie et al., 1983).

section of the review, the diversity of these adjustments is characterized by describing the results obtained with several different protocols and comparing the results obtained with intramuscular electrodes to those derived from decomposition of surface-EMG recordings.

6.1. Intramuscular recordings

In an early study of motor unit activity during a sustained contraction, Bigland-Ritchie et al. (1983) inserted a tungsten microelectrode (0.2 mm diameter with a recording surface at the tip of 10–15 μm) into adductor pollicis to record trains of action potentials discharged by motor units during an MVC that lasted 40–120 s. They were not able to track most single motor units during the fatiguing contraction, but rather calculated average discharge rates at various times during the contraction. Average discharge rate began at 27 pps and declined to 15 pps at 60 s. Fig. 10A shows the average discharge rates for 21 motor units in a single subject measured at different times during a 40-s MVC. A similar trend was observed in all five subjects. However, they were able to track a few motor units for brief periods of time and in Fig. 10B show that the adjustments in the discharge rates of three single motor units during the sustained MVC was similar to that observed in the group measurement (Fig. 10A). Similar findings were reported by De Luca et al. (1996) when they tracked four motor units in first dorsal interosseous with a needle electrode during brief (15–20 s) isometric contractions at 50% and 75% MVC force (see their Fig. 5).

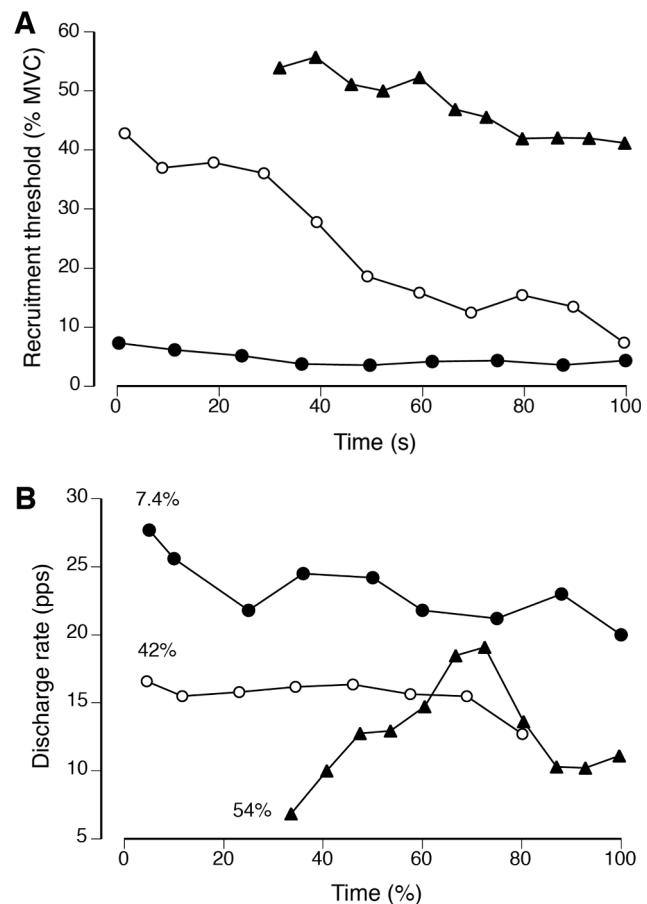


Fig. 11. Adjustments in the activity of motor units in first dorsal interosseus during a series of intermittent isometric contractions performed to task failure. Each contraction involved a gradual increase in force (16.7% MVC/s) to match the target force (50% MVC) and then a gradual decrease in force (–16.7% MVC/s). There was a 4-s rest period between each contraction. The data show the changes in recruitment threshold (top panel) and average discharge rate during the plateau phase of the contraction (bottom panel) for three motor units (each motor unit is represented by a unique symbol). The recruitment threshold force of each motor unit is indicated in the bottom panel. The motor unit indicated with the open circle stopped discharging action potentials during the force plateau, but was active during the ramp-up phase. (Reproduced with permission from Carpentier et al., 2001).

