CONSIDERATIONS FOR MUSCLE ACTIVATION AND RATE OF FORCE DEVELOPMENT IN EXERCISE PHYSIOLOGY RESEARCH

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ABSTRACT

Introduction: Muscle activation under different contraction paradigms and rate of force or torque development are commonly investigated and interpreted phenomenon within neuromuscular and biomechanical research. However, there are several considerations which should be made when investigating these parameters in research from a methodological and interpretation standpoint. Different techniques of quantifying muscle activation during high-intensity vs. low-intensity fatiguing conditions are commonly studied in isolation, however, because each measure of muscle activation has limitations, it is important to use a multi-faceted approach to analyzing muscle activation during these different contraction conditions to obtain less biased results. This multi-faceted approach to estimating muscle activation includes analyzing surface EMG amplitude in combination with individual motor unit data. Rate of force development is a topic of high research interest, especially for its purported capacity for predicting vertical jump height. However, less interest has been given to rate of force or torque development during the previously mentioned multifaceted approach to analyzing muscle activation. The current work considers whether this multifaceted approach to estimating muscle activation is affected by rate of force development, and whether rate of force development is a robust predictor of vertical jump height in multiple regression models where other predictors are included. **Methods:** Two studies were performed which analyzed muscle activation, including the behavior and properties of individual motor units, during isometric voluntary contractions. The first study did this, during a high-intensity contraction in comparison to a series of moderate intensity contractions performed until volitional fatigue, and the second study, during contractions of equal intensity and duration, but with different rates of torque development. During both studies, surface EMG signals were analyzed in terms of root mean squared amplitudes, and in terms of individual motor unit action potential amplitudes, recruitment thresholds, and firing rates. All motor unit analysis was relationship based and performed on a subject-by-subject and contraction-by-contraction basis. The third study used multiple regression techniques to analyze the predictive capacity of different estimates of rate of force development on vertical jump height from a large sample of vertical jumps performed by collegiate athletes. **Conclusions:** The results of the first study indicated the multifaceted approach to analyze muscle activation revealed greater muscle activation was achieved during a high-intensity contraction in comparison to a moderate intensity contraction at the limit of voluntary fatigue. The second study indicated rate of torque development influences motor unit behavior during the commonly utilized isometric protocols such as were used in study 1. The results of the final study indicated that estimates of rate of ground reaction force development during vertical jumps is a significant moderate predictor of vertical jump height. However, when other predictors are included in the prediction model it appears the predictive capacity of rate of force development on vertical jump height rests solely on its shared variance with another predictor, peak ground reaction force. Therefore, rate of force development may be more important than previously thought in studies investigating muscle activation via individual motor unit behavior, and less important than previously thought in predicting vertical jump height.

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CHAPTER I: A REVIEW OF RELEVANT LITERATURE

1.1 MOTOR UNIT ACTION POTENTIAL AMPLITUDES AND THE SIZE PRINCIPLE

The Size Principle

In all EMG recordings the signal is composed entirely of motor unit (MU) action potentials. The features of these action potentials, including their amplitude, shape, and frequency, is what allows researchers to investigate the behavior of MUs during muscular contractions (Adrian and Bronk 1929). It was first determined that MUs are recruited in an orderly fashion, with respect to the size of their neurons by Henneman (1957). That is, larger and larger stimuli are required to activate, or recruit, MUs with larger neurons. Henneman (1957) applied electrical stimuli of increasing intensity (5-25 volts) to the dorsal roots of decerebrated cats to elicit a reflex and recorded the action potential amplitudes and discharge trains of motor units in response to the stimuli. He reported that lower intensity stimuli recruited smaller MUs, and as the intensity increased, larger and larger MUs were recruited in response to the stimulus. In addition, as the intensity increased, MUs which were already recruited displayed longer discharge trains with a greater number of discharges. This led Henneman to conclude that the susceptibility of a neuron to discharge is a function of its size, which later became known as the Henneman size principle (Henneman and Olson 1965). This work was confirmed and advanced to show its universality in voluntary contractions in multiple human muscles such as the first dorsal interosseous (Milner-Brown et al. 1973a; Masakado et al. 1994; Hu et al. 2013a; Miller et al. 2018a; Sterczala et al. 2018a), masseter (Goldberg and Derfler 1977), vastus lateralis (Pope et al. 2016; Muddle et al. 2018; Trevino et al. 2018), biceps brachii (Moritani et al. 1987; Kossev and Christova 1998), as well as others. The size principle has been confirmed to be present in multiple contraction types, including isometric contractions (Milner-Brown et al. 1973a; Goldberg and Derfler 1977; Masakado et al. 1994; Hu et al. 2013a; Pope et al. 2016; Trevino et al. 2018; Sterczala et al. 2018a) as well as in concentric and eccentric dynamic contractions (Moritani et al. 1987; Kossev and Christova 1998; Stotz and Bawa 2001). Finally, the size principle is intact in both children and older individuals (Miller et al. 2018a, 2019; Sterczala et al. 2018a).

While the size principle has been widely reported and accepted it is not always visible in very low intensity contractions. Investigations of the MUs during contractions at or below 10% maximum voluntary contraction (MVC) have shown disorderly recruitment (Søgaard 1995; Westad and Westgaard 2005). However, in these investigations the authors concluded that such early recruited MUs likely have similar properties which would make the size principle difficult to observe, and that the findings did not, in fact, contradict the size principle.

Implications of the Size Principle and motor unit pool organization

The amplitude of a MUs action potential is much more than a simple descriptor of the MU, it is also a strong indication of the physical properties of the MU. Around the same time the size principle itself was being discovered, studies from the same laboratory (Olson et al. 1968) and by others (Hakansson 1956a) were demonstrating its utility. Hakansson (1956a) studied conduction velocities and action potential amplitudes of different size muscle fibers isolated from frog legs and reported larger muscle fibers displayed greater conduction velocities and greater action potential amplitudes.

It had been previously thought that the recorded amplitude of a MU's action potential was based upon its proximity to the recording electrode rather than its physical properties, but the research of Olson et al. (1968) established the relationship between MU size and MU action potential amplitude. Olson determined that the amplitude of a MU's action potential is based upon the number of muscle fibers that belong to the MU and the diameter of the individual muscle fibers. This study utilized nerve stimulation to decerebrated cats in progressive increments to recruit larger and larger MUs with larger and larger motoneurons. They also recorded the EMG amplitude of the action potentials from the MUs in relation to their size from several leg muscles and it was determined that as the size of the MU increased (more fibers and greater diameter fibers), the amplitude of the action potential increased as well. This research has been confirmed by numerous other studies employing different methodologies (Milner-Brown et al. 1973a; Milner-Brown and Stein 1975; Hu et al. 2013a; Pope et al. 2016; Sterczala et al. 2018b; Miller et al. 2018a; Trevino et al. 2018).

Milner-Brown et al. (1973b) utilized a technique to average MU twitch force, the force produced by a single firing of an individual MU in humans and this work allowed for further elucidation of the importance of the size principle. This technique was used to discover that MU twitch force is directly related to its recruitment threshold and action potential amplitude (Milner-Brown et al. 1973a; Goldberg and Derfler 1977), and thus larger MUs which are recruited at greater forces also possess greater force producing capabilities. MU were now understood to have quite diverse properties, with force twitches in the human first dorsal interosseous (FDI) reported to range from 0.1 to 10 g and contraction times ranging from 30 to 70 ms in a single subject. In addition, it was noted that the majority of MUs were recruited at lower force levels, or that the number of MUs recruited during an incremental increase in force declined at greater force levels.

The sum of these findings allowed for a relatively well informed picture of the organization of the properties of muscle fibers within a muscle from a neuromuscular standpoint, and that the physical characteristics of the muscle fibers were dependent on these neural properties. However, the histochemical composition of MUs remained unknown. Garnett et al. (1979) used a technique called controlled intramuscular microstimulation to deplete glycogen in several MUs of medial gastrocnemius of 13 human subjects. The contractile properties of the MUs were also analyzed during the controlled intramuscular microstimulation. The MUs were then biopsied and stained for myosin ATPase and glycogen. Although the contractile properties of MUs lie in a continuum (Enoka and Duchateau 2015), they were separated into 3 groups (slow, fast fatigue resistant, and fast fatiguing) based on their contraction times (time from action potential to peak twitch tension) and fatigability. The histochemical analysis revealed slow MUs were associated with type I muscle fibers and the fast units were associated with type IIb muscle fibers. An illustration of the properties of MUs in each of the three groups is illustrated in Figure 1.1.

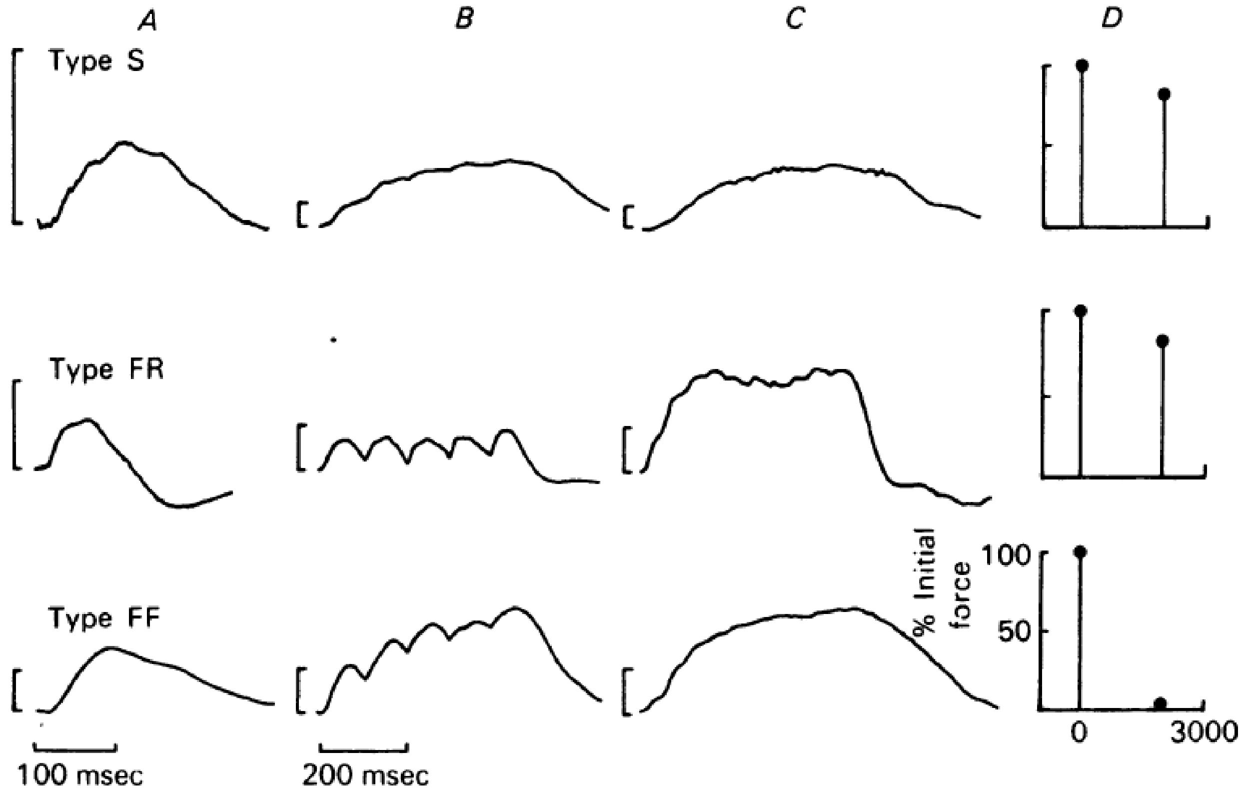


Figure 1.1 Examples of the three motor unit types found in human medial gastrocnemius. A) isometric twitch. B) isometric tetanus 10 pulses/sec, C) isometric tetanus 20 pulses/sec. D) fatigue test, control and after 3000 stimuli, expressed as a percentage of initial isometric tension. Adapted from Garnett et al. (1979).

Based on the findings of Garnett et al. (1979) and the findings of other researchers who reported associations between contractile properties of MUs and the properties attributed to different muscle fiber types (Burke et al. 1971; Eddinger and Moss 1987; Bottinelli et al. 1991; Delp and Duan 1996) MUs can be separated into categories based on their contractile properties. It can be generally stated that slow motor units are composed of type I muscle fibers, fast fatigue resistance MUs are composed of type IIa fibers, and fast fatiguing MUs are composed of type IIb fibers. This knowledge is useful in that it has allowed researchers to make inferences about muscle fiber type from analysis of MU activity (Herda et al. 2015; Pope et al. 2016; Sterczala et al. 2018a). However, it is more accurate to conceptualize the organization of the MU pool in terms of a continuous spectrum (Enoka and Duchateau 2015). Muscle fibers can coexpress different myosin heavy chain isoforms (Carroll et al. 2005), and the distributions of MU twitch tensions and contraction times are continuous (Milner-Brown et al. 1973a; Goldberg and Derfler 1977; Garnett et al. 1979).

Advancements due to modern decomposition techniques

Modern techniques for the decomposition of EMG signals from the surface of the skin has allowed for the analysis of action potential trains from many (10-50) concurrently active MUs during human contractions (Holobar and Zazula 2004, 2007; De Luca et al. 2006; Nawab et al. 2010; Hu et al. 2013b). This technology provided a very important advancement in the field of MU physiology because it became possible to study the characteristics and behavior of a legitimate sample of concurrently active MUs during a single contraction. Previously MUs would often be observed on an individual basis or in small groups of 2 or 3 concurrently active MUs (Milner-Brown et al. 1973a, b; Tanji and Kato 1973; Milner-Brown and Stein 1975; Goldberg and Derfler 1977). The MUs able to be observed during a contraction was based on their proximity to the recording electrode and/or their size relative to the size of other MUs that would be active during the contraction. This often meant that smaller MUs could only be observed during very low intensity contractions, because large action potentials of larger MUs active during higher intensity contractions obscure action potentials of smaller MUs active during the same contraction.

As previously stated, the major benefit of modern decomposition techniques is that it allowed for the analysis of many of simultaneously active MUs during muscular contractions of any intensity. Thus, the size principle, as assessed by regressing MU action potential amplitudes against recruitment thresholds was confirmed on a subject-by-subject and contraction-by-contraction basis (Hu et al. 2013a; Pope et al. 2016; Sterczala et al. 2018b; Colquhoun et al. 2018a; Muddle et al. 2018; Miller et al. 2018a; Trevino et al. 2018). The analysis of MU activity on a subject-by-subject and contraction-by-contraction basis is indeed now feasible, and elucidates the strong relationships between MU firing rates, action potential amplitudes, and their recruitment thresholds. Although many arguments have been made that all analysis of MU activity should be performed in this fashion (De Luca and Hostage 2010; De Luca and Contessa 2012; Hu et al. 2013a), there are some authors who still choose to pool data between multiple subjects and contraction intensities, and average firing rates without respect to recruitment thresholds and thus, their reports of the characteristics of MUs in relation to each other are less organized (Barry et al. 2007; Vila-Chã et al. 2010; Castronovo et al. 2015; Del Vecchio et al. 2019). For researchers who do analyze MU activity on a subject-by-subject and contraction-by-contraction basis, this quickly led to the discovery of a phenomenon referred to as the onion-skin scheme of MU control. The onion-skin scheme of MU control postulates that earlier recruited MUs will maintain greater firing rates than later recruited MUs throughout the entirety of a contraction, and that the earliest recruited MUs will be the last to turn off (De Luca and Erim 1994; De Luca et al. 1996; De Luca and Contessa 2015; Trevino et al. 2016; Sterczala et al. 2018b; Miller et al. 2019). The onion-skin scheme will be discussed in more detail in section 1.2.

1.2 MOTOR UNIT FIRING RATES

Early analysis of MU firing rates in animal preparations indicated larger motor units obtain greater firing rates than smaller MUs, and that peak firing rates of MUs were determined by their after-hyperpolarization periods (Eccles et al. 1958; Kernell 1965). Some later investigations of MU firing rates during voluntary contractions in humans also reported greater firing rates of MUs with higher recruitment thresholds (Gydikov and Kosarov 1974; Kosarov and Gydikov 1976; Tracy et al. 2005; Moritz et al. 2005; Barry et al. 2007; Jesunathadas et al. 2012). However, many other investigations of MU firing rates have provided evidence of a strong inverse relationship between MU recruitment thresholds or neuron sizes and peak firing rates during voluntary contractions in humans (Person and Kudina 1972; De Luca et al. 1982; De Luca and Erim 1994; Masakado et al. 1995; De Luca and Hostage 2010; Trevino et al. 2016) including in older individuals (Erim et al. 1999; Miller et al. 2017a; Sterczala et al. 2018a), children (Miller et al. 2018a, 2019; Chalchat et al. 2019; Herda et al. 2019a), and in individuals with different exercise training status (Herda et al. 2015; Sterczala et al. 2018b; Dimmick et al. 2018). The discrepancy in findings is not due to inconsistency in MU behavior, or to methodological differences such as the muscle tested or the EMG recording equipment used. Instead, the relationship between MU firing rates and their recruitment thresholds can appear direct or inverse depending on how the data are analyzed (De Luca and Hostage 2010).

Because of the complex nature of the relationships between muscular contractions and the pattern of firing rates of different MUs, the method by with MU firing rates are analyzed heavily influences the results that are reported. Researchers who find and report a direct relationship between MU firing rates and their recruitment thresholds have analyzed different MUs across different subjects and different contraction intensities, pooling their data into a single regression (Gydikov and Kosarov 1974; Kosarov and Gydikov 1976; Tracy et al. 2005; Moritz et al. 2005; Barry et al. 2007; Jesunathadas et al. 2012). Researchers who find and report an inverse relationship between MU firing rates and their recruitment thresholds have found it crucial to analyze MU firing rates in terms of their relationship to their recruitment thresholds and only on a subject-by-subject and contraction-by-contraction basis (De Luca and Hostage 2010; De Luca and Contessa 2012; Stock et al. 2012; Hu et al. 2013a; Herda et al. 2016; Trevino et al. 2016; Contessa et al. 2016; Miller et al. 2017a). As stated previously, while it has been argued repeatedly that grouping MU data across contractions, testing days, and subjects is inappropriate (De Luca and Hostage 2010; De Luca and Contessa 2012; Hu et al. 2013a), such analysis of MU firing rates continues to be reported and published (Vila-Chã et al. 2010; Castronovo et al. 2015; Del Vecchio et al. 2019). Regardless of how findings are reported in studies of MU behavior it is important to understand the strong relationships between MU firing rates and their recruitment thresholds and action potential amplitudes which are present, although variable, in all voluntary contractions in humans.

De Luca and Hostage (De Luca and Hostage 2010) used modern surface EMG decomposition techniques to study the relationship between MU mean firing rates and recruitment thresholds in several different muscles (FDI, vastus lateralis, and tibialis anterior) and at several different isometric contraction intensities (20, 50, 80, and 100% MVC) in 6 healthy adult subjects. The decomposition algorithm allowed for the observation of 20-30 MUs per contraction for a total of 1,273 total MUs analyzed in the study. Because the onion skin scheme of MU control was well established at this point (De Luca and Erim 1994; Masakado et al. 1995; De Luca et al. 1996; Erim et al. 1999; Adam and De Luca 2005), it was expected and confirmed that there would be strong negative relationships between mean firing rates and recruitment thresholds for each subject and contraction intensity if analyzed separately. The authors also performed analysis on data grouped across subjects to compare the findings between these two methods of analysis. Figure 1.2 below is a combination of Figures 2 and 3 adapted from De Luca and Hostage (2010) to illustrate this concept. It is clear that much stronger relationships exist when data is analyzed on a subject by subject basis. Indeed, the average r^2 for the regression of mean firing rates against recruitment thresholds decreased from ~.90 for individual data, to ~.75 for grouped data (overall average r^2 values not reported). It is also apparent that data were further grouped across muscle and contraction intensity the relationship between mean firing rate and recruitment threshold may disappear entirely.

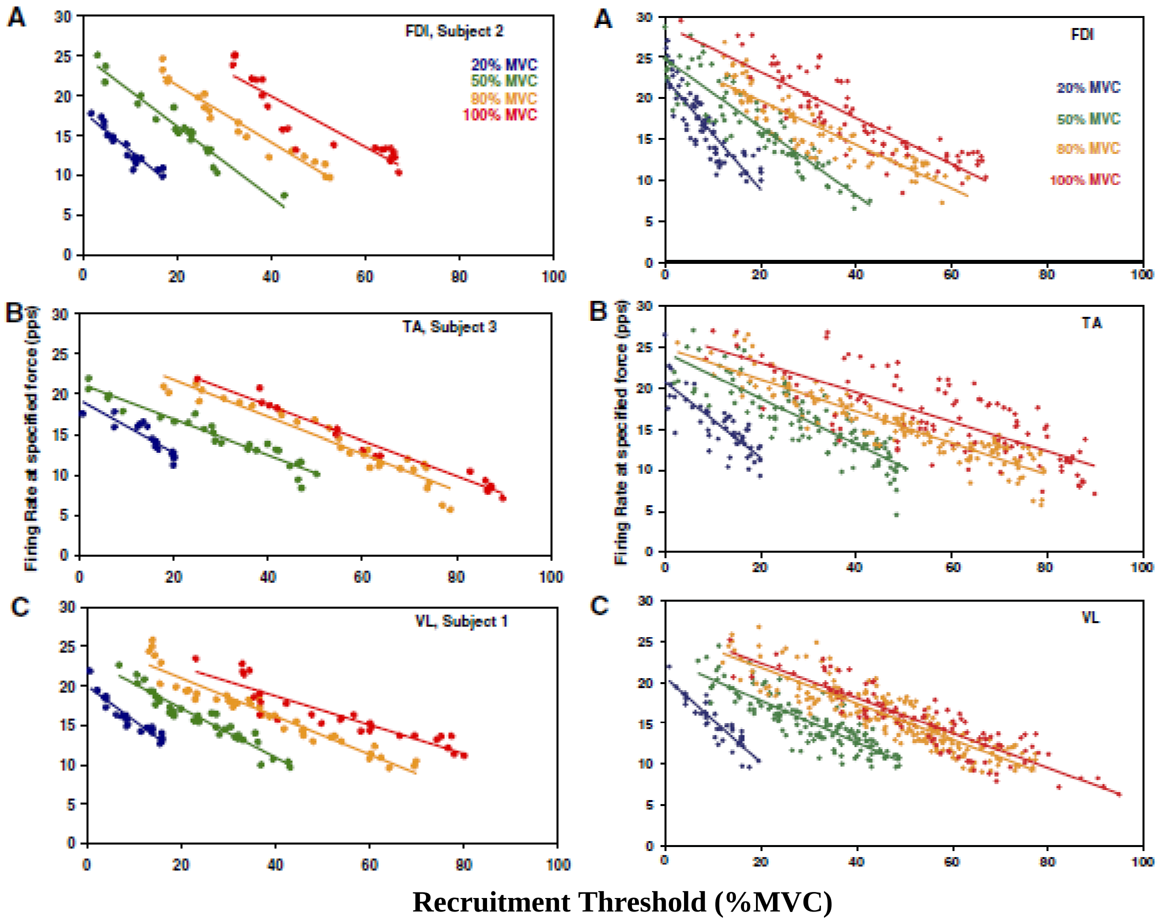


Figure 1.2 Left) Average value of the motor unit firing rates plotted as functions of recruitment threshold—separately for contractions sustained at 20, 50, 80, and 100% MVC. The data are representative of different subjects and different muscles (the vastus lateralis, the FDI, and the tibialis anterior). The regression lines are drawn through the data from individual contractions,

with each data point representing an individual motor unit. Right) Average value of the motor unit firing rates plotted as functions of recruitment threshold. Data are from all analyzed contractions from the vastus lateralis (VL), FDI, and tibialis anterior (TA) for contractions sustained at 20, 50, 80, and 100% MVC. The regression lines are drawn through the data from all the contractions at each force level, with each data point representing an individual motor unit. As expected, the regression lines for the greater contractions have higher values. Note that the data scatter is greater in these grouped data than in the data for the individual subjects. Adapted from De Luca and Hostage (2010).

For a different perspective of MU control, we turn to the works of Castronovo et al. (2015). In this study, 10 subjects completed fatiguing isometric voluntary dorsiflexion contractions at 20, 50, and 75% MVC, and EMG amplitude and MU activity of the tibialis anterior was analyzed at the beginning and near the end of the contraction. The firing rates of all active and observed MUs were averaged to calculate what was referred to as the global discharge. In addition, MU coherence, which is the strength of correlation between firing times different MUs due to common synaptic input was measured. EMG increase significantly from the beginning to the end of the contraction at both 20 and 50% MVC intensities, and increased nonsignficantly for the 75% MVC. Coherence of the MU discharge times were generally greater at higher contraction intensities and were greater at fatigue than at the beginning of each contraction. The authors also noted that there is a limitation in comparing coherence from the beginning of the contraction to the end of the contraction because they would be observing mostly different MUs which would likely have different recruitment thresholds, and thus, different properties. To correct for this a secondary analysis was performed, which showed similar findings, where coherence was compared for a limited number of MUs which were able to be tracked from the beginning of the contraction to the end of the contraction. Conversely the authors reported no differences in MU firing rates from the beginning to the end contraction and consequently stated there was no association between the increase in EMG amplitude and MU firing rates.

