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INVITED REVIEW

Resistance exercise training and the motor unit

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Abstract

Resistance exercise training (RET) is a key modality to enhance sports performance, injury prevention and rehabilitation, and improving overall health via increases in muscular strength. Yet, the contribution of neural mechanisms to increases in muscular strength are highly debated. This is particularly true for the involvement of the motor unit, which is the link between neural (activation) and mechanical (muscle fiber twitch forces) mechanisms. A plethora of literature that examines the effects of RET on skeletal muscle speculate the role of motor units, such as increases in firing rates partially explains muscular strength gains. Results, however, are mixed regarding changes in firing rates in studies that utilize single motor unit recordings. The lack of clarity could be related to vast or subtle differences in RET programs, methods to record motor units, muscles tested, types of contractions and intensities used to record motor units, etc. Yet to be discussed, mixed findings could be the result of non-uniform MU behavior that is not typically accounted for in RET research. The purpose of this narration is to discuss the effects of acute resistance exercise training studies on MU behavior and to provide guidance for future research.

Keywords Resistance exercise training · Firing rates · Action potential waveforms · Neural adaptations · Motor unit

Abbreviations

CON	Control
EMG	Electromyography
FDI	First dorsal interosseous
ISI	Interspike interval
ITT	Interoperated twitch technique
RET	Resistance exercise training
MVC	Maximal voluntary contraction
MAX	Maximum
MU	Motor unit
PIC	Persistent inward currents
pps	Pulses per second
SD	Standard deviation
TA	Tibias anterior
VL	Vastus lateralis
VMO	Vastus medialis obliquus

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Introduction

Resistance exercise training (RET) is proven to rapidly increase muscular strength and is integral in enhancing sports performance, injury prevention and rehabilitation, and improving health in all populations (Fragala et al. 2019; Maestroni et al. 2020). It is well established that muscle fibers are plastic and increase in diameter (hypertrophy) and strength during acute RET lasting only several weeks (Fry 2004). Importantly, there can be non-uniform changes in the morphology across fiber types within a muscle depending on the type of RET performed. For example, a review by Fry (2004) indicates greater hypertrophy can occur for fibers primarily expressing type II characteristics than type I fibers following high-intensity RET.

Mechanisms that are neural in origin are often cited to partially explain the increases in strength during RET (Carroll et al. 2001; Škarabot et al. 2021). This is particularly true for early increases in strength in absence of significant observable changes in muscle morphology (Moritani and deVries 1979). Other evidence often cited to support the potential of neural mechanisms increasing strength is the transfer of unilateral training to the contralateral limb and increases in electromyographic (EMG) amplitude following RET (Folland and Williams 2007). Despite extensive research and speculation, it remains unclear the extent of the neural adaptations that might be boosting increases in strength following acute RET.

There are numerous proposed locations where neural changes could occur with RET, such as supraspinal centers, descending neural tracts, or spinal circuitry, etc. (Carroll et al. 2001). Changes in underlying mechanisms involving excitatory and/or inhibitory synaptic input to the muscle along with intrinsic properties of the motoneurons are proposed. These underlying neural mechanisms are difficult to isolate during voluntary contractions in humans because of technical limitations. Currently, quantifying the output of the nervous system at the level of the muscle via motor unit (MU) action potential trains is the best method to evaluate if neural adaptations are occurring. Subsequently, proposed neural adaptations associated with RET are often supported with findings that include the firing rates of recorded MUs.

Motor unit: the link between neural and mechanical mechanisms

An alpha motoneuron originating from the central nervous system and the innervated skeletal muscle fibers is deemed the MU. The MU links the neural and mechanical (muscle fiber twitch forces) mechanisms that modulate strength (Burke et al. 1970) and, therefore, is directly influenced by RET. The diameters and contractile function varies among single fibers that primary express type 1 or II characteristics within and between muscles (Luden et al. 2008). However, the variability of discharge rates (firing rates) (Fig. 1) and twitch forces among MUs (Milner-Brown et al. 1973; Tanji and Kato 1973; Monster and Chan 1977; Kanosue et al. 1979; Masakado 1991; Van Cutsem et al. 1998) is rarely accounted for in RET research. Furthermore, MU recruitment does not occur in a linear manner (Fig. 1) and differs between muscles (De Luca and Kline 2012). To further complicate interpretations following RET is that firing rates may reach a "plateau" or have limited increases in firing rates despite increases in strength levels during a given task (Heckman et al. 2005; Hu et al. 2014). Yet,