Carpentier et al. (2001) observed different adjustments in the discharge rate of single motor units when subjects performed a series in intermittent isometric contractions with the first dorsal interosseus muscle. The task comprised ramp-and-hold contractions to a target force of 50% MVC. The ramp-up and ramp-down phases of each contraction were performed in 3 s and the plateau was sustained for 10 s with a 4-s rest before the next contraction. The average time to failure was 6.4 ± 3.6 min and was accompanied by a continuous increase in the amplitude of the surface-recorded EMG signal. Multi-unit recordings were obtained with fine-wire electrodes inserted into the muscle. The signals were decomposed into single motor unit activity with a template-matching algorithm.

The recruitment thresholds of the 67 motor units ranged from 0.5 to 55.2% MVC force ($26.2 \pm 2.0\%$ MVC force). Recruitment threshold declined by an average of $9.6 \pm 1.3\%$ MVC force at task failure, but some low-threshold units exhibited a small, but statistically significant, increase in recruitment threshold. As indicated in Fig. 11A, the decline in recruitment threshold was greatest for high-threshold motor units that were active from the beginning of the fatiguing contraction. A reduction in recruitment threshold indicates that the force contributed by earlier-recruited motor units had declined, either due to a slowing of

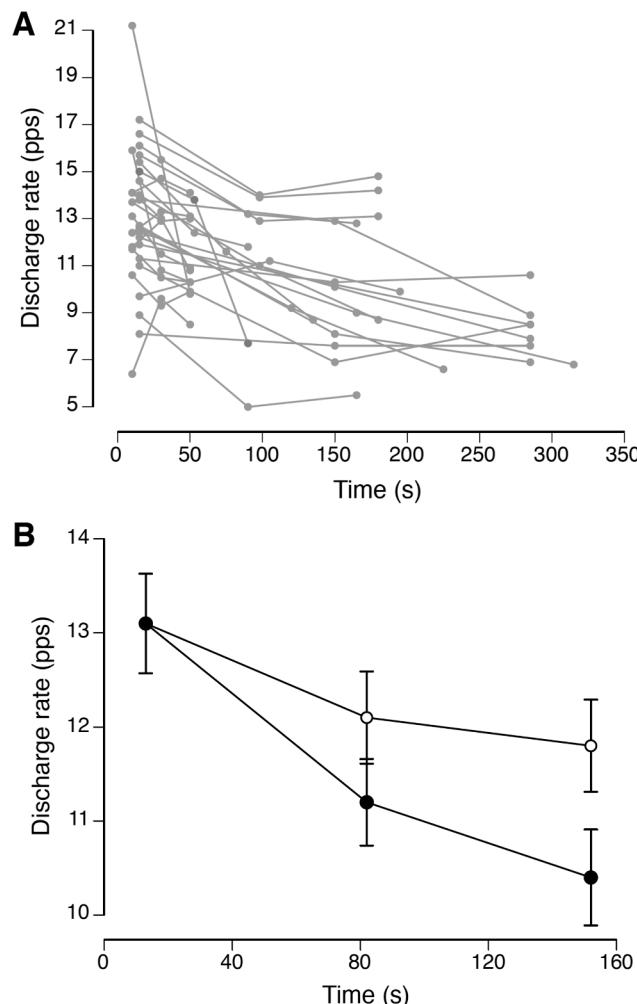


Fig. 12. Adjustments in the discharge rates of motor units in biceps brachii during two types of fatiguing contractions. (A) average discharge rate for 30 motor units at the start, middle, and end of the fatiguing contraction. (B) Mean \pm SD of average discharge rate of the same motor units during the force (open circles) and position (filled circles) tasks. Data from Mottram et al. (2005).

discharge rate or a decrease in the force capacity of the associated muscle fibers. Fig. 11B also indicates the adjustments in discharge rate for three motor units; in general, discharge rate declined for motor units that were active from the beginning of the task, but first increased and then decreased for the motor unit that was recruited during the fatiguing contraction. Similar adjustments in the activity of motor units in biceps brachii were observed when the elbow flexors also performed a series of intermittent isometric contractions (Christova and Kossev, 1998).