However, as the authors admit, recruitment of additional MUs occurred throughout the duration of each contraction which meant the average recruitment threshold of MUs observed at the end of the contraction would not be equivalent to the average recruitment threshold of MUs observed at the beginning of the contraction. The authors make no mention of the effect of recruitment threshold on MU firing rate which leads to a null result in their analysis of changes of firing rates with fatigue in the current study. The findings of this study therefore, contrast the findings of others who have described increases in firing rates in the presence of fatigue during prolonged submaximal contractions or repeated fatiguing contractions (Adam and De Luca 2005; de Ruiter et al. 2005; Mettler and Griffin 2016; Contessa et al. 2016) when several MUs are recorded per contraction and data is analyzed on a subject-by-subject and contraction-by-contraction basis. In concluding that firing rates do not increase while fatigue develops and EMG amplitude increases, Castronovo et al. (2015) also contradicts hypotheses held by some of the authors in their other works, such as Farina et al. (2010) where MU firing rates are argued to be a more appropriate indicator of excitatory drive than EMG amplitude. The most probable outcome of this protocol on MU firing rates, had they been analyzed according to recruitment thresholds, will be further discussed in section 1.3.

1.3 MOTOR UNIT RECRUITMENT PATTERNS AND FATIGUE

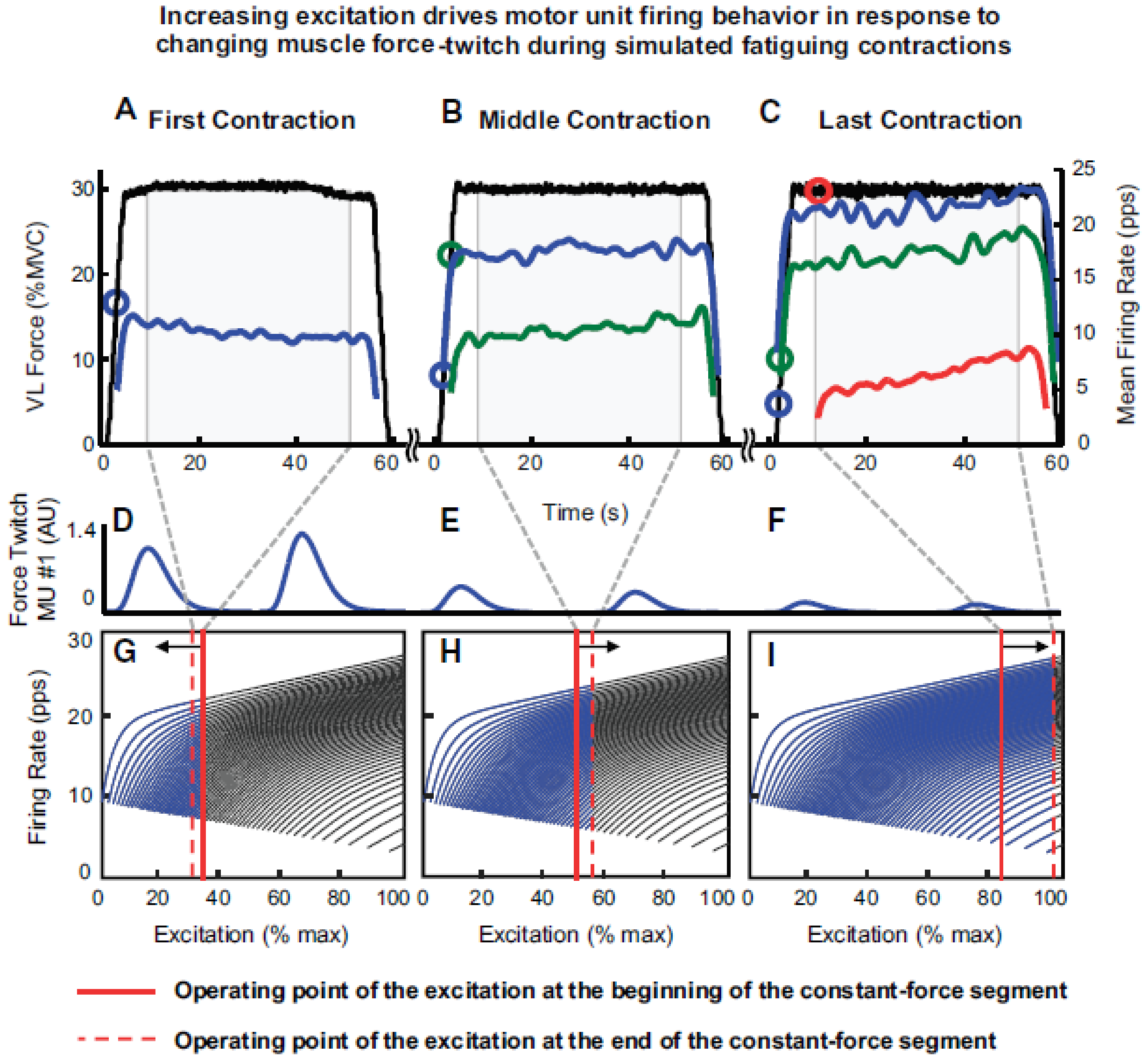
Firing rate and recruitment adaptations in response to fatigue

There has been much contention about the behavior of MUs during fatigue. Many differences in findings are undoubtedly due to differences in methodology, as studies of MU behavior during fatigue have included protocols of a single sustained MVC, a single submaximal contraction performed until the force can no longer be maintained, and repeated submaximal contractions. Some authors have reported MUs decrease firing rates as fatigue develops (Enoka et al. 1989; Garland et al. 1994; Carpentier et al. 2001; Mottram et al. 2005; Vila-Chã et al. 2012; Kelly et al. 2013; McManus et al. 2015), while others have reported increases in firing rates with fatigue (Adam and De Luca 2003, 2005; de Ruiter et al. 2005; Mettler and Griffin 2016; Contessa et al. 2016, 2018; Potvin and Fuglevand 2017; Muddle et al. 2018). Reports are inconsistent with regards to the direction of change of recruitment thresholds, including findings that in fatiguing conditions, recruitment thresholds of low threshold MUs are increased while recruitment thresholds of high threshold MUs are decreased (Enoka et al. 1989; Carpentier et al. 2001; Muddle et al. 2018) and studies that show all MUs decrease recruitment thresholds with fatigue (Adam and De Luca 2003; Contessa et al. 2016, 2018). There is however, agreement between all such studies that as fatigue develops new MUs are recruited to maintain force level. But, this is of course, only possible during submaximal contractions.

Because of the variability of firing rates (see figure 1.2) it is important to analyze a sufficient sample of MUs during each contraction to accurately describe a trend in the change in firing rates. This is another factor that influences the findings of studies aiming to determine MU behavior during fatiguing contractions (Contessa et al. 2016). However, results differ even among studies using similar protocols and surface EMG decomposition techniques. The following studies all used the same surface EMG system and decomposition algorithm (Delsys Inc, Precision Decomposition) and used seemingly similar protocols and methods of data analysis. According to research performed by Contessa and colleagues, as fatigue develops during submaximal contractions, MU firing rates increase, new MUs are recruited, and if contractions are repeated, recruitment thresholds of all MUs decrease (Contessa et al. 2016, 2018). This research was initially conducted by repeating isometric muscle actions of the VL at 30% MVC until the limit of fatigue (Contessa et al. 2016), and then confirmed in a second study by repeating muscle actions at 50% MVC in the FDI (Contessa et al. 2018). Muddle et al. (2018) performed repetitive muscle actions at both 30% MVC and at 70% MVC of the VL and found similar results to Contessa, except that recruitment thresholds of the lowest threshold MUs increased rather than decreased. McManus et al. (2015) observed MU behavior during 20% MVCs of the FDI before and after a 30% MVC fatiguing contraction and reported a trend for all MUs to decrease firing rates with fatigue. Therefore, a firm conclusion about the adaptation of MUs to fatigue cannot be established for all protocols or all muscles. Further research is needed to confirm in which situations MUs respond by increasing or decreasing recruitment thresholds or firing rates.

As to the mechanisms responsible for the discrepancy of findings of changes in MU firing rates with fatigue, there are two contentions. The first comes from those who report increases in firing rates with fatigue. They argue that the common drive theory (De Luca and Erim 1994) of input excitation dictates that MU firing rates and the number of MUs recruited both vary in unison as a direct result of input excitation, and thus firing rates cannot decrease concurrently with increases in input excitation

(Contessa et al. 2018). The combination of MU firing rates and the number of MUs recruited at a given level of excitation has been referred to by this research group as the operating point (De Luca and Hostage 2010; Contessa and De Luca 2012; Contessa et al. 2016), which is dictated by the common drive theory (see figure 1.3).


Increasing excitation drives motor unit firing behavior in response to changing muscle force-twitch during simulated fatiguing contractions

— Operating point of the excitation at the beginning of the constant-force segment

- - - Operating point of the excitation at the end of the constant-force segment

Figure 1.3. A–C) colored traces indicate the time-varying mean firing rates of 3 selected motor units in 3 contractions at the beginning (A), middle (B), and end (C) of the simulated fatigue protocol. The black lines show the simulated force. Colored circles provide the force at which motor units are recruited. D–F: force twitch of a representative motor unit at the beginning and end of the constant force segment of each simulated contraction. G–I: blue and gray curves show the relation between excitation to the motoneuron pool and firing rate for 60 out of 600 simulated motor units of the VL muscle. Solid and dotted red lines indicate the operating point of the excitation to the motoneuron pool at the beginning and end, respectively, of the constant force

segment of each simulated contraction. Blue curves indicate active motor units. The intersection of each firing rate curve with the excitation line indicates the firing rate value of motor units at the given excitation value. Adapted from Contessa et al. (2016).

The alternate explanation offered by those who report decreases in firing rates with fatigue is that as fatigue develops in earlier recruited MUs, their intrinsic excitability decreases, and/or mechanically and metabolically sensitive group III and IV afferents provide inhibitory feedback which causes fatiguing MUs to decrease their firing rates even as input excitation increases and new MUs are recruited (Kelly et al. 2013; McManus et al. 2015). It is quite possible that the common drive theory solely controls the operating point of MU activity during non-fatiguing contractions, but that during certain fatiguing conditions, decreased excitability or inhibitory feedback can cause some MUs to decrease firing rates.

A recently developed model of MU fatigue analyzed simulated recruitment and firing patterns of MUs during fatigue across different contraction intensities (Potvin and Fuglevand 2017). The model predicted MU behavior during sustained isometric contractions at 20%, 50%, 80%, and 100% MVC and describes firing and recruitment patterns for the pool of MUs according to well established theories such as the Henneman size principle (Henneman and Olson 1965) and the onion skin scheme (De Luca and Erim 1994; De Luca and Contessa 2012). The simulations found validity in that they were able to accurately predict endurance times of sustained maximal contractions performed in empirical studies in several different muscles (Bigland-Ritchie et al. 1978; Bigland-Ritchie 1981; Kent-Braun 1999; Jones et al. 2009; Kennedy et al. 2013). The parameters of the model which involve adaptation of firing rates and recruitment to fatigue fundamentally followed the findings of Contessa et al. (2016). That is, the firing rates of all activated MUs increased and new MUs were recruited as fatigue developed, regardless of the intensity of the simulated contraction. As has been discussed in this review, it is not confirmed under which circumstances MU firing rates increase or decrease during fatigue. Therefore, this assumption of the model may be incorrect, at least under some circumstances of voluntary contractions in humans. Another characteristic of the model is that all MUs, including the largest, highest-threshold MUs, are recruited before exhaustion during lower- to moderate-intensity contractions performed to fatigue. This disagrees with many previous studies which report an inability to recruit the largest MUs during fatiguing tasks (Schoenfeld et al. 2014; Jenkins et al. 2015; Muddle et al. 2018), including a study performed by one of the authors of the model (Fuglevand et al. 1993). It appears the reason the largest MUs are not recruited during sustained contractions to fatigue is inhibitory effect of central fatigue (Gandevia et al. 1996a; Amann 2011).

Regardless of the potential shortcomings of the model, it provides a useful conceptualization of the differential levels of fatigue experienced by different MUs in contractions at different submaximal force levels. For instance, the model indicated lower intensity contractions (20% MVC) are far more fatiguing to earlier recruited, smaller MUs. As the intensity of the contraction increases, the MUs which experience the greatest fatigue shifts to larger and larger MUs. High intensity contractions (80% MVC) resulted in more fatigue to the later recruited, larger MUs. Therefore, this model attempts to bring an understanding of the portion of the MU pool, on the spectrum from the smallest to the largest MUs, which experiences the greatest fatigue during sustained or repeated contractions at different intensities. This is a concept with far reaching applications. One of which is to contradict the claim many researchers have made that performing contractions at any intensity until the limit of fatigue will result in essentially the same outcome (Carpinelli 2008; Fisher et al. 2011, 2013; Burd et al. 2012). Instead, the model shows there are different levels of fatigue experienced by MUs with different physical properties when performing high or low intensity contractions. This may be the scheme that governs the different adaptations that are reported to occur under exercise training paradigms of different intensities (Fry 2004; Schoenfeld et al. 2017). However, more research is needed to confirm this.

Recruitment during fatiguing vs. high intensity contractions and implications for training

Many researchers and practitioners are highly interested in determining the most beneficial and/or practical paradigm for resistance training between high intensity training and fatiguing low intensity training (Fry 2004; Carpinelli 2008; Fisher et al. 2011, 2013; Burd et al. 2012; Schoenfeld et al. 2015, 2017). This has resulted in an attempt to analyze differences in muscle activation during such resistance training exercises (Schoenfeld et al. 2014; Jenkins et al. 2015; Looney et al. 2016), as well as MU recruitment and firing patterns in isometric contractions designed to simulate these contractions (Muddle et al. 2018). The majority of the evidence tends to explain that while beneficial adaptations can be gained from fatiguing low intensity resistance training, there are differences between low and high intensity resistance training, and high intensity training is needed for maximum gains in strength (Fry 2004; Schoenfeld et al. 2017).

Previous studies have reported greater EMG amplitude of the VL during moderate- to high-intensity contractions (75-90% of 1RM) in comparison to fatiguing lower intensity contractions (30-50% 1RM) of the leg extensors (Schoenfeld et al. 2014; Jenkins et al. 2015; Looney et al. 2016). Looney et al. (2016) analyzed differences in muscle activation during sets of back squat at different intensities performed to failure in 10 resistance trained subjects. Peak EMG amplitude of the VL and the vastus medialis (VM) were significantly greater in sets performed at 90% of a subjects' 1 repetition maximum (1RM) than in sets to failure at 50% 1RM. The authors concluded the greater EMG amplitude during the higher intensity set to failure indicated greater MU recruitment, and consequently that the lower intensity set to failure is not sufficient for recruitment of the full MU pool.

However there are limitations to interpreting EMG amplitude as a measure of muscle activation and MU recruitment (Farina et al. 2010). In addition, there is only one study comparing muscle activation between lower and higher intensity contractions that was able to analyze individual MU firing rates and recruitment (Muddle et al. 2018). In this study 18 resistance trained subjects performed repetitive isometric contractions at 70% MVC and 30% MVC until fatigue. Muddle et al. (2018) reported greater MU firing rates and action potential amplitudes of the VL during the 70% MVC protocol than the 30% MVC protocol. Therefore, the repetitive 30% MVC protocol did not necessitate the muscle activation or recruitment equal to that of the repetitive 70% MVCs before exhaustion. These findings contrasts what was predicted by Potvin and Fuglevand's model (2017) and by other researchers suggesting that low and moderate intensity contractions performed to fatigue recruit the entire MU pool (Mitchell et al. 2012).

1.4 DIFFERENCES IN MOTOR UNIT BEHAVIOR BETWEEN POPULATIONS

Motor unit behavior in children

Prior to the previously discussed (see section 1.1) recent advancements in decomposition methods of the surface electromyography (EMG) signals, all investigations of individual MU firing trains were performed using invasive intramuscular techniques (Milner-Brown et al. 1973b; De Luca et al. 1982; Enoka et al. 1989; Masakado et al. 1995; Adam and De Luca 2003). Analysis of MU behavior from the surface of the skin not only allows for the examination of MU sizes and firing rates in relation to recruitment threshold which is arguably a more appropriate and less biased method of investigation (De Luca and Hostage 2010; De Luca and Contessa 2012; Hu et al. 2013a). In addition, it allows for investigation of MU behavior in populations in which it would be less feasible to perform invasive intramuscular techniques, such as children (Miller et al. 2018a, 2019; Chalchat et al. 2019; Herda et al. 2019a).

Miller et al. (2019) compared MU activity between 22 children (8-10 years) and 13 adults (~23 years) during prolonged 30% MVCs of the FDI. As expected, the general hierarchical organization of MU activity during voluntary contractions in children was similar to what was seen for the adults with respect to the size principle (Henneman and Olson 1965; Hu et al. 2013a), and the onion skin scheme (De Luca and Erim 1994; De Luca and Contessa 2012). However, an interesting finding of the paper was that children appeared to require greater muscle activation in order to complete the task at the same relative force level than did the adults. Across the two repetitive 30% MVCs performed by children and adults, EMG root mean squared amplitude was about 56% of maximum for children, and only 31% of maximum for adults. Reflecting the increased muscle activation, MU firing rates were greater for children in comparison to adults across all recruitment threshold levels. However, the action potential amplitudes of the MUs recruited to perform the task were similar sized or greater for adults than for children. While it is true that larger MUs are recruited for higher intensity tasks, between group differences in the action potential amplitudes of MUs recruited to perform a task are dependent on both muscle activation (Hu et al. 2013a; Sterczala et al. 2018b; Dimmick et al. 2018), and differences in muscle cross sectional area (Pope et al. 2016; Trevino et al. 2018;

Herda et al. 2019b). Therefore, the greater action potential amplitudes observed concomitantly with lower muscle activation in adults compared to children is explained by the greater muscle cross-sectional area reported for the adults (Miller et al. 2019).

Motor unit behavior in aging individuals

It is well understood that the physical properties of MUs are altered with age (Ansved and Larsson 1990; Roos et al. 1997). The information presented in this review of literature thus far suggests that the behavior of MUs during voluntary contractions will likely be altered in consequence. Indeed, many early studies of MU behavior in aging individuals reported decreased firing rates in comparison to younger adults (Nelson et al. 1984; Newton et al. 1988; Howard et al. 1988; Soderberg et al. 1991; Erim et al. 1999). However, some other researchers reported similar firing rates but observed other differences in MU behavior. These included 1) increased variability in the firing rates for older individuals (Laidlaw et al. 2000; Tracy et al. 2005), 2) increased force production of lower threshold MUs (Galganski et al. 1993), and 3) increased muscle activation and coactivation of antagonist muscles during force matching tasks performed at relative intensities (Spiegel et al. 1996; Miller et al. 2017a).

The work of Sterczala et al. (2018a) provides an investigation of changes in MU size in aging individuals according to current methods of analysis for MU behavior. In this study, 14 young adults (~22 years) and 10 older (~61 years) adults performed isometric muscle actions with the FDI at 50% MVC. Action potential amplitude of observed MUs for each subject and contraction were regressed against their recruitment thresholds. It was reported that older subjects possessed smaller action potential amplitudes of the higher threshold MUs in comparison to younger adults. The authors concluded this was due to the selective atrophy of type II muscle fibers in aging individuals that has been previously reported (Lexell et al. 1988; Klitgaard et al. 1990; Hortobágyi et al. 1995).

Male and female differences in motor unit behavior

There are relatively few studies that compare MU behavior and properties between males and females, especially that analyze MUs on a contraction-by-contraction and subject-by-subject basis and regress MU properties against their recruitment thresholds. Harwood et al. (2014) analyzed MU firing rates of the elbow flexors during isometric contractions performed at 15% MVC and reported greater firing rates for males (14.3 pulses per second[pps]) than for females (13.4 pps) when firing rates were pooled. Tenan et al. (2013) observed no differences in pooled initial firing rates of MUs of the VM during isometric knee extensions, but found initial firing rates were altered by menstrual cycle phase in women. Conversely Peng et al. (2018) found pooled initial firing rates of MUs of the VM were 1.18 pps greater for females than males during a straight leg raise. Because of the methods of analyses used, it is difficult to interpret the findings of these studies and it is also the likely cause for the contradictory findings. One study that regressed firing rates recruitment thresholds and analyzed contractions separately reported no differences in MU firing rates between males and females during 10% or 50% MVCs of the FDI (Miller et al. 2017a).

Although studies analyzing differences in MU firing rates between males and females have conflicting results, there appears to be a consistently reported discrepancy in MU action potential amplitudes between males and females. Both Trevino et al. (2018) and Herda et al. (2019b) report greater action potential amplitudes of the higher threshold MUs for males in comparison to females. This suggests higher threshold MUs are larger in males than in females. In addition, the greater action potential amplitudes of higher threshold MUs was correlated with muscle CSA and type II myosin heavy chain content of the VL (Trevino et al. 2018) and with peak torque and power during isometric and isokinetic leg extensions (Herda et al. 2019b).

1.5 DEPENDENCY ON PHYSICAL PROPERTIES AND ADAPTATION TO TRAINING

Muscle cross-sectional area and muscle quality assessed via ultrasonography

Many researchers have begun utilizing B mode ultrasonography as a simple and accurate means of assessing muscle size via anatomical cross-sectional area or muscle thickness (Morse et al. 2005; Fukumoto et al. 2012; Rosenberg et al. 2014; Lopez et al. 2017). In addition, echo intensity has been validated as a measure of muscle quality in terms of the infiltration of fat and other non-contractile tissue within the muscle cross-sectional area (Pillen et al. 2009; Fukumoto et al. 2012; Rosenberg et al. 2014; Young et al.

2015; Stock et al. 2017). As a result many studies involving muscular size or quality in relation to MU properties and/or behavior have begun utilizing the technology as well (Pope et al. 2016; Sterczala et al. 2018b; Miller et al. 2018a, 2019; Trevino et al. 2018; Dimmick et al. 2018). These studies suggest physical differences between individuals or groups in muscle size and quality are reflected in the neuromuscular properties of the muscle.

A recent study by Trevino et al. (Trevino et al. 2018) revealed correlations between the size of higher threshold MUs and muscle cross-sectional area assessed via ultrasonography. Panoramic ultrasound scans of the VL were collected and subjects performed submaximal isometric muscle actions at 40% MVC. Action potential amplitudes of observed MUs during the 40% MVC were regressed against their recruitment thresholds for each subject and contraction. The authors reported a significant correlation between muscle cross-sectional area and the slopes of the MU action potential amplitude vs. recruitment threshold relationships (r = 0.836). This relationship indicated that individuals with larger muscles have larger higher threshold MUs.

Effect of training on motor unit action potential amplitudes

A recent study by Pope et al. (2016) sought to determine the effects of an 8-week high intensity resistance training on muscle size and MU properties. Subjects performed isometric ramp contractions at 100% MVC and surface EMG from the VL was decomposed to yield MU recruitment thresholds and action potential amplitudes which were used to create MU action potential amplitude vs. recruitment threshold relationships for each subject and contraction. Panaramic ultrasound scans of the VL were used to quantify muscle cross-sectional area for each subject before and after the training program. As expected, the 8-week training program results in a 13.7% increase in VL cross-sectional area. However, a novel finding was that the MU action potential amplitude vs. recruitment threshold relationships for the subjects also responded to the training. Specifically, the slope of the relationship steepened, indicating the action potential amplitude of higher threshold MUs was increased following training. The change in muscle cross sectional area accounted for ~84% of the variance in the change in the slope of the MU action potential amplitude vs.

recruitment threshold relationships, thus the authors concluded the slope of the relationship may be effectively used as a non-invasive indicator of high threshold MU specific hypertrophy.

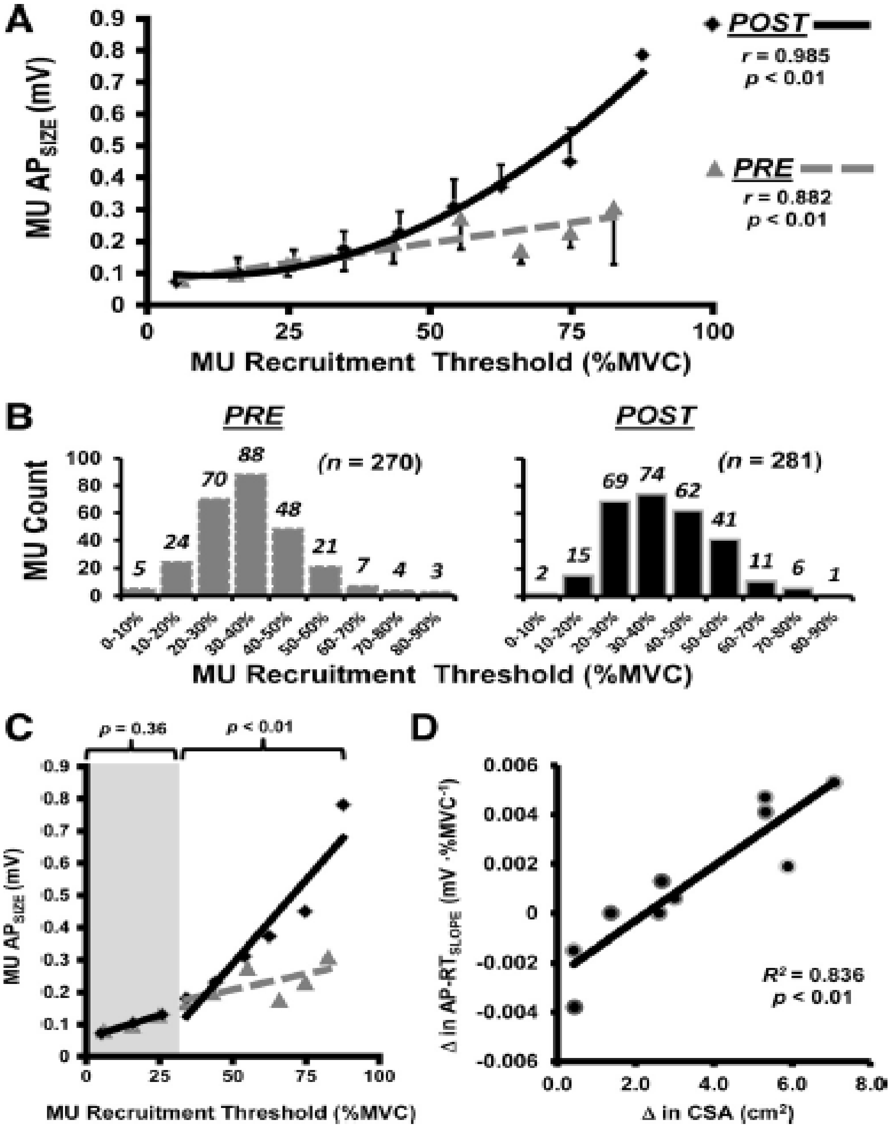


Figure 1.4 A) pooled group data from before (PRE; dashed gray regression line with triangle data points) and after (POST; solid black regression line with diamond data points) training. The data were assessed separately using polynomial regression to determine the best fit model for the relationship betweenmotor unit (MU) action potential amplitude (MU AP_{SIZE}; expressed in mV) and recruitment threshold force [RT; expressed as a %maximal voluntary contraction (MVC)]. The vertical bars represent the SD within each bin (note the bars extend above for the POST data points and below for the PRE data points). B) final number of MUs used for statistical analyses, as well as their distribution across RTs. C) when the slope coefficients were assessed separately using linear regression, only the high-threshold (RT > 30% of MVC) MUs experienced a significant increase with training. D) relationship observed between each individual's change (Δ) in cross-sectional area (CSA) and change in linear slope coefficient for their relationship between MU AP_{SIZE} vs. RT ($\text{AP-RT}_{\text{SLOPE}}$). Adapted from Pope et al. (2016).