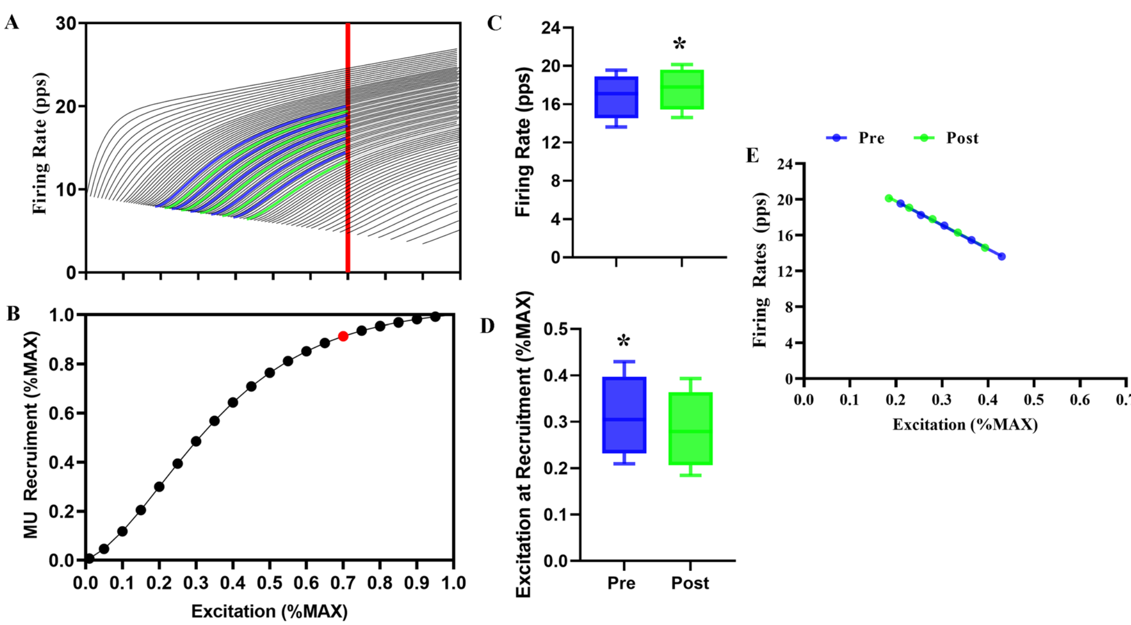

Fig. 1 Illustration of the modeled (De Luca and Hostage 2010; De Luca and Contessa 2012; Contessa and Luca 2012) MU **A** firing rate (pps) and **B** recruitment pattern for the vastus lateralis based on experimental data collected during linearly increasing isometric muscle actions to discrete force levels (increasing net excitation). MU recruitment is normalized to the maximum number of MUs (%MAX) of the vastus lateralis (~600) and is plotted as a function of excitation level (expressed as %MAX). Notice the non-uniform changes in firing rates for a given MU along with the non-linearity of recruitment from low-to-high levels of net excitation. The red (**A**) vertical line or (**B**) circle represents the input excitation of the motoneuron pool at a relative net excitation at 70% MAX. MUs selected to reflect recordings during pre- and post-resistance exercise training (RET) are highlighted in blue and green, respectively. The mean (±SD) (**C**) firing rates were significantly higher whereas the (**D**) recruitment positions were lower post-RET ($P<0.001$, $P<0.001$). A potential interpretation would be that MU recruitment (i.e., thresholds) and firing rate behavior changed pre- to post-RET. Or differences could be the result of recording MUs with relatively lower recruitment positions pre- to post-RET. For firing rates, however, differences are negated when regressed relative to recruitment position pre- to post-RET

hypotheses typically do not consider the non-uniform nature of MU behavior. Nonetheless, it is consistently speculated that increases in discharges (firing rates) of the MUs is a potential neural adaptation that leads to greater force generation (Siddique et al. 2020). In theory, changes in inhibitory and excitatory synaptic inputs or intrinsic properties of the motoneuron pool could result in higher firing rates that increases strength as represented with a rightward shift in the force-firing rate relationship (Fig. 2). Burke et al. (1970) demonstrates the effects of slight changes in firing times on the force output of single MUs. Thus, it is conceivable that increases or changes in synchronization of the MU firing times could increase muscular strength. However, interpreting changes in firing rates following RET is difficult because of the non-uniform nature of MU behavior.

Recording MUs in resistance exercise training literature

The conclusions regarding the effects of RET on MU properties are inconsistent as apparent with reported increases (Van Cutsem et al. 1998; Patten and Kamen 2000; Kamen and Knight 2004; Vila-Chã et al. 2010; Watanabe et al. 2018; Del Vecchio et al. 2019; Orssatto et al. 2022), decreases (Kidgell et al. 2006; Watanabe et al. 2018), or no change (Rich and Cafarelli 2000; Pucci et al. 2006; Beck et al. 2011a; Stock and Thompson 2014; Sterczala et al. 2020; Watanabe et al. 2020; MacLennan et al. 2021) in firing rates from pre- to post-RET. The lack of clarity could be the result of variability in RET programs, muscles tested, intensity of

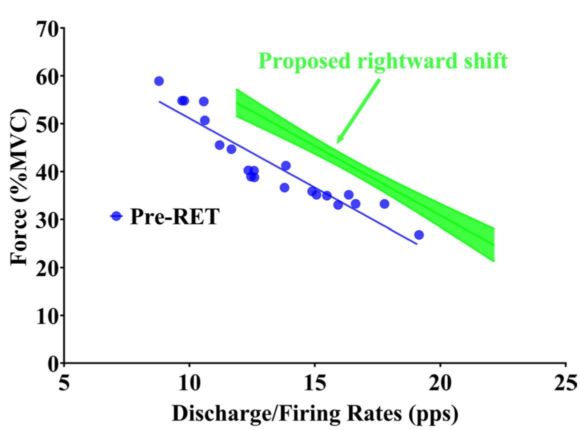

Fig. 2 Plotted is the MU recruitment thresholds relative to percent of maximal voluntary contraction (%MVC) and corresponding discharges (firing rates, pps) of the vastus lateralis obtained from an isometric muscle action performed at 70% MVC prior to 8 weeks of resistance exercise training (RET) for a subject from Sterczala et al. (2020). The green band represents the proposed rightward shift of the force-firing rate relationship based on the increases in MU firing rates (~3 pps) reported in Del Vecchio et al. (2019)