Consistent with the finding of an average increase in the recruitment threshold of low-threshold motor units ($< 25\%$ MVC force; $n = 39$), Carpentier et al. (2001) found that the peak spike-triggered average force of these units increased by $\sim 33\%$ (8 mN). In contrast, the peak spike-triggered average force for motor units with recruitment thresholds in the range of 25–50% MVC force ($n = 17$) decreased by $\sim 44\%$ (25 mN). In parallel, average discharge rate during the plateau phase decreased by $\sim 25\%$ (6.1 pps) for the low-threshold motor units ($n = 16$) and by $\sim 14\%$ (2.6 pps) for the motor units ($n = 15$) with thresholds in the upper half of the recruitment range (25–50% MVC force). These adjustments in motor unit activity were accompanied by a continuous increase (32%) in the amplitude of the surface-recorded EMG signal for first dorsal interosseus.

Person and Kudina (1972) observed similar reductions in discharge rate and the recruitment of additional motor units in rectus femoris during a sustained isometric with the knee extensors. The target force was 18% MVC. Most of the 32 motor units active from the beginning of the fatiguing contraction had an initial discharge rate of 11–19 pps that decreased at 25–40 s into the contraction to a rate of < 13 pps. The observed depression of discharge rate, however, could be overcome by a transient increase in the force exerted by the knee extensors during the voluntary contraction (their Fig. 4). Similar reductions in the discharge rates of motor units were observed in vastus lateralis and vastus medialis by Vila-Chá et al. (2012) when the knee extensors sustained isometric contractions at either 10% or 30% MVC force to failure and in deltoid by De Luca et al. (1982) when the muscle sustained an isometric contraction at 30% MVC force for 30 s.

Due to the challenge of tracking single motor units during fatiguing contractions with intramuscular electrodes, some groups have measured the adjustments in discharge characteristics during submaximal isometric contractions in which the target force was set at $\sim 3\text{--}5\%$ MVC force above the recruitment threshold of an isolated motor unit. In addition to optimizing motor-unit discrimination, this approach enables the assessment of rate coding on the steep section of the force-frequency relation (Macefield et al., 1996). Garland et al. (1994) used this approach to record the activity of single motor units in biceps brachii with fine-wire electrodes during sustained isometric contractions performed with the elbow flexors; the target force set at $6.9 \pm 6.4\%$ MVC force above the recruitment threshold force for each motor unit. Average target force was $26 \pm 12\%$ MVC force and time to task failure was 8.8 ± 7.5 min. They were able to track 45 motor units over variable intervals during the fatiguing contraction and found that discharge rate decreased with varying trajectories for 32 motor units, did not change for 7 motor units, and increased for 6 motor units. Those motor units with higher initial discharge rates experienced greater reductions in discharge rate ($r = 0.53$, $P = 0.0002$). The progressive increase in EMG amplitude for both biceps brachii and brachioradialis during the fatiguing contraction indicates that discharge rate declined for most motor units despite a continuous increase in the net excitatory input received by the motor neuron pool.

Mottram et al. (2005) used a similar protocol to compare the influence of load type on the adjustments in motor unit activity. Subjects performed sustained isometric contractions with the elbow flexor muscles while either pulling up against a rigid restraint (force task) or supporting an inertial load (position task). Subjects were required to match the target force during the force task and to maintain a constant elbow-joint angle during the position task. When the net elbow flexor torque was matched across tasks for each subject, time to task failure was briefer for the position task (Hunter et al., 2002; Maluf et al., 2005), but does appear to depend on limb posture (Rudroff et al., 2010). Average target force used by Mottram and colleagues was $3.5 \pm 21\%$ MVC force above the recruitment threshold force, which corresponded to an average value of $22 \pm 13\%$ MVC force (range: 3–49% MVC force). Each subject performed the two tasks for the same duration (161 ± 96 s; range: 45–330 s) so that the same motor unit could be tracked during both tasks (see their Fig. 1).