Effect of training on motor unit firing rates

Vila Chã et al. (2010) investigated the effects of 6 weeks of either endurance training or strength training on MU firing rates of the VL and vastus medialis obliquus (VMO) in sedentary men. The authors reported mean firing rates decreased following endurance training and increased following resistance training. However, there are several limitations. Firstly, the submaximal contractions where firing rates were measured were performed at 10% and 30% of an MVC performed at the beginning of each trial day, rather than normalized to the pre-training MVC. Because MVC strength was increased for the strength group they were performed contractions at a different force level at post-training in comparison to pre-training, which was not the case for the endurance training group. In addition, recruitment thresholds of MUs were not accounted for which does not allow for a proper understanding of the MUs involved in each task. In either case, this study suggests there are adaptations in MU firing rates in response to training, but further research is needed to fully elucidate such changes.

More recently, a study by Martinez-Valdez et al. (2017) performed a similar study and addressed some of the limitations of Vila Chã et al. (2010). Increases in firing rates were observed again following just 2 weeks of high intensity interval training. However, some MUs were tracked across the training protocol, such that the firing rates of some MUs were directly compared from pre- to post-training. Although absolute force of the contractions where MU firing rates were measured was increased at post-training, the tracking of MUs does allow for the interpretation that at least some of the increases in strength following a short high intensity interval training program results from increases in MU firing rates.

1.6 MU RECRUITMENT AND RATE OF FORCE DEVELOPMENT

Although rate of torque development is a topic of high research attention, few studies have investigated the effect of the rate of torque development on the activity of MUs, in terms of recruitment, firing patterns, and coactivation during isometric force training tasks. De Luca and Contessa (2012) performed isometric contractions of the FDI and the VL with three different rates of force development

(2%, 4%, and 10% MVC/s) during the ramp up phase of isometric contractions to achieve different contraction intensities of 50, 80, and 100%, MVC respectively. It was noted that MU firing rates in relation to recruitment thresholds were greater for the contraction that was performed at the faster rate of force development, but this contraction was also performed at a higher intensity. It would be expected that the greater excitation required to achieve the higher intensity contraction in itself would result in greater MU firing rates (Farina et al. 2010). It is possible that changes in MU firing rates at constant submaximal force levels could occur simply due to altered recruitment strategies during contractions performed with different rates of force development, although no study has measured this directly.

It has been shown that rate of torque development causes differences in MU recruitment patterns when the confounding variable of different target torques has been removed. Desmedt and Godaux (1977) analyzed MU recruitment patterns of the tibialis anterior during submaximal ankle dorsiflexion contractions at different rates of force development. They reported very high rates of force development including ballistic contractions caused MUs to be recruited at progressively lower forces. However, they reported no differences in MU recruitment patterns during slower rates of isometric force development, such as the rates that are commonly used in modern studies of MU behavior. There are a few confounding factors that likely led to finding no changes in recruitment patterns during the slower, more controlled contractions. The target force was set at an absolute 12 kg, rather than a target force relative to each subject’s MVC as is the current standard protocol for MU research (De Luca et al. 1996; Vila-Chã et al. 2010; De Luca and Contessa 2012; Herda et al. 2016; Watanabe et al. 2016; Trevino et al. 2016; Sterczala et al. 2018b; Del Vecchio et al. 2019). In addition, because of limitations of the technology at the time the study was performed, a close examination of MU recruitment and firing behavior could not be performed with relationship-based analyses as only a few MUs could be recorded per contraction.

The only attempt to critically analyze MU recruitment and firing patterns using different controlled rates of force development to achieve a relative submaximal force was performed by Masakado et al. (1995). Similarly to Desmedt and Godaux (1977), the authors reported differences in MU behavior when contractions were performed as fast as possible, but no significant differences in recruitment and firing rate patterns between different controlled rates of force development for the FDI. The rates of force development that were chosen for the study (10% MVC/s vs. 20% MVC/s) are commonly used in the literature (De Luca et al. 1982; Seki et al. 1991; Hu et al. 2013a; Trevino et al. 2016; Muddle et al. 2018), and thus the findings should be generalizable. However, because of limitations in the technology at that time, this study was also not able to provide relationship-based analysis of MU recruitment and firing behavior on a subject-by-subject and contraction-by-contraction basis. A close examination of figure 1.5, which is reproduced from Masakado et al. (1995) shows a slight trend for MUs to be recruited earlier and have slightly greater firing rates during the slow rate of force development (10% MVC/s) in comparison to the faster controlled rate of force development (20% MVC/s). It is possible that an examination of the effect of rate of force development during the linearly increasing ramp phase of submaximal isometric contractions commonly used to analyze MU behavior with modern surface decomposition techniques will elucidate this trend.

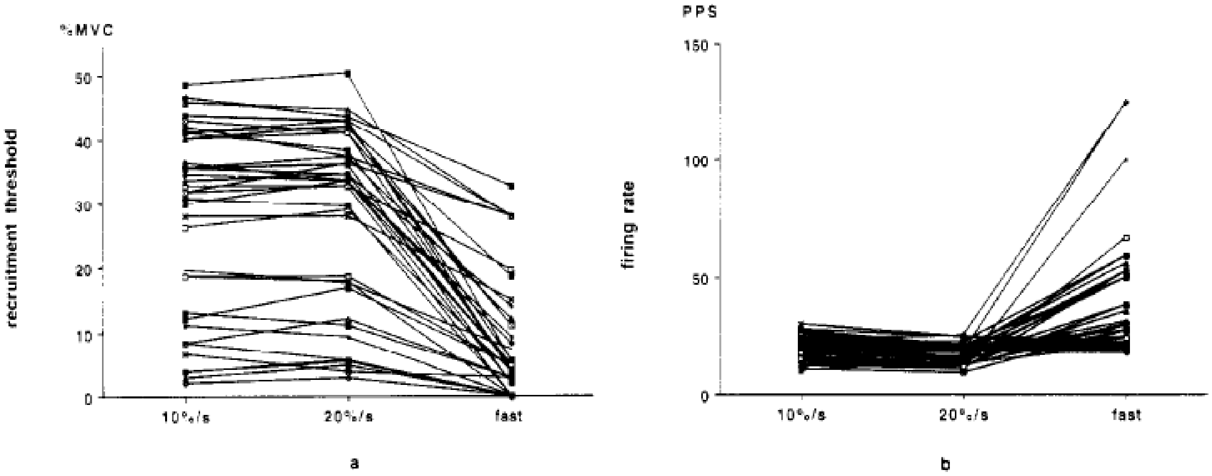


Figure 1.5 Comparison of 10% maximum voluntary contraction (MVC)/s, 20% MVC/s and fast contractions with the a) recruitment thresholds and b) firing rates (pulses per second [pps]) of 40 motor units.

1.7 VERTICAL JUMP AND RATE OF FORCE DEVELOPMENT

Vertical jump is a commonly studied and interpreted measure of explosive or athletic performance, and has been used to test the efficacy of training programs (Vanezis and Lees 2005; Peterson et al. 2006; Hara et al. 2006; McLellan et al. 2011). While it seems intuitive that greater rate of force development (RFD) capabilities would lead to greater jump performance, empirical evidence is split on whether measures of RFD during vertical jumping is directly related to vertical jump height (Vanezis and Lees 2005; Ebben et al. 2007; McLellan et al. 2011).

McLellan et al. (2011) investigated the relationship between RFD and vertical jump height, in a study where 23 physically active men performed counter-movement jumps (CMJ) and squat jumps (SJ). Jump height was measured with a Vertec jumping device and force was quantified by a force plate for all jumps. Although RFD was directly related to vertical jump height (r = 0.68), the force-time variable which had the greatest relationships with vertical jump height was peak power (r = 0.73). Another very important finding was that peak power (ICC = 0.96) and vertical jump height (ICC = 0.98) were both more reliable than peak (ICC = 0.89) and average (ICC = 0.89) RFD. Despite these results, the authors concluded that peak RFD was the greatest predictor of vertical jump performance rather than peak power, in spite of its weaker correlation with vertical jump height and its weaker reliability.

Ebben et al. (2007) sought to investigate potential gender differences in the association between RFD and vertical jump performance. For this study, 24 male and 21 female NCAA Division I Track & Field athletes completed CMJs and force-time variables were analyzed via force plate data. Correlations were examined between average RFD and time to takeoff for males and females. Although there were no significant differences between males and females for RFD (P = 0.11) or time to takeoff (P = 0.08) the means were numerically greater for males (5038 N/s) than females (4118 N/s) as expected. An interesting finding was that there was no relationship between RFD and jump height for males and females (r = 0.19), but there was an inverse relationship between time to takeoff and jump height (r = -0.33).

Vanezis and Lees (2005) separated male soccer players into a high performance group and a low performance group based on vertical jump capabilities and analyzed kinetic and kinematic data in an attempt to understand what separates individuals with high and low jumping capabilities. The results indicated the high performing jumpers produced greater joint powers at the ankle and knee joints and performed greater work at the ankle joint during CMJs in comparison to the low performing jumpers. In addition, these variables were plotted against time and the differences were visually but not statistically analyzed. Although no statistical analysis was done to compare the time dependent differences in these variables between groups, and no traditional measurement of RFD was calculated, the authors discuss the results as indicating greater rate of strength development for the high performing group than the low performing group. Where rate of strength development is a theoretical construct involving fast and forceful activation of muscles that is not necessarily captured by a specific biomechanical measurement but is somewhat estimated by several measurements involving both velocity of movement and force production.

Another study analyzing the relationship between RFD and vertical jump height introduces another important consideration. There are many methods by which RFD can be measured during a vertical jump and the specific method likely influences the relationship observed. Laffaye and Wagner (2013) analyzed CMJs from 178 US national championship level athletes in basketball, football, and baseball. In this study RFD was determined over the eccentric phase of the CMJ only, as the average RFD from the minimum to the maximum force produced during the eccentric phase of the CMJ. The authors conclude that eccentric RFD is the best measurement of RFD, through theoretical rationale only, for predicting vertical jump although it is not actually compared to other methods such as total average RFD, peak RFD, average concentric RFD, or peak concentric RFD which are all commonly used in the literature. Therefore, it is unclear how useful RFD is as a predictor of vertical jump height, which measurement of RFD accounts for the most variability in vertical jump height, and how the subject pool analyzed affects the relationship.

From a theoretical standpoint, in order for RFD to be a valid and useful predictor of vertical jump performance, or of athletic performance, it must be reliably measured during vertical jumps. However, studies analyzing the reliability of RFD have consistently shown it to be highly variable within subjects (Moir et al. 2005, 2009; Sheppard et al. 2008; McLellan et al. 2011; Nibali et al. 2015). Nibali et al. (2015) sought to determine whether kinetic and kinematic variables from maximal CMJs are reliable and whether they are influenced by familiarization. While it was concluded that many kinetic and kinematic CMJ variables are reliable and not affected by familiarization in trained athletes, average eccentric RFD (change in force divided by change in time over the entire eccentric phase) proved to be highly variable. The kinetic variables analyzed in the study, including average concentric force, concentric impulse, and jump height, had very low coefficients of variation within subjects (2.7-3.5%), however eccentric rate of force development had a very high coefficient of variation (21.3%) (Figure 1.6). Corroborating the unreliability of rate of force development during vertical jumps, Moir et al. (2005) analyzed reliability of kinetic variables during static jumps in 9 recreationally active college-aged students and found all variables to be reliable except peak RFD (ICC = 0.53, CV = 12.7%). It should be noted that average RFD was acceptably reliable, although average RFD has been shown to be less related to vertical jump height than other measures of RFD (McLellan et al. 2011).

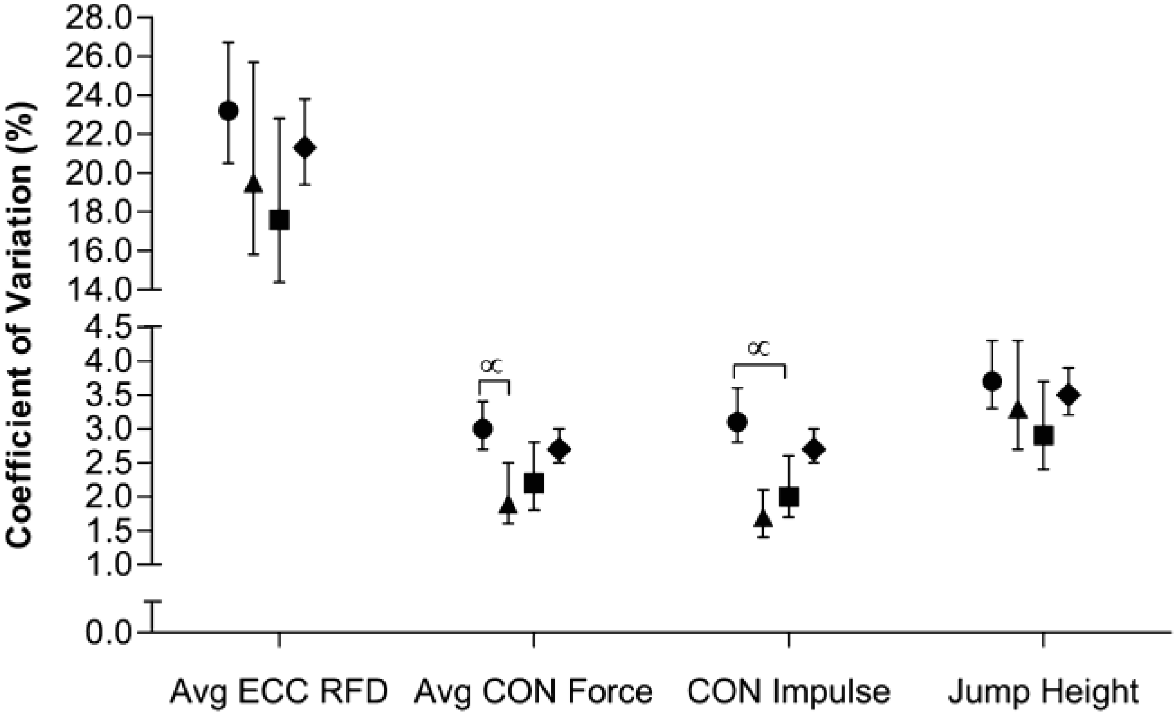


Figure 1.6. Reliability of vertical jump kinetic and kinematic variables expressed as the percent coefficient of variation (%CV) (90% upper and lower confidence limits) for athletes categorized by competitive level: high school (●), college (▲), professional (■), and all (♦). A substantial difference in the reliability of high school compared with the college or professional stratum is denoted by ∝.

1.8 ANALYSIS OF KINETIC AND KINEMATIC DATA VIA MOTION CAPTURE SYSTEMS

Motion capture systems (MCS) have commonly been used in combination with force platforms during vertical jump studies to assess many kinetic and kinematic vertical jump variables simultaneously (Leard et al. 2007; Wagner et al. 2009; Bates et al. 2013). Estimation of vertical jump height via MCS is done by quantifying the change in center of mass (or pelvis) from a normal standing position to peak height during the jump. One study has shown this method of jump height estimation to be largely valid in comparison to the impulse method of estimating jump height (Chiu and Salem 2010). However, it should be noted that the impulse method of jump height estimation is also not free from error when compared to position transducer estimated vertical jump height (Street et al. 2001; Kirby et al. 2011). A comparison of vertical jump height as assessed by MCS analyzed center of mass displacement in comparison to a position transducer would provide a more conclusive assessment of the validity of this estimation method, but there is still good evidence for its validity.

Recent advancements in technology have lead to markerless MCSs which can assess kinetic data typically collected by force plates, in addition to kinematic data. One example of a markerless MCS that has been validated to accurately quantify ground reaction forces is DARI Motion (Scientific Analytics Inc., Overland Park, Kansas). Fry et al. (2016) performed body weight squats with 5 subjects which were simultaneously recorded by the DARI Motion MCS and a traditional force plate. There were no significant differences observed between the ground reaction forces recorded from the force plate and from the MCS and there was very high agreement between the force-time curves from the force plate and the MCS (R=0.995).

Mosier et al. (2019) used the DARI markerless MCS to analyze the kinetic contribution of the upper limbs during vertical jumps. Fourteen recreationally active males performed CMJs with and without arm swings. Dual X-ray Absorptiometry (DEXA) scans were used to determine the mass of the upper limbs in relation to total body mass. During each jump the MCS recorded kinematic variables, and kinetic variables were derived from the kinematic data along with anthropometric estimates which allowed for separate derivations for the full body and for the upper limbs. The results demonstrated a

13.6% (7 cm) decrease in jump height when no arm swing was allowed, and that the upper limbs contributed 31.5% of the peak ground reaction force during the CMJs. The authors concluded the upper limbs have a great influence on the kinetics of the CMJ and that correct arm swing technique during CMJs may be an important variable to consider for performance.

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CHAPTER II: RATIONALE AND SPECIFIC AIMS

Muscle activation during different voluntary contraction conditions and rate of force or torque development are commonly investigated and interpreted phenomena within neuromuscular and biomechanical research. However, while these topics are commonly studied, there may be several underlying considerations which deserve attention from a methodological standpoint, and from an interpretation standpoint. The current work serves to investigate and discuss these considerations in several different applications of neuromuscular and biomechanical areas of exercise physiology research.

Different techniques of quantifying muscle activation, or neural drive, during high-intensity vs. low-intensity fatiguing contraction conditions are commonly used in isolation, such as global EMG characteristics, or analysis of individual motor unit behavior and properties. However, each measure of muscle activation has limitations and is not a comprehensive estimate of neural drive, thus it is important to use a multi-faceted approach to analyzing muscle activation during these different contraction conditions to obtain less biased results. Rate of force or torque development is a topic of high research interest, especially because it has been reported to predict vertical jump height, although these findings are not conclusive. However, less interest has been given to whether rate of torque development alters motor unit behavior during commonly used isometric submaximal trapezoidal contraction protocols. The current work considers whether this multifaceted approach to estimating muscle activation is affected by rate of force development. Finally, previous studies investigating rate of ground reaction force development as a predictor of vertical jump height have had several limitations, such as not controlling for variance accounted for by other variables, and small sample sizes. Multiple regression models were performed to determine whether rate of force development is able to uniquely account for variance in vertical jump height when other variables are included in the prediction model.

SPECIFIC AIMS

Chapter III:

1) To investigate whether moderate-intensity contractions performed to fatigue activate the motor unit pool to the same extent as a higher-intensity contraction.
2) To examine the benefits of analyzing muscle activation via a multifaceted approach including global EMG and single motor unit analysis in comparison to results which might be obtained by only utilizing one method in isolation.

Chapter IV:

1) To determine whether the rate of torque development during the linearly increasing torque phase of commonly used isometric trapezoidal contractions influences motor unit behavior during the steady torque portion of the contraction.
2) To discuss the implications of the effect of rate of torque development on analysis of motor unit behavior and how future researchers may approach this issue in research design.

Chapter V:

1) To examine which of the available estimates of rate of ground reaction force development is best suited to predict vertical jump height, and to examine the predictive capacity of this estimate to predict vertical jump height at the bivariate level.
2) To examine whether the predictive power of rate of ground reaction force development on vertical jump height is due to rate of force development accounting for unique variance in jump height, or whether its relationship with vertical jump height is solely due to its shared variance with other predictors.

CHAPTER III: NEURAL DRIVE IS GREATER FOR A HIGH-INTENSITY CONTRACTION THAN FOR MODERATE-INTENSITY CONTRACTIONS PERFORMED TO FATIGUE

ABSTRACT

The purpose of this study was to investigate whether moderate-intensity contractions performed to fatigue activate the motor unit (MU) pool to the same extent as a higher-intensity contraction. Participants (7 males, 2 females, age=22.78±4.15 yrs, height=173.78±14.19 cm, mass=87.39±21.19 kg) performed three isometric maximum voluntary contractions (MVC), an isometric trapezoidal contraction at 90% MVC (REP_{90}), and repetitive isometric trapezoidal contractions at 50% MVC performed to failure with the first (REP_1) and final repetition (REP_L) used for analysis. Surface EMG was recorded from the vastus lateralis. Action potentials were extracted into firing events of single MUs with recruitment thresholds (RT), MU action potential amplitudes ($MUAP_{AMP}$), and mean firing rates (MFR) recorded. Linear MFR and $MUAP_{AMP}$ vs. RT and exponential MFR vs. $MUAP_{AMP}$ relationships were calculated for each subject. The level of significance was set at $P \leq 0.05$. *B* terms for the MFR vs. $MUAP_{AMP}$ relationships ($P=0.001$, $REP_L=-4.77\pm1.82$ pps/mV, $REP_{90}=-2.63\pm1.00$ pps/mV) and predicted MFRs for MUs recruited at 40% MVC ($P<0.001$, $REP_L=11.14\pm3.48$ pps, $REP_{90}=18.38\pm2.60$ pps) were greater for REP_{90} than REP_L indicating firing rates were greater during REP_{90}. In addition, larger mean ($P=0.038$, $REP_L=0.178\pm0.0668$ mV, $REP_{90}=0.263\pm0.128$ mV) and maximum ($P=0.008$, $REP_L=0.320\pm0.127$ mV, $Rep_{90}=0.520\pm0.234$ mV) $MUAP_{AMPS}$ were recorded during REP_{90} than REP_L. Larger MUs were recruited and similar sized MUs maintained greater firing rates during a high-intensity contraction in comparison to a moderate-intensity contraction performed at fatigue. Individuals seeking maximize activation of the MU pool should utilize high-intensity resistance training paradigms rather than moderate-intensity to fatigue.

INTRODUCTION

The potential of resistance training performed at lower loads to stimulate muscle hypertrophy and strength gains similar to high-load resistance training paradigms is of high research interest (Fry 2004; Schoenfeld et al. 2017). A primary question remains, are motor unit (MU) activation patterns similar between lower-load contractions performed to fatigue and high-intensity contractions? It is hypothesized that the activation of the entire MU pool, as reported during high-intensity contractions, would maximally stimulate muscle protein synthesis and, in theory, result in overall increases muscle hypertrophy and strength (Kraemer and Ratamess 2004).

A recent meta-analysis comparing low- and high-load resistance training protocols concluded that high-load leads to greater increases in strength, but increases in muscle cross-sectional area are similar between low- and high-load resistance training (Schoenfeld et al. 2017). Schoenfeld et al. (2017) reported the average percent increase in 1 repetition maximum (RM) strength was 35.3% for high-load (>60% 1RM) in comparison to 28.0% for low-load (<60% 1RM) training, and increases in muscle size were similar between low- (7.0%) and high-load (8.3%) training protocols. Muscular endurance receives considerably less attention, although Schoenfeld et al. (2015) reported a 16.0% increase in muscular endurance following low-load training in comparison to no improvement for high-load training. Although there is conflicting evidence (Mitchell et al. 2012; Morton et al. 2016), some report muscle fiber type specificity of training, such that low-load training may preferentially hypertrophy muscle fibers that primarily express type I characteristics while high-load training may preferentially hypertrophy muscle fibers that primarily express type II characteristics (Netreba et al. 2013; Vinogradova et al. 2013). While muscles fibers are more accurately represented as possessing characteristics along a continuum rather than distinct groupings (Enoka and Duchateau 2015), it is generally thought that low-threshold MUs are primarily composed of type I fibers and high-threshold MUs are primarily composed of type II fibers (Burke et al. 1973; Bottinelli et al. 1996).