contractions used to record MUs and analytical approaches to interpret potential changes in firing rates (Fig. 3). Far less discussed in the literature, studies that report amplitudes of the action potentials (Pope et al. 2016; Sterczala et al. 2020; Jenkins et al. 2020; MacLennan et al. 2021) and twitch forces (Keen et al. 1994; Van Cutsem et al. 1998) of single MUs may provide further insight on adaptations at the level of the MU following RET. Therefore, primary objectives of this narrative review are to discuss each individual study to outline confounding variables likely contributing to inconsistencies leading to unclear results and the impact on potential physiological interpretations. Data-bases, such as PubMed, Google Scholar, etc., were searched to identify studies that included recording of single MUs pre- to post-RET. Furthermore, the mixed results among studies may be due to different approaches to record MUs. Therefore, studies incorporating intramuscular or decomposition of surface EMG will be discussed separately.

Studies utilizing intramuscular recordings of MUs in resistance exercise training

Early experiments primarily included recording MU action potential trains with sensors or electrodes inserted into the muscle. Recording AP trains with intramuscular electrodes is considered the gold standard for quantifying firing events of a single MU. The technique allows for the monitoring of MU discharges and action potential waveforms in real time (Cracraft and Petajan 1977; Van Cutsem et al. 1998; Kidgell et al. 2006). Intramuscular electrodes, however, are limited as only a few MUs (~0–4 per contraction) can be recorded and the technique is primarily used during lower intensity contractions. Therefore, it is difficult to account for the variability in the properties of MUs within a muscle, particularly for the higher-threshold MUs not recruited during lower intensity contractions. Consequently, leading to lower sensitivity in detecting changes pre- to post-RET. Furthermore, another weakness is that the few recorded MUs limits analytical approaches to statistically test potential differences. Researchers routinely "pool" or "group" firing rates without accounting for variability between individuals and perform t-tests and ANOVAs on the data. In most instances, it is unclear the approaches taken to statistically test MU firing rates when a differing number of MUs may be recorded pre- and post-RET for each subject. Despite limitations, these studies provide valuable information regarding the effects of RET on MUs (Table 1).

One of the earliest known works, Cracraft and Petajan (1977) examined single MU activity via interspike intervals (ISIs), which are used to quantify firing rates. MUs were examined at longer to shorter ISIs of the tibias anterior (TA) with an intramuscular electrode in 14 male