Similar to the preceding studies on intramuscular recordings of single motor units, the average discharge rate of most motor units declined during the two tasks but there were some motor units for which there was no change and a few that increased discharge rate. The adjustments in discharge rate of 30 motor units during the position task are shown in Fig. 12A. Despite similar elbow flexor torques and task durations, the average decline in discharge rate for the same motor units was greater during the position task than the force task (Fig. 12B). To maintain the force, therefore, the number of newly recruited motor units was greater ($P = 0.01$) during the position task (1.4 ± 0.8 per trial) than the force task (1.0 ± 0.7 per trial) so that there was a progressive and similar increase in EMG amplitude for biceps brachii and brachialis during the two tasks. Also, the coefficient of variation for

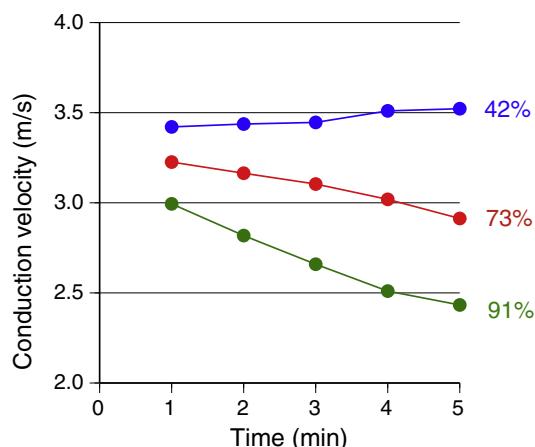


Fig. 13. Change in conduction velocity of motor unit action potentials in abductor pollicis brevis during a 5-min protocol that involved 25 ramp-up and ramp-down isometric contractions. Each line indicates the data for a single motor unit with the values at the right of each line denoting the percentage of time during the first contraction that the motor discharged action potentials. The greater the reduction in conduction velocity, the more metabolically active were the associated muscle fibers during the fatiguing contraction. (Reproduced with permission from Farina et al., 2009).

interspike interval increased during the position task ($\% \Delta 74 \pm 126$) but not during the force task ($\% \Delta -2 \pm 47$), suggesting a greater relative increase in synaptic noise during the position task (Matthews, 1999). The greater adjustments in motor unit activity during the position task were also associated with more substantial reductions in recruitment threshold than during the force task (Baudry et al., 2009).

Taken together, the preceding studies on intramuscular recordings of motor-unit activity during fatiguing contractions generally indicate that discharge rate declined for most units that were active from the beginning of the task and discharging at slightly above recruitment threshold. However, discharge rate did not change for some motor units and it increased for others. When the task involved maintaining a constant submaximal output, such as force, joint angle, or angular velocity, the decrease in discharge rate necessitated the recruitment of additional motor units that increased discharge rate initially before an eventual decline. Nonetheless, the amplitude of surface-recorded EMG signals increased continuously throughout the contraction denoting a progressive increase in the net excitatory synaptic input to the motor neuron pool. Also, the recruitment threshold force of most motor units—except those with the lowest thresholds—decreased during the fatiguing contraction due to the reduction in force capacity of the earlier recruited motor units. What is missing from many of these studies, however, is information about the concurrent adjustments in the discharge activity of multiple motor units, which could be provided by accurate decomposition of surface-recorded EMG signals.

6.2. Decomposition of surface EMG signals

As with the other rate-coding characteristics, the results are mixed on the capacity of surface-decomposition methods to replicate the range of adjustments in motor unit activity that has been observed in intramuscular recordings. In one of the more successful studies, Farina et al. (2009) used a 61-electrode grid (3 mm between electrodes) to record the activity of motor units in abductor pollicis brevis ($n = 73$) as subjects performed 25 ramp-up and ramp-down contractions. The target force was 10% MVC and the rate of change in force was $\sim 2\%$ MVC/s.