Analysis of MU activity during low-intensity fatiguing and high-intensity contractions may clarify whether similar MUs are involved in such contractions. In voluntary efforts in humans, MUs are recruited in order of increasing size, according to the size principle (Henneman and Olson 1965), and action potential amplitudes are correlated with the diameter of muscle fibers within a MU (Hakansson 1956b). Thus, the size principle can be observed by regressing action potential amplitudes against recruitment thresholds during linearly increasing isometric muscle actions (Milner-Brown et al. 1973a; Hu et al. 2013a). A recently developed model of fatigue analyzed recruitment patterns and activity of MUs during fatigue across different contraction intensities and indicated lower-intensity contractions are far more fatiguing to earlier recruited (lower-threshold) smaller MUs in comparison to high-intensity contractions which resulted in more fatigue to the later recruited (higher-threshold) larger MUs (Potvin and Fuglevand 2017). Therefore, it is plausible that low-intensity fatiguing, and high-intensity contractions will yield differing MU recruitment and firing patterns.

Recruitment thresholds of high-threshold MUs are reported to decrease as fatigue develops (Contessa et al. 2016; Muddle et al. 2018). This is observed during prolonged contractions as new MUs with larger action potential amplitudes are recruited, and during subsequent contractions, as MUs are recruited earlier at lower force levels. Based on these findings, one assumption of the model (Potvin and Fuglevand 2017) is that all MUs, including the largest highest-threshold MUs, would be recruited before exhaustion during lower- or moderate-intensity contractions performed to fatigue. However, previous studies have reported greater electromyographic (EMG) amplitude of the vastus lateralis (VL) during higher-intensity (75-90% of 1RM) than lower-intensity resistance training (30-50% 1RM) of the leg extensors performed to fatigue, including during leg extensions (Jenkins et al. 2015), leg press (Schoenfeld et al. 2014), and back squat (Looney et al. 2016). This would indicate recruitment during low- to moderate-intensity fatiguing contractions does not equal recruitment during high-intensity contractions. There are limitations, however, to interpreting EMG amplitude as a measure of excitatory drive and/or MU recruitment (Farina et al. 2010). There is limited research comparing excitatory drive between lower- and higher-intensity contractions in terms of MU firing rates and recruitment (Muddle et al. 2018). One recent study (Muddle et al. 2018) observed greater MU firing rates and larger action potential amplitudes of the VL during high-intensity contractions (70% MVC) performed to fatigue in comparison to low-intensity contractions (30% MVC) of the leg extensors performed to fatigue. The results indicated, that the repetitive 30% MVCs did not necessitate the excitatory drive or recruitment equal to that of the repetitive 70% MVCs before exhaustion was reached which contrasts what would be predicted by the model (Potvin and Fuglevand 2017) and by other researchers suggesting that low- to moderate-intensity contractions performed to fatigue recruit the entire MU pool (Mitchell et al. 2012; Morton et al. 2019). However, no study has investigated differences in neural drive and MU recruitment between a moderate-intensity contraction performed to fatigue and a single, near maximal, high-intensity contraction.

There are limitations to assessing neural drive and MU recruitment according to global EMG characteristics, not the least of which is amplitude cancellation (Farina et al. 2010). Therefore, the current study will also utilize surface EMG decomposition techniques to analyze MU firing rates, a more robust measure of neural drive (Farina et al. 2010), and MU recruitment via recruitment thresholds and action potential amplitudes (Milner-Brown et al. 1973a; Hu et al. 2013a; Contessa et al. 2016). There are still limitations of analyzing MU recruitment via action potential amplitudes, because they may be altered in the presence of fatigue (Dimitrova and Dimitrov 2003). To partially combat this, we implemented a spike trigger averaging procedure (Hu et al. 2013a, b, c; Thompson et al. 2018) to validate the firing times and to exclude any MUs from analyses where the action potential waveform was unstable during each repetition. Each measure of muscle activation has limitations, which further supports the multi-faceted approach to analyzing muscle activation in the current study.

Therefore, the purpose of the current project is to analyze MU activity during repetitive fatiguing moderate-intensity contractions (50% MVCs) in comparison to a single high-intensity non-fatigued contraction (90% MVC). Results from the present study will provide further knowledge regarding the potential differences in MU activity during such tasks. The purpose of this paper is not to infer hypertrophic or other adaptations which may result from training, however, the findings may offer possible explanations for training load specific adaptations which have been previously reported.

METHODS

Experimental approach to the problem

This investigation employed a repeated-measures design in which all subjects performed isometric leg extensions for a high-intensity contraction and for a series of repeated moderate-intensity contractions which was performed to volitional fatigue. The contractions were performed at relative intensities of 90% (high-intensity) and 50% (moderate-intensity) of maximum voluntary contraction (MVC). Surface EMG decomposition techniques were used for a multi-faceted approach to compare muscle activation via MU activity of the VL during the contractions. This allowed for a more thorough comparison of MU recruitment by observing action potential amplitudes and neural drive via the firing rates of similar sized MUs between contractions than EMG amplitude alone.

Subjects

Participants were comprised of nine healthy individuals between the ages of 18 and 29 (mean ± SD, 7 males, 2 females, age = 22.78 ± 4.15 yrs, height = 173.78 ± 14.19 cm, mass = 87.39 ± 21.19 kg) who volunteered for the study. Participants ranged from recreationally active (~1-3 hrs/wk) to resistance trained (4-8 hrs/wk). Each participant was informed of the potential risks and benefits of participating in the study and voluntarily signed an institutionally approved written informed consent form prior to any data collection. This study was approved by the Human Subjects Committee – Lawrence at the University of Kansas.

Procedures

The participants visited the laboratory two times separated by at least 24 h. The first visit was a familiarization trial followed by an experimental trial. During the first visit, the participants practiced the isometric MVCs and submaximal trapezoidal contractions several times. For all isometric testing, each participant was seated with restraining straps over the pelvis, trunk, and contralateral thigh, and the lateral condyle of the femur was aligned with the input axis of the Biodex System 3 isokinetic dynamometer (Biodex Medical Systems, Inc., Shirley, NY, USA). All isometric leg extensor strength assessments were performed on the right leg with the knee flexed at a 90° joint angle.

During the experimental trial, participants completed a warm-up consisting of three to five brief voluntary isometric contractions from 30%-80% MVC. Participants then performed three isometric MVCs with strong verbal encouragement. The peak force from the three MVCs was used to determine the target force amplitude for subsequent isometric trapezoidal muscle actions at 90% MVC (REP_{90}) and for repetitive contractions at 50% MVC which were performed to failure. The first 50% MVC was considered REP_1 and the last completed 50% MVC was considered REP_L. At least two minutes of rest were given between each MVC, the 90% MVC, and the start of the repetitive 50% MVCs. The rest interval was reduced to 8-9 s between each repetitive 50% MVC. The trapezoidal trajectories consisted of a ramp-up period, where force increased linearly at a rate of 10% MVC/s, a constant force segment at 90% or 50% MVC, which was 12 sec in duration, and a ramp-down where force decreased linearly at 10% MVC/s. Therefore, the duration of the 90% MVC was 30 s and the 50% MVCs were 22 s. Each participant was instructed to maintain their force output as close as possible to the target force presented digitally in real time on a computer monitor. The subjects did have difficulties completing the 90% MVC. The force was relatively unsteady and, in most instances, the subjects completed the isometric trapezoidal templates prior to 30 seconds as their rate of decline was quicker than the template.

Electromyographic Signal Detection and Processing

During the contractions, surface EMG signals were recorded from the VL using a 5-pin surface array sensor (Delsys, Inc., Natick, Massachusetts). The diameter of each pin is 0.5 mm, and they are placed at the corners of a 5 × 5-mm square, with the fifth pin in the center of the square. Prior to sensor placement, the surface of the skin was prepared by shaving and sterilized with an alcohol swab. To remove the dead layers of skin, hypoallergenic tape (3M, St. Paul, Minnesota) was applied to the site, then peeled back to remove contaminants (Delsys, Inc., dEMG User Guide). The surface EMG sensor was placed over the belly of the VL and fixed with adhesive tape while the reference electrode was placed over the contralateral patella.

For the 50% and 90% MVCs, action potentials were extracted into firing events of single MUs from the 4 separate EMG signals, sampled at 20 kHz, via the precision decomposition (PD) III algorithm (version 1.1.0) as described by De Luca et al. (2006). Initially, the accuracy of the decomposed firing instances were tested with the reconstruct-and-test procedure (Nawab et al. 2010). Only MUs decomposed with >90% accuracies were included in the analyses. In addition, a secondary spike trigger average (STA) procedure was included to validate the firing times and action potential waveforms generated via the PDIII algorithm. The derived firing times from the PDIII algorithm were used to STA the 4 raw EMG signals (Hu et al. 2013a, b, c; McManus et al. 2016; Miller et al. 2019). A MU was included in further analyses if there were high correlations ($r>0.70$) across the 4 channels between the PDIII algorithm (version 1.1.0) and STA derived action potential waveforms and the coefficient of variation of the STA derived peak-to-peak amplitudes across time was <0.30 (Hu et al. 2013a). It is possible to observe seemingly valid MU action potential waveforms from trigger events that do not correspond with MU discharges (Farina et al. 2014). To examine this possibility, we added Gaussian noise to the discharge times identified from the PDIII algorithm (Hu et al. 2013b; Thompson et al. 2018). The Gaussian noise added to the firing times was set at 1% of the standard deviation of the inter-spike interval for each MU (Hu et al. 2013b; Thompson et al. 2018). Correlations were performed between the MU action potential waveforms created from the STA procedure with the small amount of noise (<2 ms shift in firing times) added to the firing times and the action potential waveforms derived from the PDIII algorithm. In addition, the peak-to-peak amplitudes of the STA action potential waveforms were compared to the STA action potential waveforms with the addition of Gaussian noise. A small amount of noise added to the firing times should reduce the correlation between action potential waveforms derived from the PDIII algorithm and the STA procedures. In addition, the peak-to-peak amplitudes of the STA action potentials should be diminished with the addition of small shifts in the firing times if no true action potential waveform is consistently present (Figure 1B-C).

For each MU, recruitment threshold (RT [expressed relative to MVC]), MU action potential amplitude ($MUAP_{AMP}$), and the mean firing rate (MFR) during the steady force plateau were recorded. A 2000 ms hanning window was applied to the MU firing instances to create the MFR curves. $MUAP_{AMPS}$ were calculated for each MU according to previous methods (Hu et al. 2013a), as the average peak-to-peak amplitude values from each of the four unique action potential waveform templates using a custom-written software program (LabVIEW 2015, National Instruments, Austin, TX, USA).

If the range of RTs of the sample of MUs recorded in any contraction was less than 12% MVC the contraction was excluded from the RT based relationship analyses, as this may lead to spurious relationship coefficients which do not fall in the physiological ranges for MU data. Additionally, if less than 10 MUs were observed for a 50% MVCs or 6 MUs for a 90% MVC the data were excluded from all relationship based analyses. Data from our lab has indicated when such procedures are followed, the inter-day reliability of the relationship coefficients of interest have excellent reliability (ICCs = 0.801 – 0.901). EMG from REP_1 and REP_L and REP_{90} were expressed as root mean squared amplitude for analysis.

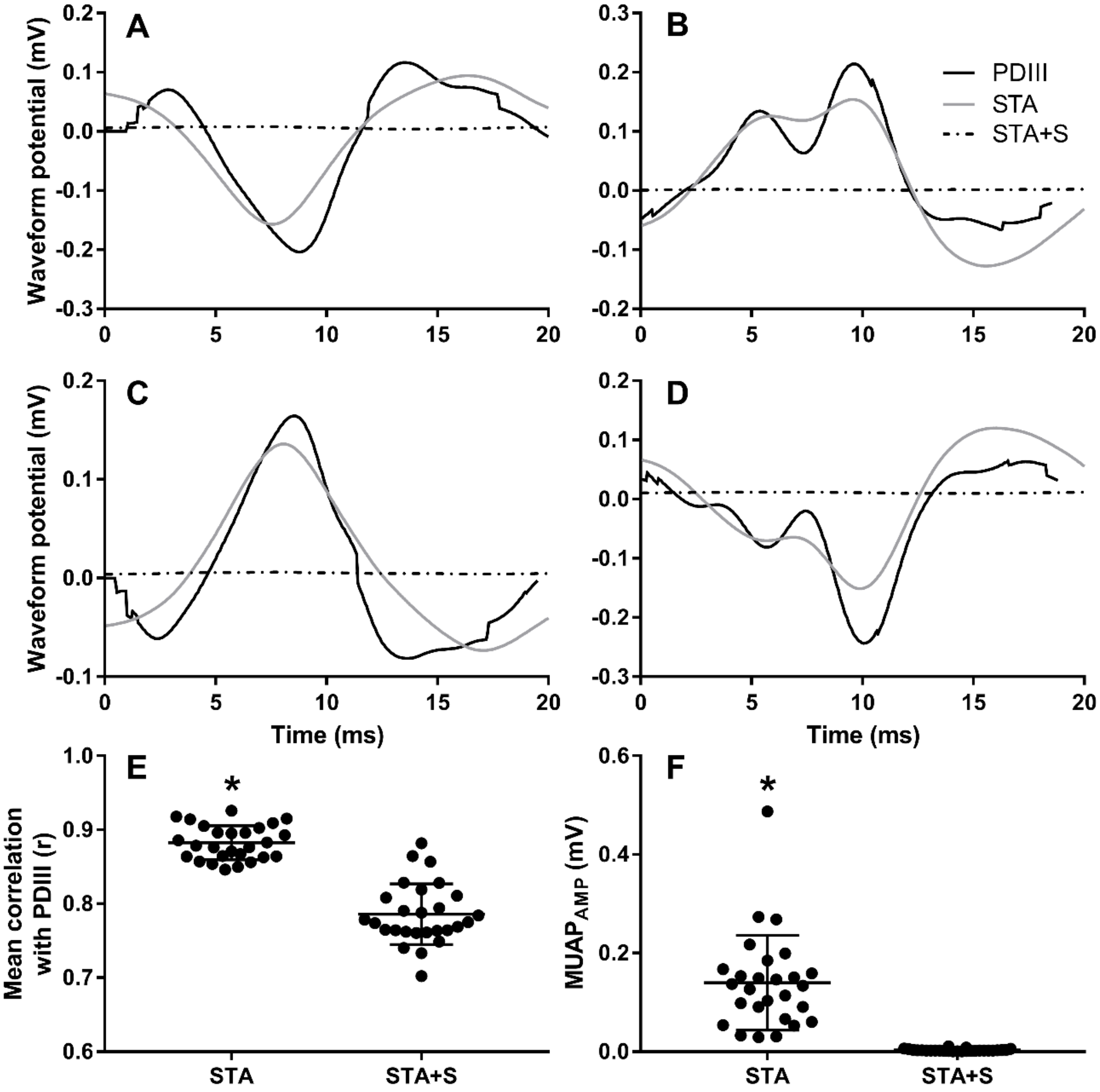

Figure 1. Motor unit (MU) action potential templates as derived from the precision decomposition system III (PDIII), the spike trigger averaging procedure (STA) and the STA with firing times shifted according to Gaussian noise (STA+S) from channels 1-4 (A-D respectively). It is clear that the motor unit action potential waveforms were not present with the shift in firing times. Column scatter plots with mean (SD) bars for the average correlation of STA and STA+G MUAP waveforms with the PDIII derived waveforms (E) and for mean MU action potential amplitudes ($MUAP_{AMPS}$) derived via STA and the STA+S (F). * Indicates that STA+S was significant less than STA.

Statistical Analyses

Linear regressions were performed on the MFR vs. RT and MUAP_{AMP} vs. RT relationships for each subject with the y-intercepts and slopes used for statistical analysis. MFRs for MUs recruited at 40% MVC were predicted according to the composite linear regression equation of the MFR vs. RT relationships for each contraction as indicated by the vertical dotted line in Figure 3A. MFR vs MUAP_{AMP} relationships were fitted with an exponential model in accordance with previous methods (Hu et al. 2013a; Miller et al. 2019) using the following equation: $MFR = Ae^{B(MUAPAMP)}$. Where A is the theoretical MFR of a MUAP_{AMP} of 0 mV, e is the natural constant, and B is the decay coefficient of MFR with increments in MUAP_{AMP}, and the A and B terms were and used for statistical analysis.

A total of 10 one-way mixed-factorial ANOVAs (REP_1 vs. REP_L vs. REP_{90}) were used to examine possible differences in the A and B terms for the MFR vs MUAP_{AMP} relationships, the slopes and y-intercepts for the MFR vs. RT and MUAP_{AMP} vs. RT relationships, the predicted MFRs for MUs recruited at 40% MVC, EMG amplitude, and mean and maximum MUAP_{AMP} (recorded MU with the greatest AP_{AMP}) for each contraction. The difference in correlations coefficients between the PDIII algorithm and STA action potential waveforms with and without Gaussian noise shifted firing times were collapsed across contraction, converted to z-scores using Fisher's Z-Transformation, and the z-scores were analyzed using a dependent samples t-test. In addition, a dependent samples t-test was used to analyze differences in mean MUAP_{amp} between waveforms from STA and STA with Gaussian noise shifted firing times to further demonstrate deterioration of the action potentials with small errors introduced to the firing times identified by the PDIII algorithm. When appropriate, paired-samples *t*-tests were used as follow-ups for significant main effects and Cohen's *d* effect sizes were calculated for each pairwise comparison. The alpha level was set at $P \leq 0.05$, and all statistical analyses were performed using SPSS, version 25 (IBM Corp., Armonk, New York).

RESULTS

The group completed an average of 10±5 repetitions. Following the removal of 39 MUs which failed to meet the validation criteria according to the STA procedures a total of 576 MUs were analyzed in the current study. As expected, the minor Gaussian noise shift in firing times resulted in a significant decrease in the mean peak-to-peak amplitudes (98%, $P<0.001$) of the STA action potentials and the correlations coefficients (11%, $P<0.001$) with the PDIII algorithm derived waveforms (Figure 1). The changes in peak-to-peak amplitudes and correlations with the shifted firing times are similar to what is previously reported by Thompson et al. (2018) and Hu et al. (2013a) who used two different EMG decomposition methods. These findings further validate the firing times and action potential shapes of the MUs recorded in the current study.

Two contractions failed to meet the criteria for inclusion in the RT based relationship analyses as their RT ranges were <12%. Each subject's relationships used for analyses were significant ($r^2 = 0.25 – 0.92$) and demonstrated the expected properties of MU activity regardless of contraction. Together, the three calculated relationships depict that the later recruited higher-threshold MUs were larger and possessed lower firing rates at steady force for each subject and contraction. The recorded MU activity in the present study conforms to the size principle and the onion-skin scheme of firing rates (Hu et al. 2013c). An illustration of the decomposed firing instances of MUs during REP_{90} and REP_L contractions as well as the action potential shapes of a few representative MUs are presented in Figure 2. MU and other EMG data for each repetition are presented in Table 1.

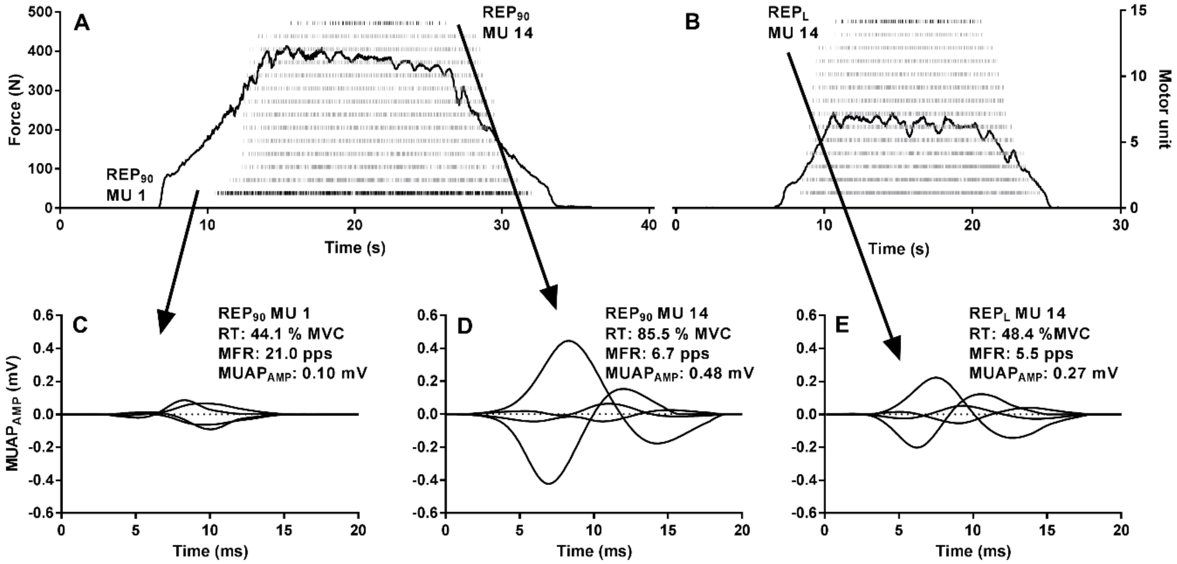

Figure 2. The normalized force and individual motor unit (MU) firing instances during the 90% maximum voluntary contraction (REP_{90}) (A) and the final 50% maximum voluntary contraction (REP_L) of the fatiguing protocol (B) for the same subject. Action potential templates (all 4 recorded channels are shown) from the first (C) and final (D) motor units (MU) recruited that were observed during REP_{90} and the final MU (E) recruited that was observed during REP_L are presented along with their recruitment thresholds (RT), mean firing rates (MFR) and MU action potential waveform amplitudes ($MUAP_{AMP}$). Of note, the defining characteristics of the MU action potentials waveforms are lost due to the scaling.

MFR vs. RT relationships

There was no significant main effect for contraction for the slopes (P=0.277) or for the y-intercepts (P=0.766) of the MFR vs. RT relationships. Therefore, the slopes and y-intercepts of the MFR vs. RT relationships were not significantly different between the high-intensity contraction and the first and last moderate-intensity contraction (Figure 3A). For the predicted MFRs of MUs recruited at 40% MVC, there was a significant main effect for contraction (P<0.001). Dependent samples t-tests indicated predicted MFRs of MUs recruited at 40% MVC were similar between REP_1 and REP_L (P=0.897, *d*=.07, 95% CI [-0.98 to 1.12]), but were greater for REP_{90} than REP_1 (P<0.001, *d*=3.03, 95% CI [1.03 to 4.97]) and REP_L (P=0.005, *d*=2.45, 95% CI [0.71 to 4.13]) (Figure 4D).

MUAP$_{AMP}$ vs. RT relationships

For the slopes, there was no significant main effect for contraction (P=0.137). For the y-intercepts there was a significant main effect for contraction (P=0.032), however, dependent samples t-tests indicated there were no significant differences between REP$_1$ and REP$_L$ (P=0.532, *d*=0.39, 95% CI [-.69 to 1.44), REP$_1$ and REP$_{90}$ (P=.057, *d*=1.15, 95% CI [-0.11 to 2.34]), or REP$_L$ and REP$_{90}$ (P=0.059, *d*=1.41, 95% CI [0.07 to 2.68]) for the y-intercepts (Figure 3B).

Table 1. Means ± standard deviations of the slopes and y-intercepts from the mean firing rate (MFR [pulses per second]) vs. recruitment threshold (RT [% maximum voluntary contraction) relationships and the motor unit action potential amplitude (MUAP$_{AMP}$) vs. RT relationships, and the *A* and *B* terms from the MFR vs. relationships, as well as EMG amplitude, mean and maximum MUAP$_{AMPS}$ for the first (REP$_1$) and last (REP$_L$) repetition of the fatiguing protocol as well as the 90% MVC (REP$_{90}$).

	REP$_1$	**REP$_L$**	**REP$_{90}$**
MFR vs. RT			
Slopes (pps/%MVC)	-0.486 ± 0.256	-0.532 ± 0.209	-0.374 ± 0.061
Y-intercepts (pps)	30.39 ± 9.35	32.45 ±11.25	33.33 ± 3.31
Predicted MFR (pps)	10.92 ± 2.32	11.14 ± 3.48	18.38 ± 2.60*†
MUAP$_{AMP}$ vs. RT			
Slopes (%MVC/mV)	0.00587 ± 0.00413	0.00596 ± 0.00280	0.00913 ± 0.00585
Y-intercepts (mV)	-0.0685 ± 0.103	-0.0318 ± 0.0862	-0.258 ± 0.210
MFR vs. MUAP$_{AMP}$			
A term (pps)	26.21 ± 5.40	28.07 ± 5.56	24.08 ± 4.49
B term (pps/mV)	-4.96 ± 1.95	-4.77 ± 1.82	-2.63 ± 1.00*†
EMG			
Amplitude (mV)	42.99 ± 20.19	69.57 ± 27.18*	100.64 ± 61.16*
MUAP$_{AMP}$			
Mean Amplitude (mV)	0.109 ± 0.0468	0.178 ± 0.0668*	0.263 ± 0.128*†
Maximum Amplitude (mV)	0.219 ± 0.0810	0.320 ± 0.127*	0.520 ± 0.234*†

* Indicates significantly greater than REP$_1$. † Indicates significantly greater than REP$_L$.

MFR vs. MUAP$_{AMP}$ relationships

For the *A* terms, there was no significant main effect for contraction (P=0.201), indicating MFRs of MUs with the smallest AP$_{\mathrm{AMPS}}$ were similar between contractions. However, there was a significant main effect for contraction for the *B* terms (P=0.001). Paired samples t-tests indicated no significant difference between REP$_1$ and REP$_L$ (P=0.731, *d*=0.10, 95% CI [-0.83 to 1.02]), but *B* terms were less negative for REP$_{90}$ than REP$_1$ (P=0.005, *d*=1.50, 95% CI [0.30 to 2.64]) and REP$_L$ (P=0.001, *d*=1.46, 95% CI [0.27 to 2.59]). The decrement in MFRs for MUs with larger AP$_{\mathrm{AMPS}}$ was less pronounced for REP$_{90}$ which indicated larger MUs maintained greater firing rates during the high-intensity contraction than the first or last moderate-intensity contractions (Figure 3C).