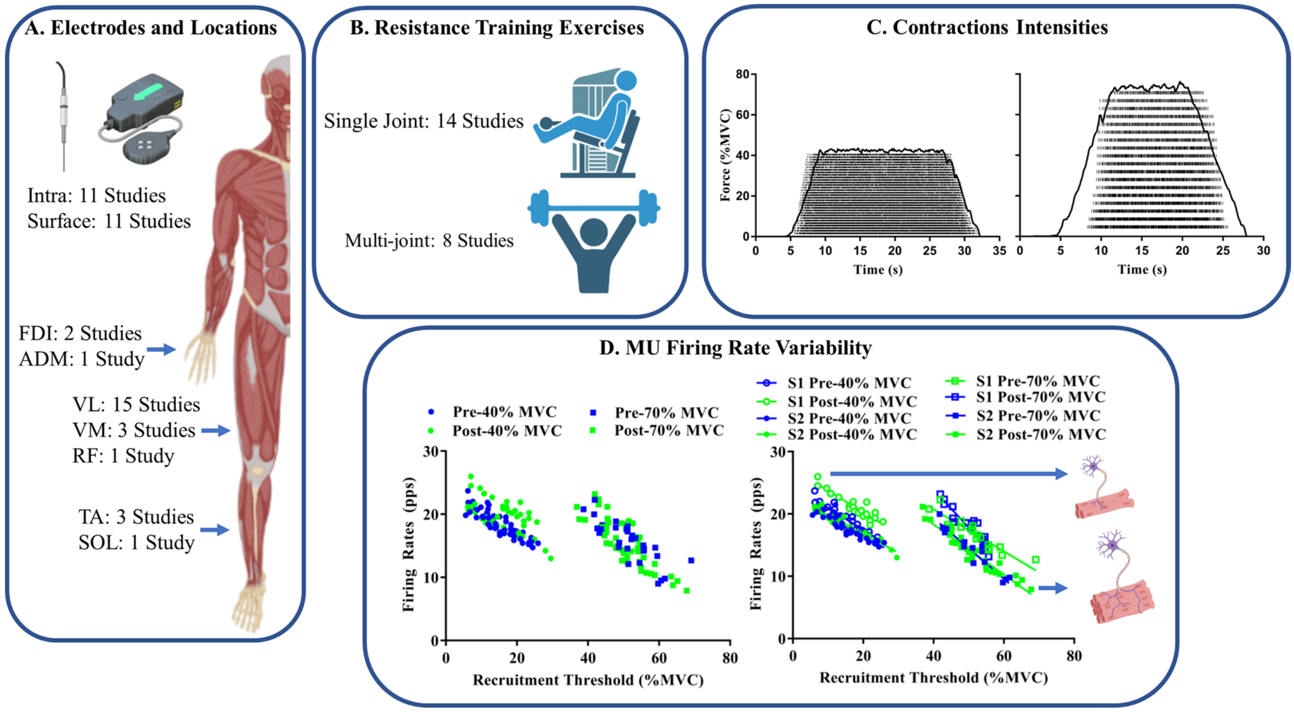

Fig. 3 The lack of clarity on the effects of resistance exercise training could be due to recording methods (**A**), various training exercises (**B**), contraction intensities used to record motor unit (MU) action potential trains (**C**), and **D** variability in MU properties depending on individuals, contraction intensity, and segment of the motoneuron pool recorded. Roughly half of the studies utilized intramuscular (intra) versus surface electromyographic electrodes with most of those studies recording MUs of lower body muscles. The majority of studies utilize a combination of either lower- or higher-intensity isometric contractions that include a "ramp up" (**C**). Importantly, differences in MU firing rates between individuals as a function of recruitment is rarely accounted for in resistance exercise training research (**D**, Left Figure). Inter-individual differences (subject [S]) and recruitment thresholds (expressed as percentage of maximal voluntary contraction [%MVC]) explains the majority of the variance in firing rates at each contraction intensity and can hinder interpretations regarding potential changes pre- to post-resistance exercise training if not accounted for as indicated in **D**. Furthermore, there is minimal discussion in the literature regarding the effects of the level of excitation in the motoneuron pool when firing rates are quantified as function of contraction intensity and recruitment threshold pre- to post-resistance exercise training. For example, smaller to moderate size MUs with higher firing rates tend to be recorded during lower and moderate-intensity contractions when the level of excitation is relatively modest, such as during a 40% MVC. However, the firing rates of smaller to moderate size MUs are not directly quantified during the higher-intensity contractions because the recordings consist of primarily higher-threshold MUs. Potentially, changes in firing rates could be a function of contraction intensity or level of excitation. Unfortunately, recording and quantifying firing rates of the same MU at discrete force levels ranging from lower- to maximal-excitation lacks feasibility on a wide scale

subjects (age = 19–35 years). Subsequently, ISIs were not examined at discrete forces or levels of excitation as typically performed in current research, such as a muscle action performed at 40% of a maximal voluntary contraction (MVC). The RET programs consisted of the following: (1) two maximal isometric contractions performed for 6 weeks (5 days/week) and (2) low-to-moderate intensity isotonic contractions performed for 6 weeks (3 days/week). The authors plotted ISIs for each MU and separated the data as a function of *non-lapses*, *lapses*, and *pauses* dependent on the duration of the ISIs. A ratio of the lapses was determined for each MU with the mean lapse ratio calculated for each subject. Therefore, firing rates were not quantified for each subject. The results did indicate that the lapse ratios decreased for isometric, whereas, increased for isotonic RET. The physiological meaningfulness of these results is unclear, however, changes in MU activity may be dependent on the type of RET.

Van Cutsem et al. (1998) examined single MUs with intramuscular recordings of the TA following 12 weeks (5 days/week) of RET that included ten "fast" concentric muscle actions of the dorsiflexors against a load of 30–40% of maximal strength in five subjects (three females) (age 18–22 years). This is the first paper in the RET literature to examine MUs while accounting for recruitment thresholds. This is a critical distinction as firing rates are typically higher for MUs with lower recruitment thresholds (*lower-threshold MUs*) (De Luca et al. 1982) when analyzed separately for individual and contraction as initially determined in research using intramuscular electrodes (Tanji and Kato 1973; Monster and Chan 1977; Kanosue et al. 1979; Masakado 1991). Quantifying firing

Table 1 Resistance exercise training studies that include intramuscular recording of motor units

References	Subjects	Intervention(s)	Muscle and Contraction	Effect
Cracraft and Petajan (1977)	RET $n = 14$ males: 19–35 years	Dorsiflexors: 6 weeks (5 days/week): isometric MVCs OR 6 weeks (3 days/week): low-to-moderate intensity isotonic contractions	TA: MU ISIs were tracked from longer-to-shorter durations	The lapses in ISIs decreased for isometric, but increased for isotonic RET
Keen et al. (1994)	RET $n = 10$ (5 males): 18–27 years. RET $n = 11$ (5 males): 59–74 years	FDI: 12 weeks (3 days/week): high-intensity (80% of 1 RM) isotonic contractions	FDI: MU twitch forces during isometric contractions	No change in MU twitch forces
Van Cutsem et al. (1998)	RET $n = 5$ (3 females): 18–22 years	Dorsiflexors: 12 weeks (5 days/week): moderate intensity (30–40% of 1RM) isotonic contractions	TA: MU twitch forces and recruitment thresholds during isometric contractions and initial firing rates during ballistic contractions	MU twitch forces and firing rates increased
Rich and Cafarelli (2000)	RET $n = 10$ males: 22.9 ± 2.1 years. CON $n = 10$ males	Leg extensors: 8 weeks (3 days/week): isometric MVCs	VL: MU firing rates at 50% MVC	No change in MU firing rates
Patten and Kamen (2000)	RET $n = 6$ (3 males): 23.2 ± 3.5 years. RET $n = 6$ (3 males): 75.8 ± 7.4 years	Abductor of 5th digit: 6 weeks (5 days/week): isometric MVCs	ADM: MU firing rates at MVC	MU firing rates increased from the 1st to 2nd visit with no changes pre- to post-RET
Kamen and Knight (2004)	RET $n = 8$ males: 18–29 years. RET $n = 7$ males: 67–81 years	Leg extensors: 6 weeks (3 days/week): high-intensity (85% of 1 RM) isotonic contractions and isometric MVCs	VL: MU firing rates at 10%, 50% and 100% MVC	MU firing rates at 100% MVC increased from the 1st to 2nd visit with no changes pre- to post-RET
Pucci et al. (2006)	RET $n = 10$ and CON $n = 20$ males: 25.0 ± 5.5 years	Leg extensors: 3 weeks (3 days/week): isometric MVCs	VL: MU firing rates at 50%, 75%, and 100% MVC	No change in MU firing rates
Kidgell et al. (2006)	RET $n = 5$: 24.8 ± 5.3 years. CON $n = 3$: 27.3 ± 6.7 years. No sex indicated	FDI: 4 weeks (3 days/week): isometric MVCs	FDI: MU firing rates at lower contraction intensities (8 ± 9% MVC)	Decrease in MU firing rates with no changes in synchronization for the RET and CON
Vila-Cha et al. (2010)	RET $n = 10$ males, ET $n = 10$ males, and CON $n = 10$ males: 26.0 ± 3.8 years	Whole-body: 6 weeks (3 days/week): three bilateral leg exercises and four exercises for upper body muscles performed at high-intensities	VL and VMO: MU firing rates at 10% and 30% MVC	MU firing rates increased for the VL and VMO at 30% MVC and the VMO at 10% MVC
Vila-Chã et al. (2012)	RET $n = 10$ males, ET $n = 10$ males, and CON $n = 10$ males: 26.0 ± 3.8 years		VL and VMO: MU firing rates during prolonged contractions at 10% and 30% MVC	No change in the decline of MU firing rates during the prolonged contractions
Vila-Chã and Falla (2016)	RET $n = 10$ males, ET $n = 10$ males, and CON $n = 10$ males: 26.0 ± 3.8 years		VL and VMO: MU firing rates at 20% and 30% MVC	Decrease in the coefficient of variation of MU firing rates