Consistent with the results of studies that used intramuscular electrodes, recruitment threshold increased slightly for the lowest threshold motor units, but decreased for those that were recruited later. In a unique contribution to the field, they found that the change in the

conduction velocity of motor unit action potentials depended on the relative duration of activity. As shown in Fig. 13, the motor unit that discharged action potentials for the greatest percentage of the initial ramp-up and ramp-down contraction (range: 16–98%) experienced the most substantial reduction in conduction velocity. Due to the association between conduction velocity of action potentials and metabolite concentration (Cairns and Dulhunty, 1995; Kössler et al., 1991), this finding suggests that the most active low-threshold motor units experienced the greatest challenge to metabolic homeostasis during the task. Due to the decrease in force contributed by some motor units—as suggested by the decrease in recruitment threshold—an additional 18 motor units were recruited after the first minute of the task. Even among low-threshold motor units, therefore, there were significant differences in the adjustments they exhibited during the 5-min task.

Another decomposition study has also been able to replicate some of the findings obtained with intramuscular electrodes (McManus et al., 2016). The purpose of this study was to compare the coherence of discharge times for motor units in first dorsal interosseous before and after a sustained submaximal contraction (30% MVC force). The motor unit activity was derived from four differential recordings of surface EMG signals. In contrast to most other groups who use this decomposition method, McManus and colleagues used spike-triggered averaging of the identified waveforms to assess the reliability of the decomposed motor units before examining the adjustments. They used the discharge times detected by the decomposition system to obtain a spike-triggered average of the motor unit action potential in each of the four interference signals. Only motor units that exhibited an adequate correlation (> 0.7) between the two estimates of the action potential (decomposition algorithm and spike-triggered average) and a low coefficient of variation for peak-to-peak amplitude during the fatiguing contraction (< 0.3) were used in the analysis. These criteria resulted in an average of just $28 \pm 14\%$ of the 70 ± 11 waveforms identified by the decomposition algorithm as being considered acceptable motor unit action potentials.

The average number of acceptable motor units in the 11 subjects (out of 15) who had at least 8 concurrently active motor units was 16.9 ± 6.7 . Average initial discharge rate at the onset of the fatiguing contraction was 12.8 ± 2.8 pps and this decreased by an average of 74.4% during the fatiguing contraction. There was a weak, but significant, correlation for those units with higher initial discharge rates to exhibit a decrease during the fatiguing contraction and for those with lower initial rates to experience an increase ($r = -0.27$, $P < 0.001$). The association between initial discharge rate and its subsequent decline was particularly strong for 6 of the 11 subjects ($r = -0.70 \pm 0.09$). Also, motor units recruited during the fatiguing contraction exhibited both an increase and a decrease in discharge rate, as observed in intramuscular recordings (Fig. 11B).

Other decomposition studies have used similar experimental protocols, but found that average motor unit discharge rate either did not change (Castronovo et al., 2015) or that it increased (Contessa et al., 2016; Muddle et al., 2018) during fatiguing contractions. Due to the possibility that the relatively limited data obtained with intramuscular electrodes during fatiguing contractions may underestimate the adjustments at the population level, I briefly describe the findings of decomposition studies with contrary results. In one of these studies, Castronovo et al. (2015) found no change in average discharge rates of motor units in tibialis anterior during isometric contractions sustained at one of three target forces (20%, 50%, 75% MVC) until task failure. The surface EMG signals were recorded with high-density electrodes and decomposed into trains of motor unit action potentials with the convolutive, blind-source algorithm. The decomposition yielded an average of 21 ± 7 motor units per subject at each of the contraction intensities. As expected, average discharge rate increased with target force (20%: 11.0 ± 0.8 pps; 50%: 14.7 ± 1.9 pps; 75%: 15.8 ± 2.6 pps) as did the coefficient of variation for interspike interval (20%: $18.0 \pm 8.3\%$; 50%: $25.0 \pm 11.1\%$; 75%: $34.0 \pm 11.7\%$).