EMG amplitude

There was a significant main effect for contraction (P=0.002). Dependent samples t-tests indicated EMG amplitude was greater during REP$_L$ than REP$_1$ (P<0.001, *d*=1.11, 95% CI [0.02 to 2.15]) and during REP$_{90}$ than REP$_1$ (P=0.007, *d*=1.27, 95% CI [0.14 to 2.35]), but was not significantly greater for REP$_{90}$ than REP$_L$ (P=0.076, *d*=0.66, 95% CI [-0.34 to 1.62]). EMG amplitude was greater for both the high-intensity contraction and the last moderate-intensity contraction in comparison to the first. A moderate effect size suggested EMG amplitude was also greater for the high-intensity contraction in comparison to the last moderate-intensity contraction (Figure 4C).

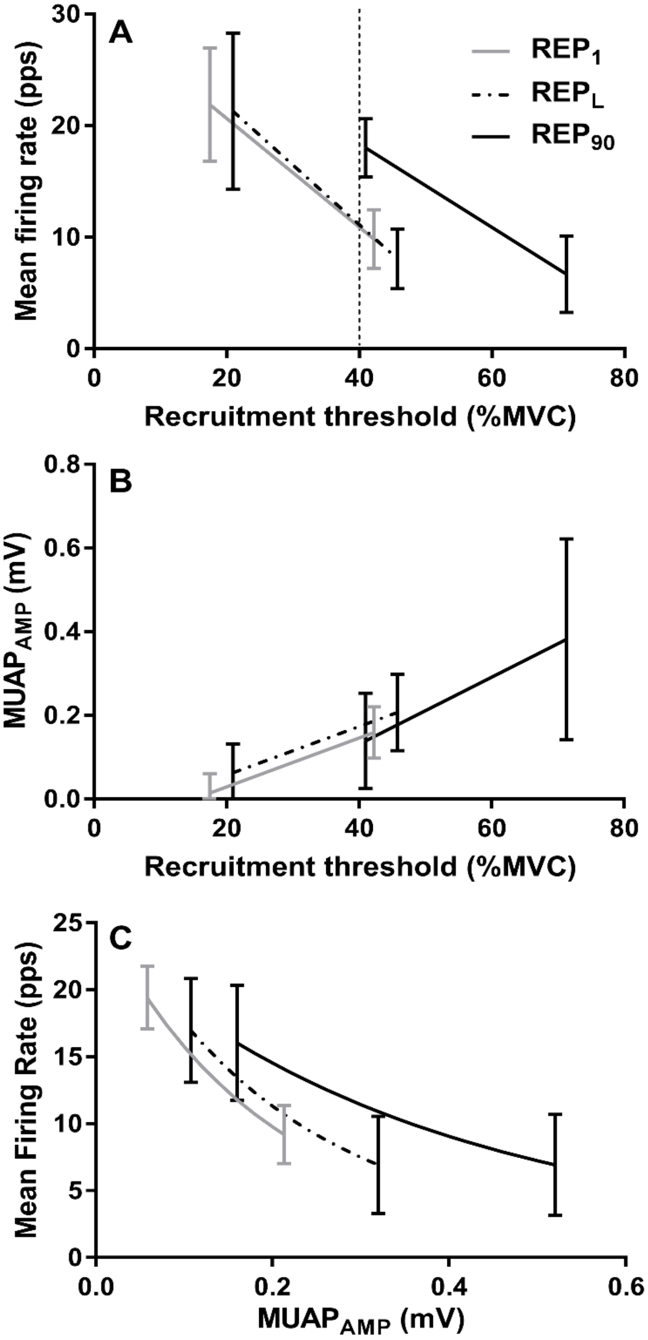

Figure 3. Average predicted mean firing rate (MFR[pulses per second]) vs. recruitment threshold (RT[% maximum voluntary contraction(MVC)]) relationships (A) for the 90% MVC (REP$_{90}$) and the first (REP$_1$) and the last (REP$_L$) 50% MVC performed during the fatiguing protocol. The dotted vertical line shows the predicted MFR of motor units (MU) recruited at 40% MVC for each of the contractions. Average predicted MU action potential amplitude (MUAP$_{AMP}$) vs. RT relationships (B) and MFR vs. MUAP$_{AMP}$ relationships (C) for REP$_{90}$, REP$_1$ and REP$_L$.

Mean and maximum MUAP$_{AMPS}$

There was a significant main effect for contraction for the mean MUAP$_{AMPS}$ ($P<0.001$). Dependent samples t-tests indicated mean MUAP$_{AMPS}$ were greater for REP$_{L}$ ($P<0.001$, *d*=1.20, 95% CI [0.08 to 2.26]) and REP$_{90}$ (P=0.004, *d*=1.60, 95% CI [0.37 to 2.77]) than REP$_{1}$ and were greater for REP$_{90}$ than REP$_{L}$ (P=0.038, *d*=0.83, 95% CI [-0.20 to 1.82]) (Figure 4A). In addition, there was a significant main effect for contraction for maximum MUAP$_{AMPS}$ ($P<0.001$). Dependent samples t-tests indicated maximum MUAP$_{AMPS}$ were greater for REP$_{L}$ (P=0.005, *d*=0.94, 95% CI [-0.11 to 1.95]) and REP$_{90}$ (P=0.002, *d*=1.72, 95% CI [0.45 to 2.93]) than REP$_{1}$, and were greater for REP$_{90}$ than REP$_{L}$ (P=0.008, *d*=1.06, 95% CI [-0.02 to 2.09]) (Figure 4B). Observed MUAP$_{AMPS}$ were largest during the high-intensity contraction despite that MUAP$_{AMPS}$ were greater for the last moderate-intensity contraction in comparison to the first when considering the average observed MUAP$_{AMP}$ and the largest MUAP$_{AMP}$ observed for each contraction.

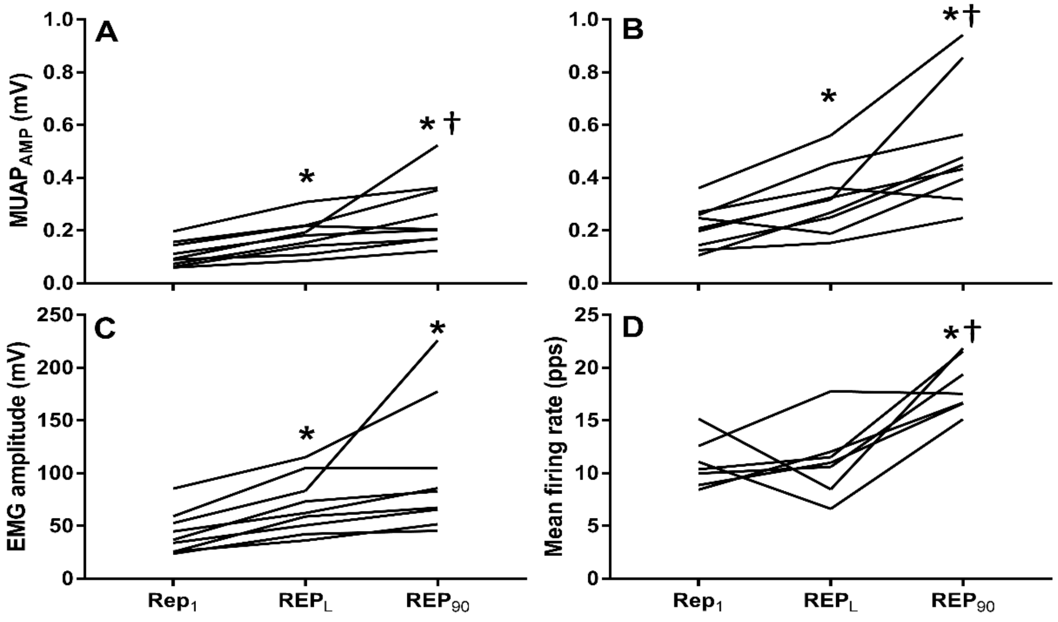

Figure 4. Spaghetti plots illustrating the change in mean motor unit action potential amplitude (MUAP$_{AMP}$) (A), maximum MUAP$_{AMP}$ (B), EMG amplitude (C), and predicted mean firing rate (pulses per second) at 40% maximum voluntary contraction (MVC) (D) from the first (REP$_{1}$) and the last (REP$_{L}$) 50% MVC performed during the fatiguing protocol and for the 90% MVC. * Indicates significantly greater than REP$_{1}$. † Indicates significantly greater than REP$_{L}$.

DISCUSSION

Previous research has reported that over the course of fatiguing protocols consisting of low- to moderate-intensity contractions, EMG amplitude increases (Vila-Chã et al. 2012; Schoenfeld et al. 2014; Jenkins et al. 2015), additional MUs are recruited (Contessa et al. 2016), and firing rates increase (Contessa et al. 2016; Muddle et al. 2018). It is suggested that as fatigue is approached, these measures of excitation and recruitment increase until all MUs are recruited and excitation is maximal (Mitchell et al. 2012; Potvin and Fuglevand 2017). Some of the findings of the current study agree with this theory. There was no significant difference between the 90% MVC and the final 50% MVC for EMG amplitude or the slopes and y-intercepts of the mean firing rate and action potential amplitude vs. recruitment threshold relationships. The initial conclusion from these analyses would be that there were no differences in MU activity between the 90% MVC and the final 50% MVC of the fatiguing protocol.

However, further analyses suggest greater excitation and MU recruitment for the 90% MVC in comparison to the final 50% MVC of the fatiguing protocol. These included: 1) greater predicted firing rates of MUs recruited at 40% MVC (Figures 3A and 4D), 2) greater firing rates of MUs with similar action potential amplitudes (smaller *B* terms for $\mathrm{MUAP_{AMP}}$ vs. RT relationships) (Figure 3C), and 3) greater mean and maximum action potential amplitudes of observed MUs (Figure 4A-B) during the 90% MVC. The greater MU action potential amplitudes tentatively suggest larger MUs were active while the greater firing rates for MUs with a given recruitment threshold or action potential amplitude indicate greater neural drive (Farina et al. 2010) during the 90% MVC in comparison to the last 50% MVC. These findings provide evidence that the operating point of MU control (Contessa et al. 2016) was greater for a high-intensity contraction than for the final repetition of a moderate-intensity fatiguing protocol.

Increased EMG amplitude and $\mathrm{MUAP_{AMPS}}$ suggested excitation increased and additional MUs were recruited for the last 50% MVC in comparison to the first 50% MVC. Although there was a slight trend for greater firing rates for the final 50% MVC (Figure 3A,C), no significant increase in firing rates was observed. These findings generally agree with previous research investigating changes in neural drive and

MU recruitment with fatigue during repetitive contractions. It is typically observed that firing rates increase, recruitment thresholds decrease, and larger MUs are needed to sustain the contractions as fatigue develops (Contessa et al. 2016; Muddle et al. 2018). Only one study (Muddle et al. 2018) has compared fatigue related changes in firing rates and MU recruitment between lower- (30% MVC) and higher- (70% MVC) intensity repetitive contractions. MU recruitment and firing rates were increased with fatigue at both intensities, but greater firing rates and recruitment of larger MUs during the high-intensity condition was reported. Results from the current study agree with those found by Muddle et al. (2018) indicating MU recruitment and neural drive during the final repetition of a moderate-intensity fatiguing protocol did not match that of a higher-intensity condition, although the high-intensity condition in the current study consisted of just a single 90% MVC.

The motoneuron inhibitory effect of central fatigue may explain the decreased neural drive and MU recruitment during the moderate-intensity isometric contraction (Amann 2011). Gandevia et al. (1996b) investigated voluntary activation via interpolated twitch over the time course of sustained isometric MVCs of the elbow flexors and reported high initial voluntary activation (>99%) which decreased over the course of the contraction (90.7%). Feedback from group III/IV afferents associated with metaboreceptors and mechanoreceptors which are activated by muscular contraction do not inhibit initial muscle activation, but increase their inhibitory effect (central fatigue) as a contraction is maintained or repeated in order to constrain peripheral fatigue (Gandevia et al. 1996b; Amann 2011). Furthermore, central fatigue prevents voluntary activation from reaching maximal levels during voluntary submaximal isometric contractions (Löscher et al. 1996) such as in the moderate-intensity contractions in the current study. During prolonged submaximal contractions, firing rates are increased and new MUs are recruited in order to maintain force as peripheral fatigue develops (Contessa et al. 2016; Muddle et al. 2018). However, as the contraction continues, group III/IV afferent feedback inhibits further increases in neural drive or MU recruitment to constrain peripheral fatigue and avoid potentially deleterious effects in the working muscles (Amann 2011).

Therefore, it is plausible that central fatigue inhibits the recruitment of the largest MUs during low- to moderate-intensity submaximal contractions performed to fatigue.

EMG amplitude has previously been observed to be greater during higher- than lower-intensity leg extensions (Jenkins et al. 2015) and leg presses (Schoenfeld et al. 2014) to fatigue. However, in these studies, EMG amplitude appeared to be similar for the last repetitions of the lower-intensity contractions in comparison to the first repetition of the higher-intensity contractions. In the current study, the difference in EMG amplitude from the final rep of the fatiguing 50% MVCs (69.57 ± 27.18%) to the 90% MVC (100.64 ± 61.16%) did not reach significance, but the Cohen's *d* indicated a moderate effect size (0.66) which tentatively suggested EMG amplitude was greater for the single high-intensity contraction than the final moderate-intensity contraction. The EMG amplitude data in the present study does provide support to researchers that caution against over interpretation of this measurements of muscle activation to monitor fatigue. The lack of significant differences between contractions according to EMG amplitude was contrasted by the findings of significant differences in action potential amplitudes and firing rates between contraction intensities. Therefore, examining MU activity via decomposition techniques provides a more complete interpretation of neural drive via firing rates and recruitment via action potential amplitudes of MUs than global EMG amplitude (Farina et al. 2010).

Limitations of the current study include that we cannot determine to what extent action potential amplitudes may have been affected by changes in the metabolic environment due to fatigue and, therefore, interpretations of action potential amplitudes from the current study should be made with caution. In addition, some of the differences in recruitment thresholds between contractions may be due to the algorithm's ability to detect certain MUs under fatiguing and/or high-intensity contractions as well as the physiological changes in recruitment thresholds that occur with fatigue.

The results of the current study also highlight the importance of analyzing this phenomenon from multiple perspectives. There may be many measures by which high-intensity contractions are indistinguishable from fatiguing moderate-intensity contractions, but conclusions should not be drawn from these alone. Many studies have reported similarities between fatiguing low- or moderate-intensity and high-intensity resistance training in terms of hormone responses (Morton et al. 2016), fiber type specific muscle glycogen depletion (Morton et al. 2019), and one study reported similar peak EMG amplitude (Schoenfeld et al. 2016). In addition, studies have reported similar responses to such training programs for strength (Hisaeda et al. 1996; Fisher and Steele 2017) and muscle hypertrophy, in terms of type I and type II fiber cross-sectional area (Morton et al. 2016) or whole muscle cross-sectional area and volume (Hisaeda et al. 1996; Mitchell et al. 2012; Fink et al. 2018). However, the majority of EMG studies report greater muscle activation (Schoenfeld et al. 2014; Jenkins et al. 2015; Looney et al. 2016; Muddle et al. 2018) for high-intensity contractions and the majority of resistance training studies report greater strength gains from high-load programs (Mitchell et al. 2012; Schoenfeld et al. 2015, 2017; Morton et al. 2016). In addition, while gains in hypertrophy from training may be similar, there is evidence for preferential type II muscle fiber hypertrophy from higher-intensity training and preferential type I muscle fiber hypertrophy for lower-intensity training (Netreba et al. 2013; Vinogradova et al. 2013). The current study is not well suited to infer hypertrophic adaptations which may be gained through longitudinal training, but the findings may offer an explanation for training load specific adaptations which have been previously reported. That is, it is plausible this effect is due to higher-threshold MUs being fatigued to a greater extent during high intensity contractions while lower-threshold MUs are fatigued to a greater extent during lower-intensity contractions (Potvin and Fuglevand 2017). Variability among responses in neural drive and recruitment patterns among the contractions was observed (Figure 4), which would likely result in different adaptions following resistance training. Therefore, variability in neural drive during low and high load resistance training among individuals may help explain variability in adaptions following these modes of resistance training.

In summary, greater neural drive and MU recruitment were observed during a single high-intensity contraction than moderate-intensity contractions before or at volitional fatigue. The current findings agree with previous research investigating MU activity during fatigue and comparing muscle activation during high- and low-intensity fatiguing protocols. However, a multifaceted approach to examining muscle activation by analyzing the activity of individual MUs provided a more comprehensive investigation than previous studies analyzing EMG amplitude alone. It is speculated that group III/IV afferent inhibition prevented neural drive and MU recruitment during the fatiguing moderate-intensity contractions to equal that of the high-intensity contraction.

Practical Application

The current findings have implications for models of MU activity during fatigue and resistance training paradigms. We have provided further evidence that moderate-intensity contractions performed to volitional fatigue appear to not equal the levels of neural drive and recruitment that are observed in high-intensity contractions. The different contractions (high-intensity vs. fatigued moderate-intensity) in the current study would presumably stress and adapt a different subpopulation of MUs and comprising muscle fibers. Individuals, coaches, and practitioners should recognize that fatiguing bouts performed at low-to-moderate intensities may not include a significant amount of activity of the higher-threshold MUs where the largest skeletal muscle fibers are generally present.

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CHAPTER IV: THE EFFECT OF RATE OF TORQUE DEVELOPMENT ON MOTOR UNIT RECRUITMENT AND FIRING RATES DURING ISOMETRIC VOLUNTARY TRAPEZOIDAL CONTRACTIONS

ABSTRACT

It is common practice to examine motor unit (MU) activity according to mean firing rate (MFR) and action potential amplitude ($MUAP_{AMP}$) vs. recruitment threshold (RT) relationships during isometric trapezoidal contractions. However, it is unknown whether the rate of torque development during the linearly increasing torque phase affects the activity of MUs during such contractions. Sixteen healthy males and females performed two isometric trapezoidal muscle actions at 40% of maximum voluntary contraction (MVC), one at a rate of torque development of 5% MVC/s ($SLOW_{40}$) and one at 20% MVC/s ($FAST_{40}$) during the linear increasing torque phase. Surface electromyography (EMG) was recorded from the vastus lateralis (VL) via a 5-pin surface array sensor and decomposed into action potential trains of individual MUs, yielding MFR and $MUAP_{AMP}$ which were regressed against RT separately for each contraction. Surface EMG amplitude recorded from leg extensors and flexors was used to quantify muscle activation and coactivation. MFR vs. RT relationship slopes were more negative ($P=0.003$) for the $SLOW_{40}$ (-0.491±0.101 pps/%MVC) than $FAST_{40}$ (-0.322±0.109 pps/%MVC) and the slopes of the $MUAP_{AMP}$ vs. RT relationships ($P=0.022$, $SLOW_{40}=0.0057\pm0.0021$ mV/%MVC, $FAST_{40}=0.0041\pm0.0023$ mV/%MVC) and muscle activation of the extensors ($P<0.001$, SLOW40=36.3±7.82%, $FAST_{40}=34.0\pm6.26\%$) were greater for $SLOW_{40}$ than $FAST_{40}$. MU Firing rates were lower and action potential amplitudes were larger in relation to recruitment thresholds for a contraction performed at a slower rate compared to a faster rate of isometric torque development. Differences in MU activity can exist as a function of rate of torque development during commonly performed isometric trapezoidal contractions.

INTRODUCTION

The Onion-Skin scheme of motor unit (MU) control describes the organization of MU recruitment with regards to firing rate activity during submaximal isometric voluntary contractions in humans (De Luca and Erim 1994; Masakado et al. 1995; De Luca and Hostage 2010; De Luca and Contessa 2012, 2015), where earlier recruited lower-threshold MUs maintain greater firing rates than later recruited higher-threshold MUs regardless of force and time. In addition, action potential amplitudes are correlated with the diameter of muscle fibers within a MU (Hakansson 1956b) and, therefore, the size principle (Henneman 1957) can be observed by regressing action potential amplitudes against recruitment thresholds (Milner-Brown and Stein 1975; Goldberg and Derfler 1977; Masakado et al. 1994; Conwit et al. 1999; Hu et al. 2013a; Pope et al. 2016; Sterczala et al. 2018b; Martinez-Valdes et al. 2018; Miller et al. 2018b). The Onion-Skin scheme and the size principle as measured with the MU action potential amplitudes regressed against recruitment thresholds (Hu et al. 2013a; Sterczala et al. 2018b) are most apparent when MU activity is characterized on a subject-by-subject and contraction-by-contraction basis. As a result, it is common practice to examine potential differences in MU activity as a function of contraction intensity (De Luca and Contessa 2012; Hu et al. 2013a), fatigue (Adam and De Luca 2005; Contessa et al. 2016), exercise interventions (Stock et al. 2012; Pope et al. 2016), coactivation (Contessa et al. 2018), and contractile properties of the muscle (Trevino et al. 2016; Colquhoun et al. 2018a) by comparing the MU firing rate and action potential amplitude vs. recruitment threshold relationships.

Many studies analyzing individual MU activity in humans use isometric trapezoidal contractions with a linearly increasing torque (ramp-up) phase preceding a constant torque phase where a submaximal torque level relative to maximum voluntary contraction (MVC) is maintained followed by a linearly decreasing torque (ramp-down) phase where torque is returned to baseline (De Luca and Hostage 2010; Stock et al. 2012; Hu et al. 2013a; Trevino et al. 2016; Del Vecchio et al. 2018; Martinez-Valdes et al. 2018). It is also common amongst such research to use contraction intensities of 40% MVC (Vander Linden et al. 1991; Hu et al. 2013a; Herda et al. 2015; Trevino et al. 2016; Sterczala et al. 2018b) and analyze motor units from the vastus lateralis (Adam and De Luca 2005; De Luca and Contessa 2012; Stock et al.

2012; Contessa et al. 2016; Colquhoun et al. 2018b). Thus, these methods were also used in the current study. However, very little is known about the effect of the rate of torque development during the linearly increasing torque phase on the activity of MUs, in terms of recruitment, firing patterns, and coactivation during such contractions. Although 10% MVC/s is a common rate of force/torque development used in studies of motor unit activity, various rates of torque development have been used to achieve different contraction intensities (De Luca and Contessa 2012; Stock et al. 2012; Trevino et al. 2016) including 5% MVC/s (Vander Linden et al. 1991; Klein et al. 2001; Del Vecchio et al. 2019) and 20% MVC/s (Seki et al. 1991; Masakado et al. 1995). For the current study, the rates of torque development examined were 5% and 20% MVC/s in order to ensure the differences in rate of torque development were sufficient to observe any potential differences in motor unit activity.

De Luca and Contessa (2012) performed isometric contractions of the first dorsal interosseous and the vastus lateralis (VL) with three different rates of linearly increasing force development of 2%, 4%, and 10% MVC/s to achieve different contraction intensities of 100%, 80%, and 50% MVC, respectively. The authors reported greater firing rates in relation to recruitment threshold for the higher intensity contraction that was performed at the faster rate of force development. The greater excitation required to achieve the higher intensity contraction will result in greater MU firing rates (Farina et al. 2010). However, there could also be changes in firing rates in relation to recruitment thresholds as a function of altered recruitment strategies during different rates of force development. Desmedt and Godaux (1977) reported MUs of the tibialis anterior were recruited at progressively lower forces with increases in rates of force development during ankle dorsiflexion ballistic contractions with no differences observed during slower rates of isometric force development. However, the target force was set at an absolute 12 kg for each subject and few MUs were recorded per contraction, which did not allow for a systematic examination of MU recruitment and firing rate patterns as can be performed with relationship-based analyses. In contrast, Masakado et al. (1995) observed non-significant differences in recruitment and firing rate patterns between different slower rates of force development (10% MVC/s vs. 20% MVC/s) for the first dorsal interosseous. However, similar to Desmedt and Godaux (1977) a thorough examination of MU activity on a contraction-by-contraction basis could not be performed as few MUs were recorded. Therefore, it remains unclear if MU recruitment and firing rate patterns differ between different slower rates of force development. While some studies have investigated altered motor unit activity (Desmedt and Godaux 1977; Masakado et al. 1995; De Luca and Contessa 2012) or muscle activation (Tomko et al. 2018) during contractions at different rates of torque development, limitations in their methodologies inhibit the generalizability of their findings to current methods of collecting and analyzing MU activity during voluntary contractions. To our knowledge, no study has compared MU activity across slower rates of torque development at the same relative submaximal force levels while using high-yield decomposition techniques that allow for MU activity to be analyzed on a subject-by-subject and contraction-by-contraction basis in order to avoid biases of recruitment thresholds and inter-individual variability (De Luca and Hostage 2010; De Luca and Contessa 2012).

Currently, interpretations of motor unit activity are made without respect for the influence of the rate of torque development on the findings. If MU activity is significantly affected by rate of torque development, 1) the findings of such studies may not be generalizable to all rates of torque development, 2) additional care may be needed in order to ensure compliance with torque trajectories during ramp phases, and 3) it is possible that relationships observed between MU properties and contractile properties of the muscle may be better elucidated at other rates of torque development. Therefore, the examination of MU activity during different rates of force development via firing rate and action potential amplitude vs. recruitment threshold relationships and EMG amplitude is warranted. We have examined mean firing rate and MU action potential amplitude vs. recruitment threshold and mean firing rate vs. MU action potential amplitude relationships of the VL between two 40% MVC leg extensions which only differed with respect to the rate of torque development (5% MVC/s vs. 20% MVC/s) during the linearly increasing torque phase. In addition, muscle activation (EMG) of the leg extensors (VL, vastus medialis [VM] and rectus femoris [RF]) and flexors (semitendinosus [ST] and biceps femoris [BF]) was measured to examine potential differences in coactivation that may have altered MU activity of the VL (Contessa et al. 2018) between the contractions with different rates of torque development.