RET resistance exercise training, *CON* control, *MVC* maximal voluntary contraction, *TA* tibialis anterior, *ISI* interspike intervals, *FDI* first dorsal interosseous, *RM* repetition maximum, *VL* vastus lateralis, *ADM* abductor digiti minimi, *VMO* vastus medialis oblique rates without accounting for recruitment thresholds limits interpretations regarding potential increases in MU firing rates pre- to post-RET. Recording different segments of the MU pool, such as recording more lower vs. higher-threshold MUs will lead to a wrong interpretation that there were changes in firing rates. Furthermore, Van Cutsem et al. (1998) and Milner-Brown et al. (1973) utilizing intramuscular electrodes demonstrate that the twitch forces are greater for MUs with higher recruitment thresholds (*higher-threshold MUs*). Van Cutsem et al. (1998) reported that the twitch forces of single MUs, as measured with a spike trigger averaging technique, increased pre- to post-RET with this especially evident for the later recruited higher-threshold MUs (Fig. 3, p. 299). This finding does contradict Keen et al. (1994) who examined the effects of 12 weeks (3 days/week) of dynamic isotonic high-intensity (80% of maximal strength) RET on MU twitch forces with intramuscular electrodes of the first dorsal interosseous (FDI) in younger ($n = 10$; age = 18–27 years; five males) and older ($n = 11$; age = 59–74 years; five males) subjects. However, Keen et al. (1994) did not account for recruitment thresholds during the analytical processes. It is plausible that a propensity of recording a greater percentage of lower- versus higher-threshold MUs pre- vs post-RET could alter interpretations. Indeed, Van Cutsem et al. (1998) reported that exact phenomenon where there were significantly more lower-threshold MUs recorded following RET in comparison to pre-testing. Therefore, without accounting for recruitment thresholds the findings of Van Cutsem et al. (1998) may indicate no effect of RET on MU twitch forces. However, the differences between studies could also be related to the specific muscles tested with the FDI possessing a shorter MU recruitment range than the TA (De Luca and Kline 2012).

In addition, Van Cutsem et al. (1998) recorded the firing rates of MUs at the onset of the ballistic contractions performed to different torque levels while Keen et al. (1994) did not report firing rates. For Van Cutsem et al. (1998), the firing rates were quantified with the average times of the first three ISIs. The authors reported higher firing rates and a greater tendency for doublets (two spikes < 5 ms) following RET. Authors concluded training-induced neural adaptations contributed to the increases in the speed of contraction of the dorsiflexor muscles following RET. It cannot be discounted that the increase in firing rates were a function of recording more MUs with lower recruitment thresholds as indicated by the authors and in the histogram presented in Fig. 2 (p. 298). As previously mentioned, quantifying different segments of the MU pool (lower vs higher recruitment thresholds) pre- to post-RET could mislead interpretations of changes in firing rates (Fig. 4). The variability of firing rates among MUs as a function of recruitment position makes physiologically interpretations difficult when recruitment thresholds differ.

Rich and Cafarelli (2000) examined MU firing rates of the vastus lateralis (VL) at 50% MVC with intramuscular recordings following 8 weeks (3 days/week) of RET (isometric MVCs) of the leg extensors in males (age = 22.9 ± 2.1 years) with ten participating in the RET while ten males served as controls. Voluntary and non-voluntary strength increased, however, there were no changes in firing rates at 50% MVC. The authors speculated that the increases in voluntary and non-voluntary muscular strength did not appear to be a function of MU activity but were likely mechanical in origin. This is first instance where MU firing rates were not altered as a function of RET and contradicts earlier works. Recruitment thresholds for each MU were not quantified and limits interpretations. Furthermore, the largest MUs with the greatest twitch forces for the VL were likely not recruited during the 50% MVC as modeled (De Luca and Kline 2012) and previous work would suggest (Muddle et al. 2018; Miller et al. 2020). Thus, a segment of the motoneuron pool that significantly contributes to maximal strength was not measured pre- and post-RET. Of note, the research design incorporated in this study is often replicated, such as including the duration of the intervention, muscle tested, and performing isometric contractions at discrete force levels to quantify MU firing rates.