The adjustments in discharge activity during the fatiguing contraction were quantified by comparing 10-s averages obtained at the start and end of the task. EMG amplitude increased from the beginning to the end of the fatiguing contraction for the two lower target forces (20% and 50% MVC), but not for the contraction at 75% MVC force. Despite these changes in EMG amplitude, average discharge rate was not statistically different between the start and end of the fatiguing contraction for any of the target forces (initial values: 20%, 10.4 ± 0.9 pps; 50%, 13.7 ± 1.8 pps; 75%, 14.7 ± 2.5 pps). Nonetheless, the coefficient of variation for interspike interval increased during the fatiguing contraction at the two target lower forces (20%: $18 \pm 8\%$ to $26 \pm 13\%$; 50%: $25 \pm 11\%$ to $38 \pm 10\%$), but not at 75% MVC force ($34 \pm 12\%$ to $36 \pm 11\%$). These findings suggest that despite a progressive increase in net excitatory synaptic input onto the motor neurons during the fatiguing contraction at the two lower target forces, average discharge rate did not change but instead became more variable.

In another of these contrary decomposition studies, Contessa et al. (2016) found that motor units in vastus lateralis increased discharge rate during a series of intermittent, isometric contractions with the knee extensor muscles. The target force of 30% MVC, which was held for 48 s in each contraction, was reached with ramp-up and ramp-down rates of 10% MVC/s. The intermittent contractions were performed until the average force decreased by > 5% from the target force. Average discharge rates for 100 motor units during three of the intermittent contractions (early, middle, and late) performed by one subject are shown in Fig. 14. The main findings of the study are indicated by the thick blue, green, and red lines. As observed in intramuscular recordings (Fig. 11A), the blue and green circles indicate that the recruitment threshold force decreased for motor units with moderate values and additional motor units (red line) were recruited as the task progressed. However, the upward shift of the blue and green lines indicates that the average discharge rates of motor units with similar action-potential amplitudes increased with task duration. Similar results were observed in all five subjects (their Fig. 2). Combined with the continuous increase in EMG amplitude for vastus lateralis, vastus medialis, and rectus femoris (lower traces in Fig. 14), these results suggest that task failure in this protocol must have been entirely attributable to reductions in the force capacity of the activated muscle fibers.

Contessa et al. (2018) suggest that one potential explanation for the different findings in rate coding between studies that used

intramuscular electrodes and those that decompose surface-recorded interference signals may be changes in the distribution of activation among synergist muscles. However, a number of studies have demonstrated that differences in the adjustments during fatiguing contractions are often not associated with different rates in change in EMG amplitude for synergist and antagonist muscles (De Luca and Mambrini, 1987; Hunter et al., 2002; Klass et al., 2008; Lévénez et al., 2005; Maluf et al., 2005; Psek and Cafarelli, 1993; Rudroff et al., 2007; Rudroff et al., 2010; Vila-Chá et al., 2012). Rather, the key issue appears to be the extent to which the waveforms identified by a decomposition algorithm are edited with acceptance criteria. For example, the spike-triggered averaging assessment of reliability by Lowery and colleagues (McManus et al., 2016) resulted in ~72% of the waveforms identified in first dorsal interosseous during a fatiguing contraction (isometric contraction sustained at 30% MVC force until failure) being rejected due to not meeting stringent inclusion criteria. Consistent with this interpretation, the decomposition methods that have been able to replicate many of the findings derived from intramuscular recordings have used extensive manual editing of the output produced by the decomposition algorithms (Holobar et al., 2014; Lapatki et al., 2019; McManus et al., 2017; Muceli et al., 2015; Negro et al., 2016).

7. Conclusions

There have been significant advances in decomposition methods since the technology was described by Prof. Merletti in the 2006 Basmajian lecture (Merletti et al., 2008). Fundamentally, these methods depend on the capacity to distinguish surface-recorded motor unit action potentials based on their shape and location. This capacity can be limited by too few detection points (Blok et al., 2002; Farina et al., 2008; Kleine et al., 2007), high levels of signal noise (Holobar et al., 2009; Hu et al., 2013), and the anatomy of the underlying tissues (Holobar et al., 2009; Radeke et al., 2014; Vieira et al., 2011). Nonetheless, there has been considerable progress in all three components of the decomposition approach: detection systems, decomposition algorithms, and evaluation of the identified waveforms.