METHODS

Subjects

Ten healthy males (age=21.1±2.1 years, stature=170.4±24.8 cm, mass=82.4±32.4 kg) and 6 healthy females (age=19.6±1.2 years, stature=167.8±5.7 cm, mass=63.8±9.9 kg) participated in this study. Exclusion criteria included any previous or current neuromuscular diseases or musculoskeletal injuries to the ankle, knee or hip joints.

Compliance with Ethical Standards

The authors declare that they have no conflict of interest. The institutional review board for human subjects research at The University of Kansas approved this study and it was conducted in accordance with the *Declaration of Helsinki*. All subjects read and signed an informed consent form and completed a pre-exercise health status questionnaire.

Isometric Testing

The participants visited the laboratory two times separated by at least 24 hours. The first visit was a familiarization trial followed by an experimental trial. During the first visit the participants completed 4 practice MVCs (2 extension and 2 flexion) and 6-10 practice submaximal trapezoidal contractions depending on how quickly they were able to learn the task. The subject’s torque output from each practice trial was visually inspected for accuracy with the torque trajectory. Subjects were determined to be properly familiarized when they were able to comply closely with the given torque trajectory.

For isometric testing each participant was seated with restraining straps over the pelvis, trunk, and contralateral thigh, and the lateral condyle of the femur was aligned with the input axis of the Biodex System 3 isokinetic dynamometer (Biodex Medical Systems, Shirley, NY) in accordance with the Biodex User’s Guide (Biodex Pro Manual, Applications/Operations, 1998). All isometric leg extensor strength assessments were performed on the right leg at a flexion of 90°. Isometric strength was measured using the torque signal from the isokinetic dynamometer. A brief warm-up consisting of 6 isometric leg extensions between 30-90% of perceived MVC was performed prior to the experimental protocol. During the experimental trials, participants performed two isometric knee extension MVCs and two isometric knee flexion MVCs. Strong verbal encouragement was provided for motivation during each MVC trial. Subjects were asked to give full effort during each of the MVCs. Also, for each MVC, a countdown was given, and the word “push” was spoken at a relatively high frequency and at a volume slightly greater than normal conversational volume for the duration of the MVC. Following the MVCs, subjects completed two submaximal isometric trapezoidal knee extensions at 40% MVC. The highest torque output averaged over a 0.25-seconds epoch for the MVCs determined the maximal torque output for each participant and the torque level for the 40% MVCs. The average CV between MVCs was 4.8% indicating MVC torque was very consistent between MVCs. The two 40% MVCs were completed with different rates of torque development during the linear increasing torque phase. One increased at 5% MVC/s ($SLOW_{40}$) and the other at 20% MVC/s ($FAST_{40}$) to the desired torque level, which was held constant for 12 seconds for a $SLOW_{40}$ or for 18 seconds for a $FAST_{40}$. Torque was decreased to baseline at a rate of 10% MVC/s for both 40% MVCs. Therefore, the duration of each 40% MVC was 24 seconds. Three minutes of rest were given prior to each MVC, and 5 minutes of rest were given prior to each 40% MVC. The order of the 40% MVCs with respect to their rate of torque development ($SLOW_{40}$ vs. $FAST_{40}$) was randomized for each subject. During the 40% MVCs participants maintained their torque output as close as possible to the torque trajectory template displayed digitally on a computer monitor.

EMG Recording

During the contractions, surface EMG signals were recorded from the vastus lateralis (VL) using a 5-pin surface array sensor (Delsys, Inc., Natick, Massachusetts). The diameter of each pin is 0.5 mm, and they are placed at the corners of a 5 × 5-mm square, with the fifth pin in the center of the square. Bipolar surface electrodes (Delsys, Inc., Natick, Massachusetts) recorded EMG activity from the leg extensors (VL, RF, and VM) and flexors (ST and BF) during all contractions. Before sensor and reference electrode placement, the surface of the skin was prepared by shaving, removing superficial dead skin with adhesive tape, and sterilizing with an alcohol swab. To remove the dead layers of skin, hypoallergenic tape (3M, St. Paul, Minnesota) was applied to the site, then peeled back to remove contaminants (Delsys, Inc., dEMG User Guide). The specific locations of the sensors were as follows: VL) 67% of the distance from the anterior superior iliac spine to the lateral border of the patella, VM) 80% of the distance from anterior superior iliac spine to the medial epicondyle of the femur, RF) 40% of the distance from anterior superior iliac spine to the superior border of the patella, ST) 50% of the distance from ischial tuberosity to medial epicondyle of tibia, BF) 50% of the distance from ischial tuberosity to lateral epicondyle of tibia. The sensors were secured in their locations by adhesive tape. The reference electrode was placed over the left patella (Horita and Ishiko 1987; Rattey et al. 2006; Jubeau et al. 2010; Trevino et al. 2016).

EMG Decomposition

For the 40% MVCs, the surface array sensor action potentials were extracted into firing events of single MUs from the 4 separate EMG signals, sampled at 20 kHz, via the precision decomposition III algorithm (version 1.1.0) as described by De Luca et al. (2006). The precision decomposition III algorithm provides 4 unique action potential waveforms for each EMG channel. Initially, the accuracy of the decomposed firing instances were tested with the reconstruct-and-test procedure (Nawab et al. 2010). Only MUs decomposed with >90% accuracies were included in the analyses. In addition, a secondary spike trigger average (STA) procedure was included to validate the firing times and action potential waveforms generated via the precision decomposition III algorithm. The derived firing times from the precision decomposition III algorithm were used to STA the 4 raw EMG signals (Hu et al. 2013a, b, c; McManus et al. 2016). A MU was included in further analyses if there were high correlations (r>0.70) across the 4 channels between the precision decomposition III algorithm (version 1.1.0) and STA derived action potential waveforms and the coefficient of variation of the STA derived peak-to-peak amplitudes across time was <0.30 (Hu et al. 2013a). For each MU, recruitment threshold (RT), MU action potential amplitude ($MUAP_{AMP}$), and the mean firing rate (MFR) during the constant torque period were determined. A 2000 ms hanning window was applied to the MU firing instances to create the MFR curves. $MUAP_{AMPS}$ were calculated for each MU according to previous methods (Hu et al. 2013a; Pope et al. 2016; Miller et al. 2018b; Sterczala et al. 2018a), as the average peak-to-peak amplitude values from each of the four unique action potential waveform templates using a custom-written software program (LabVIEW 2015, National Instruments, Austin, TX, USA). For the 40% MVCs, a linear model was fitted to the MFR vs RT relationships (De Luca et al. 1996; Herda et al. 2015; Miller et al. 2017a) and $\mathrm{MUAP}_{\mathrm{AMP}}$ vs. RT relationships (Hu et al. 2013a; Sterczala et al. 2018a) for each subject with the y-intercepts and slopes used for statistical analysis. The following exponential model (Sterczala et al. 2018b, a; Miller et al. 2018b) was applied to the MFR vs. $\mathrm{MUAP}_{\mathrm{AMP}}$ relationships:

$$MFR = Ae^{B(MUAPAMP)}$$

Where A is the theoretical MFR of a $\mathrm{MUAP}_{\mathrm{AMP}}$ of 0 mV, e is the natural constant and B is the decay coefficient of MFR with increments in $\mathrm{MUAP}_{\mathrm{AMP}}$. Pearson product moment correlations were performed to test for significance. Any contractions without an observed recruitment range of MUs > 12% MVC, or with less than 10 MUs accurately decomposed after the reconstruct-and-test and STA procedures were excluded from further analysis.

Signal Processing

All 4 channels of the 5-pin EMG sensor, which was the only sensor that recorded EMG from the VL, are needed for decomposition. However, only channel 1 of the 4 channels was used for amplitude analysis in order to match the bipolar EMG recording sensors used for amplitude analysis of the VM, RF, BF, and ST. The torque (N•m) and the EMG (mV) signals from channel 1 of the surface array sensor (VL) as well as the signal from each of the bipolar EMG electrodes recording from the RF, VM, ST, and BF were recorded with a NI cDAQ (National Instruments, Austin, TX USA) for each MVC and with a NI BNC 2090a (National Instruments, Austin, TX USA) for each 40% MVC. The sampling frequency for torque and EMG signals was 2,000 Hz for the MVCs and 20,000 Hz for the 40% MVCs. Data was stored on a personal computer for subsequent analysis. The EMG signals were bandpass filtered (zero phase fourth-order Butterworth filter) at 10–500 Hz, while the torque signal was low-pass filtered with a 10-Hz cutoff (zero-phase fourth order Butterworth filter). EMG amplitude was expressed as root mean square amplitude values calculated by custom written software (LabVIEW v 15.0; National Instruments, Austin, TX). All EMG calculations were performed on the filtered signals. MVC torque and peak EMG amplitude of agonist muscles (VL, VM, and RF) were recorded during the highest 0.25 sec average torque (N•m) that occurred during the two extension MVCs, while peak EMG of antagonist muscles (ST and BF) were determined from the highest 0.25 sec average torque during the two flexion MVCs. EMG amplitude values from the 40% MVCs were normalized (N-EMG) as a percentage of the peak EMG for further analysis. For the 40% MVCs, MFR, N-EMG, torque, and CV of torque were analyzed over a 10 sec epoch at the beginning of the constant torque phase. The total duration of the contraction and the duration of the epoch of analysis were equated between SLOW_{40} and FAST_{40} contractions in order to minimize differences in the time related changes in motor unit activity such as potentiation, firing rate adaptation, and fatigue (Dorfman et al. 1990; Adam and De Luca 2005; Potvin and Fuglevand 2017; Miller et al. 2017b). MUs not active the entire 10 sec epoch were excluded from analysis. For analysis of N-EMG, the average N-EMG of the three extensor muscles (VL, VM, and RF) was considered extensor N-EMG and the average of the two flexor muscles (ST and BF) was considered flexor N-EMG. N-EMG amplitude at torque levels of 24-26% MVC during the linearly increasing torque phase was recorded during the SLOW_{40} and FAST_{40}. This epoch around 25% MVC was selected to quantify N-EMG during the linear increasing torque phase as it is near the upper recruitment range of MUs that were observed for the SLOW_{40} and is also within the recruitment rage of the FAST_{40}.

Statistical Analysis

Recording only MUs encompassing a small range of RTs could potentially lead to spurious coefficients from the regressions (Pope et al. 2016; Colquhoun et al. 2018b; Herda et al. 2019b; Miller et al. 2019). Therefore, contractions were included in the analyses if they met both of the following criteria: 1) at least 10 MUs were identified and 2) the range of RTs of the MUs observed was greater than 12% MVC. Because of the repeated measures design of the study, subjects who did not meet the inclusionary criteria for both contractions were not included in further analyses. Four subjects were eliminated, thus statistical analyses were completed on the remaining 12 subjects. Males and females were analyzed together as the primary interest was changes in MU activity as a function of different rates of torque development rather than previously reported sex-related differences in firing rates and action potential amplitudes (Tenan et al. 2013; Peng et al. 2018; Trevino et al. 2018). Following the reconstruct-and-test and STA validation procedures, 232 MUs did not meet the criteria and were not included in the analyses. Additionally, 13 MUs which were not active during the entire steady force and were not included in the analyses.

Paired samples t-tests were used to analyze possible differences between SLOW_{40} and FAST_{40} for the lowest and highest RT and MUAP_{AMP} of MUs observed in each 40% MVC, for torque and CV of torque during the constant torque period, and for root mean squared error (RMSE) between torque and the torque trajectory template. Paired samples t-tests were also used to compare the coefficients of the MFR and MUAP_{AMP} vs. RT relationships and the MFR vs. MUAP_{AMP} relationships between SLOW_{40} and FAST_{40}. Two separate two-way repeated-measures ANOVAs (rate of torque development [SLOW_{40} vs. FAST_{40}] × muscle group [extensors vs. flexors]) were used to analyze potential differences in N-EMG between the agonists (extensors) and the coactivation of the antagonists (flexors) during the linear increasing torque and the constant torque phases. In addition, paired samples t-tests were performed as a follow-up to significant interactions where necessary. Nonparametric Wilcoxon signed ranks tests were performed in place of parametric t-tests for all data that a Shapiro-Wilk's test determined were not normally distributed. An α of 0.05 was used to determine statistical significance. Statistical analyses were performed using IBM SPSS Statistics v. 25 (SPSS Inc., Chicago, IL). All figures were created using GraphPad Prism v. 7 (GraphPad Software, San Diego, CA).

RESULTS

A total of 703 MUs met the inclusion criteria following the reconstruct-and-test and STA validation procedures. Subsequently, 26.2±7.4 MUs were analyzed per SLOW_{40} and 32.4±8.8 MUs were analyzed per FAST_{40}. All MFR vs. RT (r=-0.84 to -0.98), MFR vs. MUAP_{AMP} (r=-0.77 to -0.96), and MUAP_{AMP} vs.

RT (r=0.63 to 0.92) relationships were significant. A representative illustration of the 40% MVCs and the MU data observed from one subject is depicted in Figure 1.

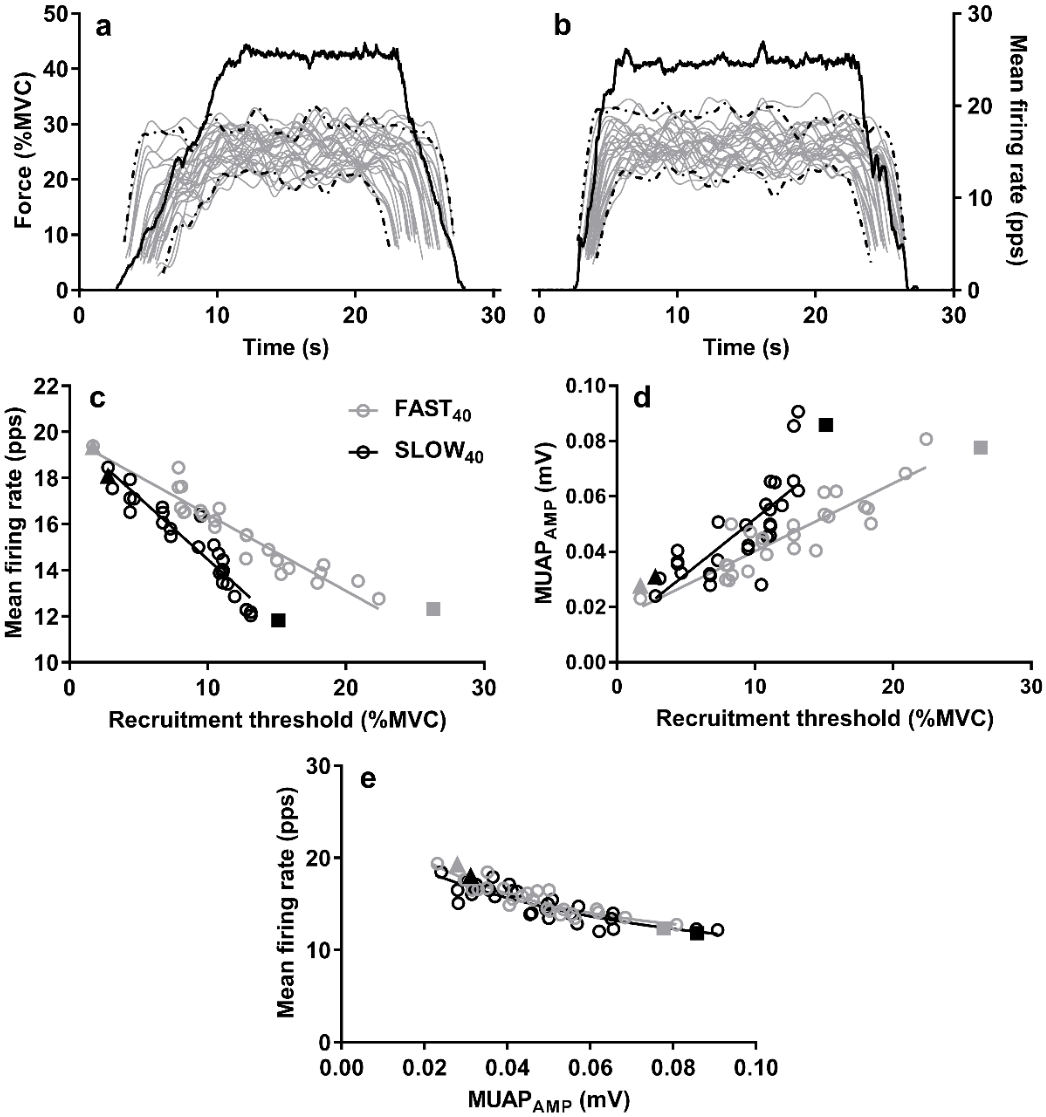

Figure 1. Illustration of the slow ($SLOW_{40}$) (a) and fast ($FAST_{40}$) (b) rate of torque development contractions from a representative subject. Thick black lines represent the subject's torque tracing. Thin grey lines represent motor unit (MU) mean firing rate (MFR [pulses per second]) curves. The dashed black lines are MFR curves of the first and last recruited MUs which are further illustrated in the subsequent plots. The subject's MFR vs. recruitment threshold (RT) (c), MU action potential amplitude ($MUAP_{AMP}$) vs. RT (d), and MFR vs. $MUAP_{AMP}$ (e) relationships plotted with lines of best fit

For all recorded MUs, RTs were similar ($P=0.978$) between $SLOW_{40}$ (6.97±5.11 %MVC) and $FAST_{40}$ (6.95±6.19 %MVC) for the lowest-threshold MUs, but differed for the highest-threshold MUs with greater RTs (Wilcoxon: $P=0.012$) recorded during the $FAST_{40}$ (35.8±7.31 %MVC) than $SLOW_{40}$ (28.2±9.87 %MVC). However, the range of observed $MUAP_{AMPS}$ was similar between the 40% MVCs as there were no differences between the smallest observed $MUAP_{AMPS}$ ($P=0.559$, $SLOW_{40}=0.044\pm0.015$ mV, $FAST_{40}=0.043\pm0.013$ mV) or largest observed $MUAP_{AMPS}$ ($P=0.248$, $SLOW_{40}=0.195\pm0.092$ mV, $FAST_{40}=$ 0.208±0.095 mV).

There were no differences in torque ($P=0.354$, $SLOW_{40}=85.6\pm24.6$ N•m, $FAST_{40}=86.0\pm24.5$ N•m) or CV of torque (Wilcoxon: $P=0.117$, $SLOW_{40}=2.24\pm1.18\%$, $FAST_{40}=2.24\pm0.71\%$) during the constant torque period between $SLOW_{40}$ and $FAST_{40}$. Although compliance with the torque trajectory template was high for both 40% MVCs, the $FAST_{40}$ torque trajectory template was more difficult to match as the RMSE between the subject's torque output and the torque trajectory template was greater for $FAST_{40}$ (2.50±0.59% MVC) than $SLOW_{40}$ (2.18±0.61% MVC) ($P<0.001$).

Motor Unit Relationships

For the MFR vs. RT relationships, paired samples t-tests indicated no differences ($P=0.478$) in the y-intercepts between $SLOW_{40}$ (24.1±3.77 pps) and $FAST_{40}$ (23.5±4.04 pps). However, the slopes were more negative ($P=0.003$) for the $SLOW_{40}$ (-0.491±0.101 pps/%MVC) than $FAST_{40}$ (-0.322±0.109 pps/%MVC). The higher-threshold MUs had lower firing rates during the $SLOW_{40}$ (Figure 2).

For the $MUAP_{AMP}$ vs. RT relationships, there were no differences (Wilcoxon: $P=0.209$) in the y-intercepts between $SLOW_{40}$ (-0.016±0.043 mV) and $FAST_{40}$ (-0.006±0.049 mV). However, the slopes were greater ($P=0.022$) for the $SLOW_{40}$ (0.0057±0.0021 mV/%MVC) than the $FAST_{40}$ (0.0041±0.0023 mV/%MVC). For a given higher RT the $MUAP_{AMPS}$ were greater during the $SLOW_{40}$ than the $FAST_{40}$ (Figure 3).

For the MFR vs. $MUAP_{AMP}$ relationships, paired samples t-tests indicated no differences in the *A* terms ($P=0.951$, $SLOW_{40}=22.7\pm2.69$ pps, $FAST_{40}=22.8\pm3.55$ pps) or the *B* terms ($P=0.189$, $SLOW_{40}=$-

4.72±1.40 pps/mV, $FAST_{40}$=-4.44±1.47 pps/mV) between the $SLOW_{40}$ and $FAST_{40}$. Therefore, firing rates were equivocal for MUs with similar AP_{AMPS} between $SLOW_{40}$ and $FAST_{40}$ (Figure 4).

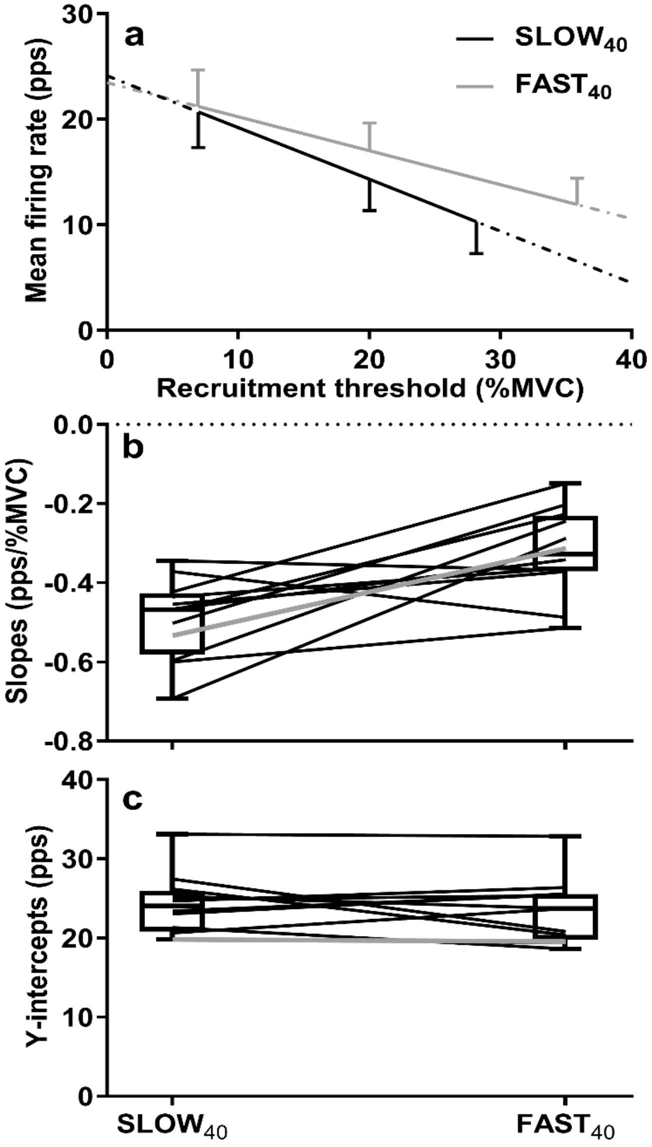

Figure 2. Average predicted mean firing rate (MFR [pulses per second]) vs. recruitment threshold (RT [%MVC]) relationships (a) for slow ($SLOW_{40}$) and fast ($FAST_{40}$) rate of torque development contractions. The solid lines indicate the predicted mean firing rates within the average observed recruitment threshold ranges for each contraction, while the dotted lines extending the predictions indicate the mean firing rates for motor units in the expected real recruitment range. Spaghetti plots of individual responses and box-and-whisker plots of the $SLOW_{40}$ and $FAST_{40}$ slopes (b) and y-intercepts (c). The grey lines in (b) and (c) indicate the responses from the subject illustrated in figure 1

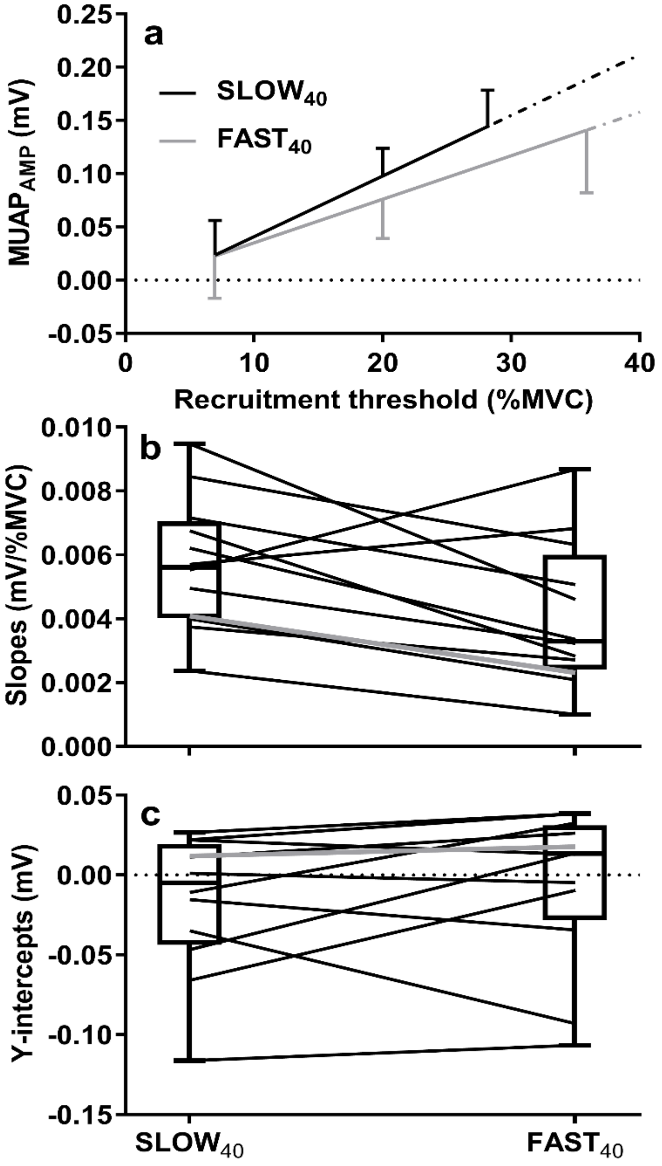

Figure 3. Average predicted motor unit action potential amplitude (MUAP$_{AMP}$ [mV]) vs. recruitment threshold (RT [%MVC]) relationships (a) for slow (SLOW$_{40}$) and fast (FAST$_{40}$) rate of torque development contractions. The solid lines indicate the predicted action potential amplitudes within the average observed recruitment threshold ranges for each contraction, while the dotted lines extending the predictions indicate the action potential amplitudes for motor units in the expected recruitment range for the contraction. However, the predictions were not extended in the 0-6% MVC range as the trajectories would predict action potential amplitudes less than 0 mV for the first recruited MUs which is not physiologically accurate. Spaghetti plots of individual responses and box-and-whisker plots of the SLOW$_{40}$ and FAST$_{40}$ slopes (b) and y-intercepts (c). The grey lines in (b) and (c) indicate the responses from the subject illustrated in figure 1