Two studies, Patten and Kamen (2000) and Kamen and Knight (2004) reported increases in MU firing rates from an initial baseline visit to the 2nd visit prior to the start of RET. Patten and Kamen (2000) examined MU firing rates of the abductor digiti minimi muscle during isometric MVCs of the abduction of the fifth digit with intramuscular recordings following 6 weeks (5 days/week) of RET (isometric MVCs) in six younger (age = 23.2 ± 3.5 years; three males) and six (age = 75.8 ± 7.4 years; three males) older subjects. One hand would be used during training with testing also performed on the untrained hand. The authors reported increases in MU firing rates of both hands for the younger and older subjects from the initial baseline visit to the 2nd visit, prior to the start of RET. Firing rates remained elevated for the trained and untrained hand for the younger subjects throughout RET with firing rates decreasing for the older subjects. Kamen and Knight (2004) examined MU firing rates of the VL at 10%, 50%, and 100% MVC following 6 weeks (3 days/week) of RET that included a combination of isotonic (85% of maximal strength) and isometric MVCs in younger ($n = 8$; age = 18–29 years) and older ($n = 7$; age = 67–81 years) male subjects. The load was gradually increased during the isotonic RET. Similar to Patten and Kamen (2000), the authors reported increases in MU firing rates during the 100% MVC, but not the 10% or 50% MVCs, from the 1st experimental to the 2nd experimental visit prior to the start of the RET for the young and older subjects. From thereon, no changes in MU firing rates occurred during submaximal and maximal MVCs despite

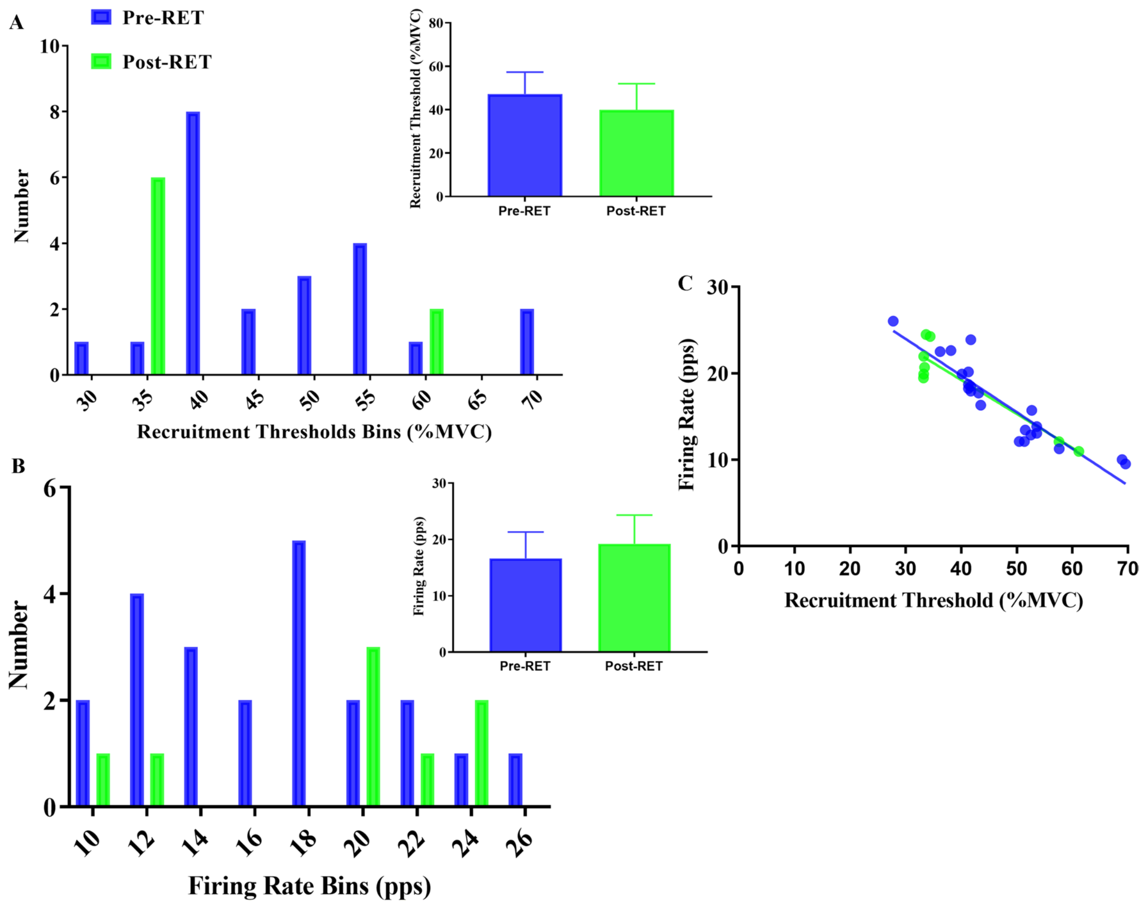

Fig. 4 Plotted histograms and bar graphs (mean ± SD) of the **A** recruitment thresholds (expressed as percentage of maximal voluntary contraction [%MVC]) and **B** firing rates along with the (**C**) firing rate versus recruitment threshold relationship pre- and post-8 weeks of resistance exercise training (RET) for a subject from Sterczala et al. (2020). The greater propensity for recording more relatively lower-threshold motor units post-RET likely explains the mean increase (2.6 pps) in firing rates. The firing rate versus recruitment threshold relationship illustrates the similarities of the firing rate patterns pre- to post-RET when regressed against recruitment threshold