With these advances, some decomposition methods have been able to replicate the findings related to peak discharge rate, force oscillations, the influence of rate coding on rate of force development, and the adjustments during fatiguing contractions that have been observed in intramuscular recordings. None of the decomposition methods,

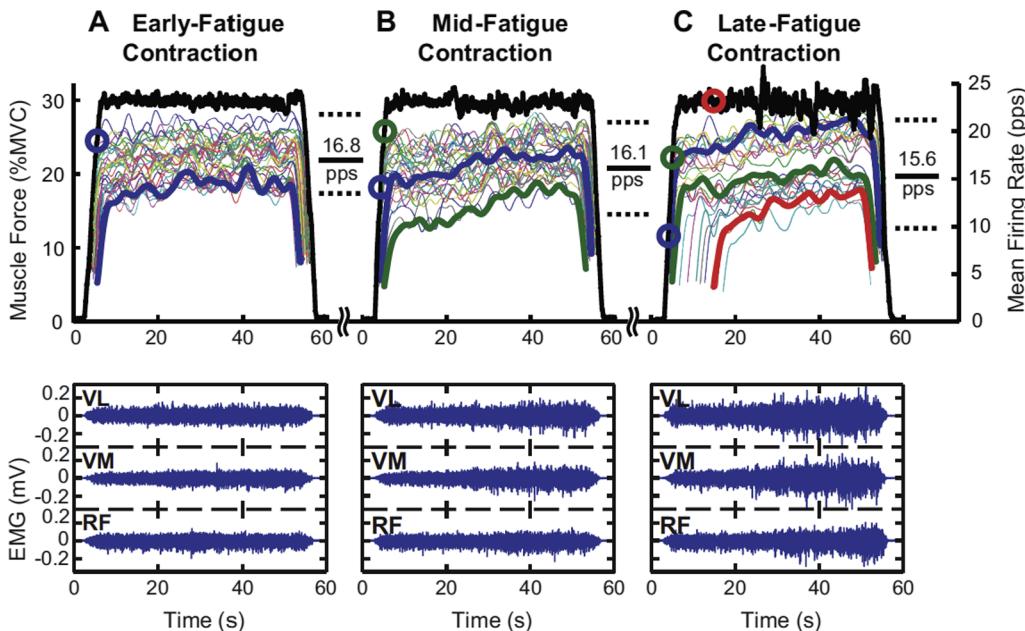


Fig. 14. Adjustments in motor unit activity during a series of intermittent, isometric contractions with the knee extensors. Each contraction was sustained for 48 s at a target force of 30% MVC. The colored lines in the upper row show the average discharge rate for motor units in the vastus lateralis muscle. Each of the thick colored lines shows the average discharge rates for a motor unit action potential with a similar amplitude (not the same motor unit) across the three contractions. The lower panel shows the surface-recorded EMG signal for vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) at the three time points during the task. (Reproduced with permission from Contessa et al., 2016).

however, have been able to detect the selective saturation of discharge rate exhibited by low-threshold motor units during gradual increases in force during isometric contractions. This limitation is likely attributable to the relatively low energy in the action potentials of low-threshold motor units (Farina et al., 2014; Holobar et al., 2009), although at least one decomposition study was able to identify low-threshold motor units (Del Vecchio et al., 2017).

As an alternative to the invasive procedures associated with intramuscular recordings, however, surface recordings of multiple interference EMG signals appear capable of significantly advancing our knowledge on the strategies used by the nervous system to control muscle force (Farina and Negro, 2015; Farina et al., 2016). An underappreciated feature of this approach, however, is that the strategy used to evaluate the waveforms identified by a decomposition algorithm can severely limit the quality of the information that can be extracted from these signals (McManus et al., 2017; McManus et al., 2016). Nonetheless, current efforts are continuing to advance the technology so that it can be applied to a broader range of task conditions (Glaser et al., 2017; Glaser and Holobar, 2017) with translation into clinical practice (Farina et al., 2017; Holobar and Glaser, 2018; Kapelner et al., 2018).

Conflict of interest

I, Roger M. Enoka, have no financial or personal relationships with other people or organizations that could inappropriately influence the content of my review paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jelekin.2019.03.010>.

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