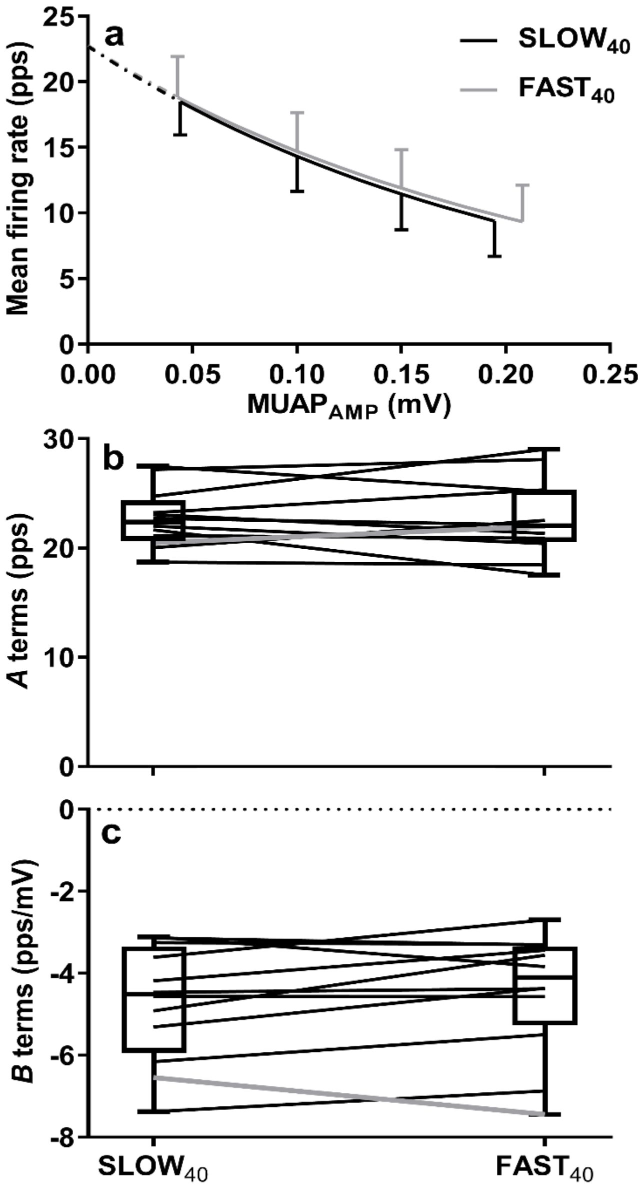

Figure 4. Average predicted mean firing rate (MFR [pulses per second]) vs. motor unit action potential amplitude ($\mathrm{MUAP_{AMP}}$ [mV]) relationships (a) for slow ($\mathrm{SLOW_{40}}$) and fast ($\mathrm{FAST_{40}}$) rate of torque development contractions. The solid lines indicate the predicted mean firing rates within the average observed action potential amplitude ranges for each contraction, while the dotted lines extending the predictions indicate the mean firing rates for motor units in the expected real action potential amplitude range. Spaghetti plots of individual responses and box-and-whisker plots of the $\mathrm{SLOW_{40}}$ and $\mathrm{FAST_{40}}$ *A* terms (b) and *B* terms (c). The grey lines in (b) and (c) indicate the responses from the subject illustrated in figure 1

Extensor and Flexor N-EMG

For N-EMG during the constant torque phase there was a significant two-way interaction (P=0.032, rate of torque development × muscle group). Paired samples t-tests indicated extensor N-EMG was greater than flexor N-EMG for SLOW_{40} (P<0.001, extensor N-EMG=36.3±7.82%, flexor N-EMG=6.50±3.82%) and FAST_{40} (P<0.001, extensor N-EMG=34.0±6.26%, flexor N-EMG=6.22±3.52%). In addition, extensor N-EMG was greater (P=0.015) for SLOW_{40} than FAST_{40}, however, flexor N-EMG was not significantly different (P=0.183) between the SLOW_{40} and FAST_{40}.

For N-EMG at 25% MVC during the linearly increasing torque phase, there was no two-way interaction (P=0.142, rate of torque development × muscle group) or main effect for rate of torque development (P=0.088). However, there was a main effect for muscle group (P<0.001). Dependent samples t-tests indicated N-EMG was greater for the extensors than the flexors regardless of contraction (P<0.001). N-EMG was not significantly greater at 25% MVC during the linearly increasing torque phase for SLOW_{40} than FAST_{40} for the extensors (SLOW_{40}= 15.0±3.28%, FAST_{40}=13.4±2.68%) or flexors (SLOW_{40}=3.48±2.49%, FAST_{40}=3.22±2.61 %).

DISCUSSION

MU firing rates were lower and action potential amplitudes were larger in relation to recruitment thresholds for isometric contractions performed at a slower rate compared to contractions performed at a faster rate of torque development. MU activity is commonly observed to be altered by the intensity of the targeted force/torque (Erim et al. 1999; De Luca and Hostage 2010; Hu et al. 2013a; Colquhoun et al. 2018b), different between populations (Erim et al. 1999; Herda et al. 2015; Sterczala et al. 2018a), or altered following exercise interventions (Vila-Chã et al. 2010; Pope et al. 2016). The novel findings of the present study suggest that differences in MU activity can exist as a function of rate of isometric torque development.

Greater slopes of the MU action potential amplitude vs. recruitment threshold relationships indicated action potential amplitudes were greater at higher recruitment thresholds for the SLOW_{40} than the FAST_{40}. The largest action potential amplitudes were similar (Figure 3.a) within the average recorded recruitment ranges of MUs for the $SLOW_{40}$ (RT range = 6.97 to 28.2% MVC) and $FAST_{40}$ (RT range = 6.95 to 35.8% MVC). However, this does not imply that the largest recruited MUs during the contractions possessed similar action potential amplitudes. For instance, the VL has been shown to continue recruitment of MUs to 95% MVC (De Luca and Hostage 2010) and, furthermore, N-EMG was doubled from 25% MVC during the linearly increasing torque phase (~15% N-EMG) in comparison to the constant torque phase (~35% N-EMG) for both contractions. Thus, larger MUs continued to be recruited during the linearly increasing torque phase from the observed upper end of the recruitment range of 28.2% MVC to 40% MVC for the $SLOW_{40}$. The dotted lines in Figure 3.a extend the predicted $MUAP_{AMP}$ vs. RT relationships for $SLOW_{40}$ and $FAST_{40}$ beyond the average recorded recruitment range to include the upper range of recruitment which would be expected during 40% MVCs of the VL. In support of greater recruitment during $SLOW_{40}$, N-EMG for the extensor muscles was 7% greater during the constant torque phase of $SLOW_{40}$ relative to $FAST_{40}$.

A limitation of EMG decomposition is that not all MUs can be recorded during any given contraction. Furthermore, another limitation of this study was that MUs were not tracked across contractions. However, the strong relationships between recruitment thresholds and AP_{AMPS} and firing rates indicate MUs with similar recruitment thresholds will demonstrate similar AP_{AMPS} and firing rates within a contraction. In addition, the relationship-based analysis of MU activity has been shown to be reliable between contractions (Colquhoun et al. 2018b). Therefore, any changes in the characteristics of a MU in relation to recruitment threshold will be easily quantified with the relationship-based approach. Subsequently, it has recently been reported that changes in recruitment thresholds and firing rates in tracked MUs across contractions does not provide any additional information that is not conveyed by the untracked MUs (Del Vecchio et al. 2019). Although unlikely, it cannot be ruled out that a bias in the Precision Decomposition III algorithm contributed to the lack of recorded of higher-threshold (28-40% MVC) MUs during the $SLOW_{40}$ which would be expected to possess larger action potentials.

The slopes of the mean firing rate vs. recruitment threshold relationships were significantly less negative for the $FAST_{40}$ than $SLOW_{40}$, but the y-intercepts were similar. Thus, MUs recruited at similar torque levels had greater firing rates for the FAST_{40} than the SLOW_{40} and the effect was more pronounced for higher-threshold MUs (Figure 2.a). When firing rates were expressed relative to MU action potential amplitudes, however, the firing rates were similar between SLOW_{40} and FAST_{40} (Figure 4). Therefore, MUs with similar action potential amplitudes had similar firing rates regardless of rate of isometric torque development. The lower slopes of the mean firing rates vs. recruitment threshold relationships were due to shifting the recruitment of similar MUs to lower torque levels in a contraction at a slower isometric rate of torque development. Together, the mean firing rate vs. recruitment threshold and MU action potential amplitude relationships suggests the additional excitation (N-EMG) necessary to achieve the targeted torque during the SLOW_{40} primarily resulted in the recruitment of larger MUs rather than significant increases in the firing rates of the already active MU pool.

Previous investigation of MU recruitment and isometric rate of force development yielded partially conflicting results (Desmedt and Godaux 1977; Masakado et al. 1995). Desmedt and Godaux (1977) reported MUs of the tibialis anterior were recruited at lower forces during ankle dorsiflexion contractions at ~50% MVC (12 kg) with greater rates of force development, and the effect was augmented even up to ballistic speeds where most MUs were recruited prior to the onset of measurable force production. However, the authors reported no changes in recruitment thresholds between the slower isometric rates of force development tested between ~1.5 kg/s and ~6 kg/s which are similar to the 5% MVC/s and 20% MVC/s rates of torque development tested in the current study. The mechanism responsible for earlier recruitment at greater rates of torque development has yet to be identified (Desmedt and Godaux 1977; Masakado et al. 1995; Maffiuletti et al. 2016). A potential explanation for the increased recruitment and MU action potential amplitudes observed during the SLOW_{40} in the present study may be a function of muscle spindle activity. De Luca and Kline (2012) suggest that at low contraction intensities (i.e. <10% MVC) when MUs fire at lower rates where their twitches are not fused, muscle spindles exist in a dynamic state (spindles are shortened and stretched repeatedly), increasing excitation to the motoneuron pool through Ia afferent feedback. With the current protocol, muscles spindles would remain in this dynamic state for four times the duration during SLOW_{40} in comparison to FAST_{40}, as the subjects would reach 10% MVC in 2 s during

$SLOW_{40}$ or 0.5 s during $FAST_{40}$. It is plausible the muscle spindles remaining longer in the dynamic state lead to the observed increase in recruitment for $SLOW_{40}$. In support, Kennedy et al. (2001) reported delayed recruitment of medial gastrocnemius MUs during plantar flexion contractions when muscle fibers were at short, non-optimal lengths, and speculated reduced afferent feedback from muscle spindles may have been responsible for the delayed recruitment. Future research should investigate the current phenomenon under vibration, which is known to remove feedback from muscle spindles (Kouzaki et al. 2000). If this hypothesis is correct, vibration would decrease recruitment during slower rates of torque development. It is also possible that post-activation potentiation plays a role in the current findings; however, if post-activation potential were a major factor in the current findings the expected result would be for the $SLOW_{40}$ to show reduced muscle activation in comparison to the $FAST_{40}$ which was not observed (De Luca et al. 1996). This would be the expected finding because the muscle fibers were activated for a longer duration before the steady force during the $SLOW_{40}$ allowing for slightly more time for potentiation to occur.

In the current study, subjects were better able to comply with the torque trajectory template for the $SLOW_{40}$ than $FAST_{40}$ as the RMSE was 15% greater for $FAST_{40}$. It is possible that the increased torque compliance for the $SLOW_{40}$ was a function of increased synergistic MU activity of the leg extensors and flexors. Thus, earlier recruitment of larger MUs and greater activation of agonists and antagonists may have better modulated the torque output to match the torque trajectory template. In support, extensor N-EMG amplitude was significantly greater for $SLOW_{40}$, however, there was no significant difference for N-EMG of the leg flexors between $SLOW_{40}$ (6.50±3.82%) and $FAST_{40}$ (6.22±3.52%). It is unclear how torque could be similar between contractions if overall recruitment was greater for $SLOW_{40}$ than $FAST_{40}$ given that firing rates and coactivation of antagonists were also similar. A limitation of the current study is that EMG was only measured from 5 of the muscles that cross the knee joint, where EMG of semimembranosis, medial and lateral gastrocnemii, and other muscles of the quadriceps, may have fully elucidated the activation strategy of all the muscles in both contractions. It is plausible that the bipolar surface EMG technique used was not sensitive to detect minor differences in already low muscle activation of the leg flexors during a moderate intensity contraction of the leg extensors. Future research should utilize ultrasonography and mechanomyography (Guo et al. 2010) in addition to EMG to examine potential differences in coactivation of the leg flexors at different rates of torque development and/or utilize higher contraction intensities where coactivation would be greater for the leg flexors (Tracy and Enoka 2002).

The results of the present study suggest great care must be taken to ensure the adherence of a subject's torque output with the torque trajectory template provided, as significant deviations in the rate of torque development during the linearly increasing torque phase will alter the recruitment of MUs shifting the slopes of the firing rates and action potential amplitudes in relation to recruitment thresholds. In addition, it should be investigated whether alternate rates of torque development in lieu of the standard 10% MVC/s commonly used for isometric trapezoid contractions are more efficacious for research seeking to determine subtle differences in MU activity between populations or following exercise interventions.

Previously, less negative slopes of mean firing rate vs. recruitment threshold relationships have been observed for contractions performed at greater intensity compared to contractions at lower intensity (De Luca and Hostage 2010) and for individuals with greater type I myosin heavy chain isoform content of the VL (Trevino et al. 2016). Trevino et al. (2016) reported ~73% of the variance in type I myosin heavy chain isoform content of the VL between subjects was explained by the slopes of the mean firing rate vs. recruitment threshold relationships from a 40% MVC. Similarly, Trevino et al. (2018) reported the slopes of the action potential amplitude vs. recruitment threshold relationships during 40% MVC leg extensions were highly correlated with cross-sectional area and myosin heavy chain isoform content of the VL. The current study provides evidence that large changes in the slopes of the mean firing rate and MU action potential vs. recruitment threshold relationships (52% and 28%, respectively) may be observed within subjects at the same contraction intensity by manipulating the rate of torque development of the linearly increasing torque phase of the isometric contraction.

In summary, MUs of similar size were recruited earlier at lower torque levels, and overall recruitment was greater, during an isometric trapezoidal contraction with a slower rate of torque development. This change in recruitment led to altered slopes of the mean firing rate and MU action potential amplitudes vs. recruitment threshold relationships which are commonly analyzed to characterize firing rate and recruitment patterns of a muscle (De Luca and Hostage 2010; Hu et al. 2013a; Herda et al. 2015; Colquhoun et al. 2018a; Miller et al. 2018b; Trevino et al. 2018). However, firing rates were similar when expressed relative to action potential amplitudes. Therefore, MU recruitment, but not firing rates of the motoneurons were altered by modulating rate of torque development during isometric trapezoidal muscle actions of the leg extensors. These findings highlight the necessity of ensuring subjects' torque output matches the provided torque trajectory template in future research. In addition, future research should examine if differences in MU activity as a function of rates of torque develop may be related to sensory processes.

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CHAPTER V: RATE OF FORCE DEVELOPMENT AND THE INFLUENCE OF SEX IN PREDICTING VERTICAL JUMP HEIGHT

ABSTRACT

Previous studies have disagreed on whether estimates of RFD are significant predictors of vertical jump height, and on which estimate of RFD should be used, and are often performed with limited sample sizes. Therefore, the purpose of the current investigation is to assess the utility of RFD as a predictor of vertical jump height. This study utilized a database of maximal countermovement vertical jumps analyzed via motion capture system from 2,258 NCAA Division I athletes. Kinematic and kinetic variables were derived from the motion capture system (DARI Motion, Scientific Analytics Inc., Lenexa, KS, USA). The variables used as predictors of vertical jump height were sex, height, weight, loading depth of the countermovement, peak ground reaction force, and 4 different estimates of rate of force development. Forward sequential multiple regression models were used to assess the variance in vertical jump height which could be accounted for by each predictor variable. Peak RFD was a significant moderate predictor of vertical jump height at the bivariate level ($r = 0.408$, $p < 0.001$). However, when peak ground reaction force was included in the prediction model the unique variance in vertical jump height which was accounted for by peak RFD was diminished ($\rho = -0.051$, $\beta = -0.051$), and it became apparent that peak ground reaction force accounted for the most unique variance in vertical jump height ($\rho = 0.503$, $\beta = 1.109$). Of note, sex was also an important predictor of vertical jump height ($\rho = 0.246$, $\beta = 0.94$). Furthermore, mediation analysis revealed the direct effect of peak RFD on vertical jump height was just 0.004. Although peak RFD was a moderate predictor of vertical jump height at the bivariate level, multiple regression analysis revealed this is due solely to its shared variance with peak ground reaction force, which uniquely predicts vertical jump height. According to the models, peak rate of force development may not be uniquely useful as a predictor of vertical jump height during maximal countermovement jumps.

INTRODUCTION

It has been reasoned that an individual's capacity to produce force at a high rate during isometric leg extensions or during vertical jumps would be related to jump performance (Vanezis and Lees 2005; McErlain-Naylor et al. 2014). Studies that have directly examined relationships between the rate of ground reaction force development (RFD) during a vertical jump and the jump height achieved have conflicting results. In addition, issues such as small sample size (McLellan et al. 2011), and failures to fully interpret regression analysis including accounting for variance shared between predictors of jump height via multiple regression techniques (Ebben et al. 2007; McLellan et al. 2011; Laffaye and Wagner 2013) have limited the findings. Thus, a thorough analysis of the efficacy of estimations of RFD as predictors of vertical jump height is warranted.

One investigation of the relationship between RFD and vertical jump height was performed in a study where 23 physically active men performed counter-movement jumps and squat jumps (McLellan et al. 2011). Peak RFD during the jumps was directly related to the vertical jump height achieved (r = 0.68). The authors concluded that peak RFD was the greatest predictor of vertical jump performance, although peak power appeared to be a stronger predictor of jump height (r = 0.73). Laffaye and Wagner (2013) analyzed CMJs from 178 male US national championship level athletes in basketball, football, and baseball, and found a moderate relationship between RFD during the eccentric phase of the jump and vertical jump height (r = 0.50). Conversely, a study by Ebben et al. (2007) which consisted of 24 male and 21 female NCAA Division I Track & Field athletes found no such relationship when correlations were performed between average RFD and jump height separately for males and females. It should be noted that the estimation of RFD was performed differently for each of these studies, as peak RFD, average RFD, and average RFD during the eccentric phase only. It is likely that the method of estimating RFD influence the magnitude of the relationship with vertical jump height, and indeed, McLellan et al. (2011) reported peak RFD (r = 0.68) was a stronger predictor of jump height than average RFD (r = 0.49).

Furthermore, each of these studies has reported correlation coefficients between predictors and vertical jump height, while no research involving dynamic RFD during countermovement vertical jumps has discussed the unstandardized or standardized weights of the predictors on jump height. It is plausible that there is there is a discrepancy between the quantity of variance which can be accounted for by predictors of vertical jump height and the effect a real change in the predictor may have on vertical jump height. Thus, interpretation of standardized beta weights in addition to the correlation coefficients of predictors of vertical jump height in multiple regression analysis will provide a greater understanding of how manipulation of these predictors may affect vertical jump height predictions.

Another issue facing estimations of RFD as predictors of vertical jump height is their reliability in relation to other commonly studied kinetic variables. Studies analyzing the reliability of RFD have consistently reported high variability within subjects even when vertical jump height itself is consistent (Moir et al. 2005, 2009; Sheppard et al. 2008; McLellan et al. 2011; Nibali et al. 2015). For example, Nibali et al. (2015) investigated the reliability of kinetic and kinematic variables from several trials of counter-movement jumps in 113 high school athletes, 30 collegiate athletes, and 35 professional athletes. Average force (CV = 2.7%) and impulse (CV = 2.7%) during the concentric phase were very reliable as was vertical jump height (CV = 3.5%), However, RFD during the eccentric phase was highly variable (CV = 21.3%). Therefore, it appears the athletes in this study were able to achieve similar jump heights across trials although these jumps were performed with relatively different rates of force development.

The final challenge to the utility of RFD as a predictor of vertical jump height is whether the variability in vertical jump height that is predicted by RFD is uniquely explained by RFD, or whether the apparent strength of RFD as a predictor is due to its shared variance with other variables involved in vertical jumps. Ground reaction force is often seen to be moderately correlated with vertical jump height, whether it is estimated as the average (Laffaye and Wagner 2013) or peak (McLellan et al. 2011) force during the jump. Loading depth, or the depth of the countermovement in a jump, may also be an important factor in the relationship between RFD and vertical jump height, as greater loading depth allows for a longer duration of force production (Moran and Wallace 2007; McErlain-Naylor et al. 2014). Moran and Wallace (2007) reported significantly greater vertical jump height when countermovement jumps were performed with 90° in comparison to 70° of knee joint flexion. Therefore, when height and weight are controlled, and the variance due to loading depth of the countermovement and peak ground reaction forces are considered concurrently with RFD, is RFD still able to uniquely predict vertical jump height?

The purpose of the current study was to analyze and assess the utility of RFD as a predictor of vertical jump height under multiple statistical scenarios. These scenarios include RFD as a bivariate predictor of vertical jump height, and while accounting for other previously identified vertical jump-related variables. This will be completed in males and females separately as well as when data from both sexes are combined, in hierarchical multiple regression models where the variance in vertical jump height is first predicted by demographic variables which cannot be changed by training (sex and height), then by a physical variable which can be changed (weight), and finally by kinetic and kinematic variables which can be modified by technique or training (loading depth, RFD, and peak ground reaction force). Such analysis may elucidate whether unique variance in vertical jump height is accounted for by RFD, or whether its apparent utility as a bivariate predictor is due to its shared variance with other predictors. An advantage of the current study is the use of a large quantity of data obtained from a database which provides the statistical power necessary for hierarchical multiple regression models with many factors. This database has been made possible by recent advancements in motion capture technology, which has been validated for the estimation of kinetic variables without the use of a force plate (Fry et al. 2016; Mosier et al. 2019) and allows for quicker data collections making the collection of a large volume of data possible. The large sample of both male and female collegiate athletes from multiple sports will provide sufficient between-subjects variability and will protect the analysis from spurious findings due to small sample sizes.

METHODS

Data

All data for the current project were previously deidentified and were obtained from the DARI Vault database housed by Scientific Analytics Inc. The data consists of demographic as well as kinetic and kinematic variables assessed by a markerless motion capture system, DARI Motion (Scientific Analytics Inc., Lenexa, KS, USA) from maximal countermovement vertical jump tests. All data in the sample used were collected from NCAA Division I athletes and were collected between the years of 2016 and 2018. The sample consisted of 2,258 athletes (891 females, age 19.7±1.2 years, mass = 67.5±10.3 kg, stature = 171±8 cm; 1367 males, age = 19.9±1.3 years, mass = 93.3±21.2 kg, stature = 186±7 cm). A breakdown of the number of male and female subjects from the sports in which they competed is found in table 1.

Table 1. Sample size for males and females for each sport and

	Males	Females	Total
Baseball	166		166
Basketball	83	19	102
Cross Country	11	21	32
Fencing	47	43	90
Football	594		594
Golf	14	11	25
Hockey	25		25
Lacrosse	107	55	162
Rowing		97	97
Soccer	97	193	290
Softball		138	138
Swimming and Diving	55	62	117
Tennis	43	28	71
Track and Field	125	146	271
Volleyball		78	78
Total	1367	891	2258

The DARI Motion markerless motion capture system has been validated to accurately estimate ground reaction forces when compared to a traditional force plate (Fry et al. 2016), and has recently been used to estimate ground reaction forces during vertical jumping (Mosier et al. 2019). The motion capture system records from eight cameras simultaneously and data is recorded at 60 frames per second. For all jump trials in the database the countermovement vertical jump protocol was consistent. The athletes were instructed to begin with feet planted and perform a countermovement jump with a full arm swing vertically as high as possible.