continued increases in muscular strength. If you consider baseline testing a de facto RET session, then it appears the increase in strength from baseline to the next visit is neural in origin with mechanical mechanisms increasing strength thereon. Of note, recruitment positions of the MUs were not quantified for Patten and Kamen (2000) and Kamen and Knight (2004) and it is unclear if recruitment thresholds of recorded MUs changed across experimental visits. Nonetheless, the initial increases in firing rates may indicate neural mechanisms. A learning effect that is neural in origin may be occurring between the 1st and 2nd experimental visit in absence of a familiarization sessions. Most studies, however, include familiarization sessions prior to baseline testing that may diminish the impact of the learning effect on MU firing rates during RET.

Published in 2006, Pucci et al. (2006) examined the effects of isometric leg extensor training (3 weeks, 3 days/week) on MU firing rates of the VL recorded at 50, 75, and 100% MVC with intramuscular electrodes pre- and post-RET in 10 male subjects who performed the RET while 20 other male subjects were in the control group (age = 25.0 ± 5.5 years). Voluntary strength increased pre- to post-RET in absence of increases in non-voluntary twitch forces and firing rates recorded during the 50, 75, and 100% MVCs. The authors also reported a small but significant increase in percent voluntary activation with the interoperated twitch technique (ITT) for the trained and untrained groups. The ITT is a difficult procedure to administer with the interpretations of physiological mechanisms limited (Taylor 2009). An increase in percent voluntary activation could signal an increase in MU recruitment. Regardless, the authors suggest that increases in firing rates might not be the primary neural adaptation to increase strength.

Vila-Chã published a series of papers (2010, 2012, 2016) that examined the effects of 6 weeks (3 days/week) of RET on MU firing rates of the vastus medialis obliquus (VMO) and VL with intramuscular electrodes during isometric contractions at lower intensities (10 to 30% MVC) that included

30 male subjects (age = 26.0 ± 3.8 years) with 10 of the male subjects completing the RET intervention while the remaining 20 participated in endurance training or served as controls. The authors incorporated an applicable RET program in comparison to previous studies as it included the whole-body and the intensity increased from 60–70% to 70–85% of maximal strength while the sets were maintained at 3–4 and the repetitions decreased from 13–15 to 8–12 repetitions by the end of the training. Exercises included leg press, leg extension, and leg curl along with exercises for upper body. MU firing rates increased throughout the RET for the VL and VMO during the 30% MVC (Vila-Chã et al. 2010). For the 10% MVC, there was only an increase in MU firing rates for the VMO at only 3 weeks in comparison to baseline (Vila-Chã et al. 2010). Vila-Chã et al. (2012) with the same research design and sample reported no time-related differences in MU firing rates during a longer duration muscle action at 10% MVC and until task failure for the 30% MVC following RET. Whereas, Vila-Chã and Falla (2016) reported a decrease in the coefficient of variation of MU discharges during the lower intensity contractions following RET. The authors suggest that early increases in strength could be the result of increases in firing rates (Vila-Chã et al. 2010) that can be explained by increased excitability governed by descending pathways and that "*synchronization and the common modulation of motor unit discharge rates*" may lead to lower coefficient of variation (Vila-Chã and Falla 2016). The authors did not report recruitment thresholds, however, performing contractions at a lower intensity might dimmish the variability in firing rates among the active MUs since recruitment thresholds would be more similar. The works of Vila-Chã et al. (2010), Vila-Chã and Falla (2016) indicate that traditional linear periodization whole-body RET may increase MU firing rates and synchronization of the VL at lower contraction intensities.

Kidgell et al. (2006) examined the synchronization of MUs of the FDI following 4 weeks (3 days/week) of RET that consisted of maximal finger abduction isometric contractions. There were five and three subjects (no indication of sex; 25.8 ± 5.0 years) in the RET and CON groups, respectively. MUs were recorded during relatively low contraction intensities (8 ± 9% MVC) where subjects maintained a certain discharge rate. In contrast to Vila-Chã and Falla (2016), there were no changes in synchronization of MUs pre- to post-RET. Although not the primary purpose, the authors report decreases in discharge rates with increases in the coefficient of variation following the intervention for the RET and CON. The discharge properties were obtained during similar mean contraction intensities pre- and post-intervention, however, the high standard deviation suggests the forces where dischargers were analyzed could have varied pre- to post-RET for subjects. Overall, isometric RET of the FDI did not influence synchronization nor did it likely affect other MU discharge properties at a relatively low contraction intensity when considering the CON underwent similar changes.