A theory-based approach was used to identify variables from the database which may be important predictors of vertical jump height, or which may be useful in a predictive model of vertical jump height. Thus, kinetic and kinematic variables which have been previously reported to be related to vertical jump height were included, along with demographic variables. These variables included sex (Ebben et al. 2007), height, weight (Dowling and Vamos 1993), loading depth (Moran and Wallace 2007; Kirby et al. 2011), RFD, (McLellan et al. 2011; Laffaye and Wagner 2013) and GRF (Dowling and Vamos 1993; McLellan et al. 2011; Laffaye and Wagner 2013). Because the focus of the analysis was the use of rate of force development as a predictor of vertical jump height in relation to other predictors, 4 separate estimates of RFD were analyzed. Complex kinetic variables which have previously been shown to be strong predictors of vertical jump height such as power and impulse were not included as they are essentially combinations of force-time variables which allow less opportunity for a prescription for improvement (Dowling and Vamos 1993).

The kinematic variables used in the current investigation included vertical jump height and loading depth. Vertical jump height (m) was calculated as the difference between the estimated center of mass during the highest recorded frame of the jump and standing height. Loading depth (m) was calculated as the difference between the center of mass during the lowest recorded frame of the countermovement and standing height.

The kinetic variables used in the current investigation were derived from the motion capture data. P-GRF (N) was the greatest instantaneous ground reaction force value recorded before take off of the jump. Peak RFD (P-RFD[N/s]) was the greatest instantaneous RFD estimated during the countermovement jump prior to take off. Average RFD (N/s) was calculated from the minimum recorded ground reaction force during the countermovement to the peak ground reaction force prior to take off. Peak concentric RFD (N/s) was the greatest instantaneous RFD estimated during the concentric portion of the countermovement jump only. Average concentric RFD (N/s) was calculated from the beginning of the concentric phase of the countermovement jump to the peak ground reaction force prior to take off.

Statistical Analyses

Bivariate correlations were performed between all variables and all variables of interested are reported by means ± standard deviations separately for females and males. The estimation of RFD which had the largest zero-order correlation with vertical jump height was selected for inclusion in the subsequent multiple regression models as a predictor of vertical jump height. An ANOVA model was used to test for interactions between sex and the other independent variables of interest which indicated a significant sex × weight interaction ($p < 0 .001$).

To analyze RFD as a predictor of vertical jump height, three forward sequential hierarchical multiple regression models were performed. Variables were entered into the models in steps according to a theoretical framework. Demographic variables were entered first in order of the level of control the subject has over that variable, followed by kinetic and kinematic variables which were entered in chronological order in which they occur, or are estimated, during a vertical jump. The first model included the full sample of both females and males, and the variables were entered in 7 steps in the following order: sex, height, weight, sex × weight, loading depth, P-RFD, and P-GRF. Because the first model includes the interaction between sex and weight it violates the assumption of multicollinearity. To ensure the behavior of the model was not simply due to variance inflation causing unstable coefficients the model was repeated separately for each sex, excluding sex and the sex × weight interaction as predictors. The second model included only females from the sample and the variables were entered in 5 steps in the following order: height, weight, loading depth, P-RFD, and P-GRF. The third and final model included only males and the variables were entered in 5 steps in the same order as the female only model.

Finally, a mediation analysis was performed to test whether the relationship between P-RFD and vertical jump height was mediated by P-GRF according to the methods described in Hayes (2017). Hayes states that mediation analysis is a causal path analysis which can show how one variable's effect on a dependent variable can be separated into its direct and indirect (through a mediator) effects. The mediation analysis consisted of statistically evaluating the bivariate regressions of vertical jump height on P-RFD and P-GRF as well as P-GRF on P-RFD, and a multiple regression model where P-RFD and P-GRF predicted vertical jump height. The path model for the mediation analysis is shown in Figure 1.

Missing data (<1%) were excluded pairwise and the alpha was set at 0.05. The assumption of multicollinearity was considered violated if the variance inflation factor (VIF) exceed 10.0, or the tolerance value was less than 0.100. All statistical analyses were performed using SPSS, version 25 (IBM Corp., Armonk, New York).

RESULTS

Bivariate correlations and Descriptive Statistics

The bivariate correlations between all variables are shown in Table 2. Of the four estimations of RFD, P-RFD, was the best predictor of vertical jump height ($r^2 = 0.166$), although P-RFD during the concentric phase only performed nearly as well ($r^2 = 0.165$). The best single predictor of vertical jump height was sex ($r^2 = 0.434$) followed by P-GRF ($r^2 = 0.264$). Descriptive statistics for variables included in the subsequent hierarchical multiple regression models are shown in Table 3.

Table 2. Intercorrelations of kinetic, kinematic, and demographic variables during countermovement jumps. N = 2258

	VJH (m)	Sex	Height (m)	Weight (kg)	Loading Depth (m)	P-RFD (N/s)	A-RFD (N/s)	PC-RFD (N/s)	AC-RFD (N/s)
Sex	0.659†								
Height (m)	0.491†	0.697†							
Weight (kg)	0.312†	0.596†	0.715†						
Loading Depth (m)	0.118†	0.021	-0.039*	-0.149†					
P-RFD (N/s)	0.408†	0.450†	0.485†	0.667†	-0.085†				
A-RFD (N/s)	0.378†	0.402†	0.393†	0.532†	-0.046*	0.688†			
PC-RFD (N/s)	0.406†	0.443†	0.475†	0.654†	-0.090†	0.993†	0.683†		
[#]AC-RFD (N/s)	0.314†	0.283†	0.260†	0.379†	-0.006	0.604†	0.885†	0.611†	
P-GRF (N)	0.514†	0.647†	0.672†	0.908†	-0.164†	0.790†	0.683†	0.784†	0.559†

Sex: 0 = female, 1 = male, VJH = vertical jump height, P-RFD = Peak rate of force development, A-RFD - average rate of force development, PC-RFD = peak rate of force development during the concentric phase only, AC-RFD = average rate of force development during the concentric phase only, P-GRF = peak ground reaction force. *Significant at 0.05 level. †Significant at 0.001 level. [#]Indicates N = 2257.

Table 3. Mean±SD for females and males for demographic, kinetic, and kinematic data.

	Female	**Male**
N	891	1367
VJH (m)	0.451±0.073	0.606±0.094
Height (m)	1.71±0.076	1.86±0.074
Weight (kg)	67.5±10.3	93.3±20.2
Loading Depth (m)	0.410±0.092	0.415±0.094
P-RFD (N/S)	8362±3227	12799±4874
P-GRF (N)	1629±319	2492±584

N = sample size, VJH = vertical jump height, P-RFD = peak rate of force development, P-GRF = peak ground reaction force.

Combined Sexes Model

The model summary and variable coefficients for the final two steps for the sexes combined model can been seen in Tables 4 and 5 respectively. The adjusted R^2 value for the final step of the model indicates the predictors account for 63.8% of the variance in vertical jump height. It should be noted that the model suffers from multicollinearity for all steps following the inclusion of the sex × weight interaction according to the high VIF values and low tolerance values for sex, weight, and the interaction variable. However, this is expected when including interaction variables in multiple regression models. Step 6 of the model introduces P-RFD. In this step of the model P-RFD appears to account for the largest quantity of unique variance in vertical jump height, as evidenced by the largest partial correlation of any predictor in this step ($\rho = 0.305$, $\beta = 0.300$). By contrast, loading depth accounts for very little unique variance in vertical jump height ($\rho = 0.111$, $\beta = 0.079$).

Table 4. Model Summary for hierarchical stepwise multiple regression, where demographic, kinetic, and kinematic data were used to predict vertical jump height (m). This model includes data from both sexes and the significant interaction between sex and weight.

Model Step	R	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	p
1	0.659	0.433	0.087	0.434	1727	<0.001
2	0.66	0.435	0.086	0.002	7.76	0.005
3	0.676	0.456	0.085	0.021	86.9	<0.001
4	0.679	0.461	0.084	0.005	21.3	<0.001
5	0.684	0.467	0.084	0.006	26.8	<0.001
6	0.719	0.516	0.08	0.05	231	<0.001
7	0.8	0.638	0.069	0.122	762	<0.001

1. Sex: 0= female, 1 = male
2. Sex, Height (m)
3. Sex, Height, Weight (kg)
4. Sex, Height, Weight, Sex × Weight
5. Sex, Height, Weight, Sex × Weight, Loading Depth (m)
6. Sex, Height, Weight, Sex × Weight, Loading Depth, P-RFD (N/s)
7. Sex, Height, Weight, Sex × Weight, Loading Depth, P-RFD, P-GRF (N)

Table 5. Model coefficients for the final two steps (6 and 7) of the hierarchical stepwise multiple regression, where demographic, kinetic, and kinematic data were used to predict vertical jump height. This model includes data from both sexes and the significant interaction between sex and weight.

Model Step		Standardized Coefficients (Beta)	p	Correlations Zero-order	Partial	Collinearity Statistics Tolerance	VIF
6	**(Constant)**		0.07				
	Sex	1.069	<0.001†	0.659	0.242	0.026	38.07
	Height (m)	0.172	<0.001†	0.491	0.149	0.366	2.729
	Weight (kg)	-0.14	0.008*	0.312	-0.056	0.078	12.807
	Sex × Weight	-0.618	<0.001†	0.582	-0.108	0.015	66.676
	Loading Depth (m)	0.079	<0.001†	0.118	0.111	0.957	1.045
	P-RFD (N/S)	0.3	<0.001†	0.408	0.305	0.549	1.821
7	**(Constant)**		0.279				
	Sex	0.94	<0.001†	0.659	0.246	0.026	38.206
	Height (m)	0.218	<0.001†	0.491	0.214	0.364	2.746
	Weight (kg)	-0.8	<0.001†	0.312	-0.313	0.061	16.378
	Sex × Weight	-0.691	<0.001†	0.582	-0.14	0.015	66.72
	Loading Depth (m)	0.134	<0.001†	0.118	0.21	0.935	1.07
	P-RFD (N/S)	-0.051	0.016*	0.408	-0.051	0.353	2.834
	P-GRF (N)	1.109	<0.001†	0.514	0.503	0.099	10.07

Sex: 0 = female, 1 = male, P-RFD = peak rate of force development, P-GRF = peak ground reaction force. *Significant at 0.05 level. †Significant at 0.001 level.

When P-GRF is introduced into the model in the final step, the multiple R^2 increases from 0.516 to 0.638, and the partial correlation and beta coefficients of P-RFD are decreased and the signs are reversed (ρ = -0.051, β = -0.051). In the final step of the model P-GRF is the largest unique predictor of vertical jump height (ρ = 0.503, β = 1.109). In addition, the inclusion of P-GRF reveals a slight suppression effect for loading depth. The partial correlation and beta coefficients of loading depth were increased from (ρ = 0.111, β = 0.079) to (ρ = 0.210, β = 0.134) with the inclusion of P-GRF in the final step of the model.

The causal path model for the mediation analysis is shown in Figure 1, where the relationship between the independent variable, P-RFD and the dependent variable VJH is proposed to be mediated by P-GRF. The zero-order correlation between P-RFD and VJH is 0.408, the correlation between P-RFD and P-GRF is 0.790, and is 0.514 between P-GRF and VJH. In the mediation analysis multiple regression model P-RFD and the proposed mediator, P-GRF, predicted VJH. The partial correlation of P-RFD was

0.003 while the partial correlation of P-GRF was 0.343. The standardized direct effect of P-RFD on vertical jump height was 0.004 ($p = 0.883$) while the standardized direct effect of P-GRF on vertical jump height was 0.511 ($p < 0.001$). The standardized indirect effect of P-RFD on VJH through P-GRF was 0.406 ($p < 0.001$). The mediation analysis indicated that P-GRF is a full mediator of the relationship between P-RFD and vertical jump height, where a 1-standard deviation increase in P-RFD will yield a 0.004-standard deviation increase in vertical jump height if P-GRF is held constant. Thus, changes in P-RFD are of little effect on vertical jump height when P-GRF is held constant.

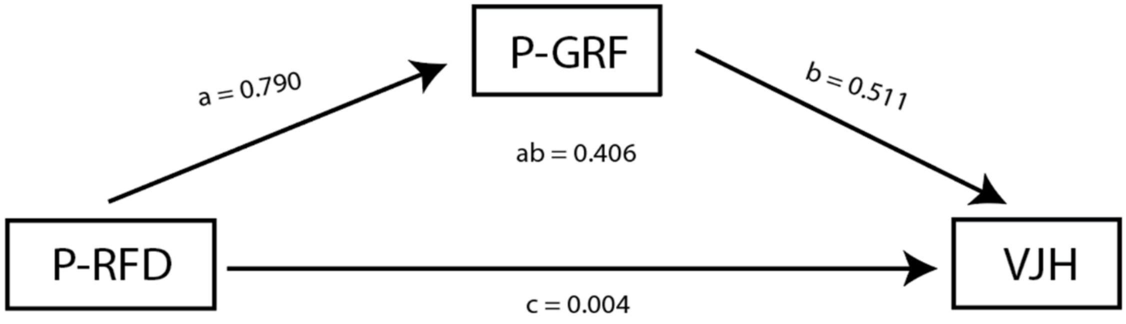

Figure 1. Path causal model for the mediation test to determine whether peak ground reaction force (P-GRF) mediates the relationship between peak rate of force development (P-RFD) and vertical jump height (VJH). a is the zero-order correlation between P-RFD and P-GRF. b is the direct effect of P-GRF on VJH and c is the direct effect of P-RFD on VJH. ab is the indirect effect of P-RFD on VJH.

Female Only and Male Only Models

The variable coefficients for the final two steps for the female only model and the male only model can been seen in Tables 6 and 7 respectively. The multiple R^2 values for the final step of each model indicated the model accounted for 34.7% of the variance in vertical jump height for females, and 37.7% of the variance in vertical jump height for males. Neither the female only nor the male only model violated the assumption of multicollinearity based on the VIF and tolerance values.

The coefficients in the 4th and 5th steps of the female only and male only models indicated the predictors behaved very similarly between all three models as expected. The only notable differences between the female only and male only models were that height and weight accounted for more variance in vertical jump height in the final step of the male only model (height ρ = 0.264, β = 0.263; weight ρ = -0.589, β = -1.308) than in the female only model (height ρ = 0.129, β = 0.121; weight ρ = -0.410, β = -0.594). P-RFD uniquely accounted for a moderate portion of variance in vertical jump height for both the female only (ρ = 0.305, β = 0.327) and male only models (ρ = 0.305, β = 0.364) before P-GRF was included in the model. However, it should also be noted that the overall predictive power of these models was quite low without the inclusion of P-GRF (female only $R^2 = 0.113$, male only $R^2 = 0.162$). As expected, in the final step of the models the partial correlations and beta coefficients of P-RFD were diminished and their signs were reversed (female only ρ = -0.079, β = -0.088; male only ρ = -0.048, β = -0.059), and the predictive power of loading depth was slightly increased (female only ρ = 0.219, β = 0.185; male only ρ = 0.217, β = 0.183).

Table 6. Model coefficients for the final two steps (4 and 5) of the hierarchical stepwise multiple regression, where demographic, kinetic, and kinematic data were used to predict vertical jump height. This model includes data from females only.

Model Step		**Standardized Coefficients (Beta)**	**p**	**Correlations**		**Collinearity Statistics**	
				Zero-order	**Partial**	**Tolerance**	**VIF**
4	**(Constant)**		<0.001†				
	Height (m)	0.121	0.001†	0.134	0.111	0.75	1.334
	Weight (kg)	-0.077	0.049*	0.105	-0.066	0.647	1.546
	Loading Depth (m)	0.086	0.007*	0.081	0.091	0.99	1.01
	P-RFD (N/S)	0.327	<0.001†	0.312	0.305	0.843	1.186
5	**(Constant)**		0.002*				
	Height (m)	0.121	<0.001†	0.134	0.129	0.75	1.334
	Weight (kg)	-0.594	<0.001†	0.105	-0.41	0.372	2.689
	Loading Depth (m)	0.185	<0.001†	0.081	0.219	0.95	1.052
	P-RFD (N/S)	-0.088	0.019*	0.312	-0.079	0.519	1.927
	P-GRF (N)	0.928	<0.001†	0.441	0.514	0.271	3.694

P-RFD = peak rate of force development, P-GRF = peak ground reaction force. *Significant at 0.05 level. †Significant at 0.001 level.

Table 7. Model coefficients for the final two steps (4 and 5) of the hierarchical stepwise multiple regression, where demographic, kinetic, and kinematic data were used to predict vertical jump height. This model includes data from males only.

		Standardized		Correlations		Collinearity Statistics	
Model Step		**Coefficients (Beta)**	**p**	**Zero-order**	**Partial**	**Tolerance**	**VIF**
4	**(Constant)**		0.001†				
	Height (m)	0.195	<0.001†	0.019	0.174	0.684	1.461
	Weight (kg)	-0.495	<0.001†	-0.199	-0.35	0.476	2.101
	Loading Depth (m)	0.119	<0.001†	0.168	0.125	0.935	1.07
	P-RFD (N/S)	0.364	<0.001†	0.116	0.305	0.644	1.552
5	**(Constant)**		0.784				
	Height (m)	0.263	<0.001†	0.019	0.264	0.675	1.482
	Weight (kg)	-1.308	<0.001†	-0.199	-0.589	0.193	5.18
	Loading Depth (m)	0.183	<0.001†	0.168	0.217	0.918	1.089
	P-RFD (N/S)	-0.059	0.074	0.116	-0.048	0.419	2.386
	P-GRF (N)	1.194	<0.001†	0.075	0.507	0.151	6.641

P-RFD = peak rate of force development, P-GRF = peak ground reaction force. *Significant at 0.05 level. †Significant at 0.001 level.

DISCUSSION

Model Performance and the Influence of Sex on the Prediction of Vertical Jump Height

The full sexes combined model was able to account for 64% of the variance in vertical jump height, which is similar to previous multiple regression models which have attempted to predict vertical jump height without including power and impulse as predictors (Dowling and Vamos 1993; McErlain-Naylor et al. 2014). Kinetic variables and vertical jump height have been shown to be greater for males than females (Moir et al. 2005; Ebben et al. 2007; Rubio-Arias et al. 2017; McMahon et al. 2017), although sex is typically not used as a predictor of vertical jump height. In the current study sex was the predictor which accounted for the most variance in vertical jump height at the zero-order level ($r = 0.659$). While its capacity to uniquely predict variance in vertical jump height was reduced in the final step of the model when all other predictors were included, it remained a useful predictor ($\beta = 0.940$, $\rho = 0.246$). Consequently, the female only and male only multiple regression models explained far less variance in vertical jump height. The R^2 values for the female only and the male only models indicated models were only able to account for 34.4% and 37.4% of the variance in vertical jump height respectively.

Body Mass as a Predictor of Vertical Jump Height

Vertical jumping involves the upward acceleration of an individuals' body mass. Indeed, accounting for body weight has proved to be an important factor for predicting vertical jump height (Thompson et al. 2013a) to the extent that it is common to normalize kinetic variables and other predictors of jump height by body weight (Dowling and Vamos 1993; Vanezis and Lees 2005; Kirby et al. 2011). However, to observe the variance in vertical jump height which could be accounted for by weight and other predictors separately, weight was included in the models as a unique predictor rather than normalizing peak RFD and peak GRF by body weight.

In the current study bodyweight behaved differently as a predictor for vertical jump height in male and female athletes. To the authors' knowledge, this is the first study to report this phenomenon. There was a significant sex by weight interaction, and the zero-order correlation between the sex by weight interaction variable and vertical jump height was 0.521. According to this interaction, higher vertical jumps were predicted for heavier males. However, in the final step of the full model when other predictors that share variance with this interaction were included in the model, the beta weight and partial correlation signs switched ($\beta = -0.691$, $\rho = -0.140$) indicating the unique variance explained by the interaction dictates that when all other variables are held constant, being a heavier male was disadvantageous for vertical jump height. In addition, the beta weights and partial correlations for weight were stronger in the male only model ($\beta = -1.308$, $\rho = -0.589$) than the female only model ($\beta = -0.594$, $\rho = -0.410$), which suggested being heavier is more disadvantageous for male athletes than female athletes in terms of vertical jump height.

Rate of Force Development vs Peak Ground Reaction Force as a Predictor of Vertical Jump Height

Rate of force development appears to be a moderate predictor of vertical jump height at the zero-order level as reported in previous research (McLellan et al. 2011; Laffaye and Wagner 2013). In the current study this was also the case when RFD predicted vertical jump height in multiple regression models where the variance due to sex, height, weight, and loading depth are controlled. However, when peak GRF was added to the model the unique predictive capacity of peak RFD was diminished. Peak GRF accounted for the most unique variance in vertical jump height of the predictors included in the full model, and in the female only and male only models. It is plausible the predictive capacity of peak RFD on vertical jump height is due largely to sharing variance with peak GRF. Indeed, the zero-order bivariate correlation between peak RFD and peak GRF is 0.790, and the mediation analysis revealed peak GRF is a full mediator of the relationship between peak RFD and vertical jump height. In the current sample, if peak GRF is held constant, a 1-standard deviation increase in peak RFD is predicted to increase vertical jump height by just 0.004 standard deviations. Thus, greater peak RFD without subsequently greater peak GRF did not lead to greater vertical jump height. It appears the predictive capacity of RFD on vertical jump height rests solely on the shared variance between RFD and peak GRF. It could also be stated that peak GRF was predictive of vertical jump height, and that those who produced a greater peak GRF during the jump tended to have greater peak RFD, but athletes with a high peak RFD without a high peak GRF were not predicted to jump high.

It is important to understand the context of the current statistical models and the limitations of the current data set, as extrapolation of findings may lead to erroneous conclusions. The findings are that while estimations of RFD are moderate predictors of vertical jump height, it appears this predictive capacity is due solely to its shared variance with peak GRF which fully mediates the relationship. However, these data are confined to a cross-sectional sample of maximal countermovement vertical jumps, which differ from many jumps performed in sport in that they are not time constrained by external factors, although jumps performed in sport settings are often time constrained by factors related to the objectives of the sport. For example, an athlete may be required to jump quickly to catch a batted ball overhead before it gets past her. Maximal countermovement vertical jump tests as performed in the current study are also time constrained, but only for the purpose of achieving maximal height, because vertical movement that is too slow will not create enough velocity for the body to leave the ground. Therefore, extrapolations of the results from the current study to apply to all jumps performed in sport settings is not appropriate. In addition, the findings apply only to literal estimations of the rate of ground reaction force development during maximal countermovement vertical jumps, and do not apply to the theoretical concept that high rate of strength development (fast and forceful muscle action) in lower limb muscles is an important factor for vertical jump and other sport performance as described by Vanezis and Lees (2005) and others (Thompson et al. 2013b, a). The more plausible conclusion is that the theoretical concept of a high rate of strength development in lower limbs is better captured by measures other than peak RFD or the other estimations of RFD in the current study. Specifically, peak power (Dowling and Vamos 1993; Peterson et al. 2006; McBride et al. 2010; McLellan et al. 2011) and individual joint powers (McErlain-Naylor et al. 2014) are consistently shown to be strong predictors of vertical jump height that are related to the concept of high rate of strength development. Therefore, the current findings do not suggest that the concept of high rate of strength development is not important for vertical jumping or other athletic performances, but only that estimations of RFD may not be the best measures of this concept and are not uniquely valuable in predictions of maximal vertical jump height.

One explanation for the lack of unique predictive power of RFD when peak GRF is included in the models may be that there is a trade-off between loading depth and RFD. It is reported that descending to a greater loading depth during the countermovement phase leads to a greater impulse and subsequently, greater vertical jump height (Moran and Wallace 2007; McBride et al. 2010; Kirby et al. 2011), which may be in spite of potentially lower RFD. In the current study the predictive power of loading depth, although modest ($\rho = 0.210$) was only realized after peak GRF was included in the final step of the model. In addition, there was a significant but weak negative correlation between loading depth and peak RFD ($r = -0.085$).

A limitation of the current study is that repeated jumps for the sample were not available. It is possible that high inter-subject variability in the capacity for high RFD obscures this relationship which may be stronger in a repeated measures design. The existence of such a trade-off may explain 1) the stronger predictive capacity of power, which encompasses the distance over which force is produced (work), and how quickly that work is performed, and 2) why Nibali et al. (2015) found vertical jump height to be a highly reliable measure, while RFD varied widely between jumps on a within-subjects basis. That is, subjects were achieving very similar jump heights across trials while producing different RFDs during the propulsive phase, which indicates jump height may not be dependent on a high RFD. Another limitation of the current study is the motion capture analysis was limited to a sampling rate of 60 Hz, which could introduce error; however, we believe the trade-off of lower sampling rate for a significantly larger sample size (2,258) was appropriate for the current analysis.

Implications for Coaching Maximal Countermovement Jumps

The current data may have implications for coaching maximal countermovement vertical jumping technique. Because the relationship between peak RFD and vertical jump height is fully mediated by peak GRF it is possible that instructing athletes to focus on maximal force production rather than speed during vertical countermovement jumps would lead to greater performance. Previous research has indicated greater vertical jump performance when athletes were instructed by coaches to keep an external focus of attention versus an internal focus of attention (Kershner et al. 2019). Data from the current study suggests that between athletes, maximal force production rather than RFD predicts vertical jumping performance; however, further research is needed to investigate whether such instructional cues could affect vertical jump height within subjects in a repeated measures design.

Conclusions

Peak rate of force development is a moderate predictor of vertical jump height at the zero-order level. However, it appears the predictive capacity of peak rate of force development is simply due the variance shared between peak rate of force development and peak ground reaction force. In the current study, peak ground reaction force fully mediated the relationship between peak rate of force development and vertical jump height. Consequently, in the final step of the vertical jump height prediction model, the unique predictive power of peak rate of force development was diminished. The strength of the current study was in the large sample size, however interpretations of results should be made with caution due to the cross-sectional nature of the study. Future studies should attempt to re-examine these findings using a repeated measures design.

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