Studies utilizing surface EMG decomposition to record MUs in resistance exercise training

The advancements in signal processing techniques applied to surface EMG signals has led to examining the effects of RET on MUs recorded from the surface of the skin (Beck et al. 2011a, b; Vila-Chã and Falla 2016; Pope et al. 2016; Watanabe et al. 2018, 2020; Del Vecchio et al. 2019; Sterczala et al. 2020; Jenkins et al. 2020; MacLennan et al. 2021; Orssatto et al. 2022) (Table 2). The EMG decomposition techniques are validated with two-source methods that compare MU action potential trains recorded with intramuscular and surface electrodes (De Luca et al. 2006; Holobar et al. 2009). However, a limitation of decomposition procedures is that MUs cannot be monitored in real time and only a few MUs can be validated with intramuscular electrodes. Therefore, spike trigger averaging (Hu et al. 2013; Thompson et al. 2018; Herda et al. 2020) along with other procedures (Holobar et al. 2014; Hernandez-Sarabia et al. 2020) are utilized to indirectly verify the accuracies of MU firing rates and action potential waveforms. The firing rates of recorded MUs via the decomposition techniques are highly reliable (Martinez-Valdes et al. 2016; Colquhoun et al. 2018b; Parra et al. 2021). The benefit of the decomposition procedures is that the larger yield of recorded MUs allows for a better estimation of firing rate behavior of the active motoneuron pool and inclusion of analytic approaches that accounts for variability among MU properties and subjects.

Beck et al. (2011a) is the first study that examined the effects of RET on MU firing rates with the utilization of surface EMG decomposition. The intervention included 8-weeks (3 days/week) of progressive high-intensity RET of the leg extensors in 11 males (age = 22.5 ± 4.2 years). The program included leg press and extension exercises along with bench press. The authors recorded MUs of the VL during an isometric leg extension to 80% MVC that included a "ramp-up", steady force segment followed by a slow ramp down back to baseline (trapezoidal contraction) with testing occurring every week. The vast majority of MUs were likely activated during the 80% MVC (De Luca and Contessa 2015) (Fig. 1). MU firing rates were regressed against recruitment thresholds separately for subjects and contractions. The primary objective was to examine potential changes in the relationship between MU firing rates quantified during steady force and recruitment threshold. The slope of the relationship remained negative as firing rates were greater for the earlier recruited lower-threshold MUs and was unchanged during and following the RET. There was no indication of

Table 2 Resistance exercise training studies that include decomposition of surface EMG signals to record motor units

References	Subjects	Intervention(s)	Muscle and Contraction	Effect
Beck et al. (2011a, b)	RET $n = 11$ males: 22.5 ± 4.2 years	Leg extensors: 8 weeks (3 days/week): high-intensity (80% of 1 RM) isotonic contractions	VL: MU firing rates and recruitment thresholds at 80% MVC	No change in firing rates
Beck et al. (2011a, b)	RET $n = 8$ males: 21.8 ± 4.2 years	Leg extensors: 8 weeks (3 days/week): High-intensity (80% of 1 RM) isotonic contractions	VL: MU firing rates at 80% MVC	No change in the cross-correlation coefficients between the first active MU and next nine recruited MUs
Orssatto et al. (2022)	RET $n = 17$ (12 females): 68.5 ± 2.8 years	Whole-body: 6 weeks (2 days/week): High-intensity with loads and velocities of the movements increasing	Soleus: MU PICs, firing rates, and recruitment thresholds were measured during 20% and 40% isometric triangular and 20% MVC trapezoidal contractions	PICs, firing rates, and recruitment thresholds increased
Stock and Thompson (2014)	RET $n = 15$ and CON $n = 11$ males: 24 ± 3 years	Lower-body: 10 weeks (2 days/week): High-intensity barbell deadlifts	VL and RF: MU firing rates and recruitment thresholds at 50% MVC	No change in firing rates at recruitment or at 50% MVC
Del Vecchio et al. (2019)	RET $n = 14$ males: 23.9 ± 2.9 years. CON $n = 14$ males: 25.1 ± 2.9 years	Dorsiflexors: Isometric MVCs, maximal ballistic contractions, and isometric ramp contractions to 75% MVC	TA: MU firing rates and recruitment and derecruitment thresholds at 35%, 50%, and 70% MVC	MU recruitment thresholds decreased and firing rates increased at steady force
Sterczala et al. (2020)	RET $n = 16$ males: 20.7 ± 1.9 years. CON $n = 8$ males: 19.4 ± 2.5 years	Lower-body: 8 weeks (3 days/week): Three bilateral isotonic leg exercises performed at high-intensities	VL: MU firing rates, action potential amplitudes, and recruitment thresholds at 70% MVC	No changes in MU firing rates. MU action potential amplitudes increased for the higher-threshold MUs
Pope et al. (2016)	RET $n = 20$ males: 22.2 ± 2.6 years	Whole-body: 8 weeks (3 days/week): Seven isotonic exercises with three that targeted the leg extensors	VL: MU action potential amplitudes and recruitment thresholds at 100% MVC	MU action potential amplitudes increased for the higher-threshold MUs
Jenkins et al. (2020)	RET $n = 9$ & CON $n = 18$ females: 20.8 ± 3 years	Whole-body: 8 weeks (2 days/week): Progressive high-intensity (> 60% of 1 RM) isotonic exercises	VL: MU action potential amplitudes and recruitment thresholds at 70% MVC	MU action potential amplitudes increased for the higher-threshold MUs
Watanabe et al. (2018)	RET $n = 25$ (12 males) & CON $n = 25$ (12 males): 61–83 years	Lower-body: 6 weeks (days/week): Bilateral leg press at 70% MVC	VL: MU firing rates and recruitment thresholds recorded during ramp contractions performed to 90% MVC	Changes (increases and decreases) in MU firing rates were dependent on recruitment threshold
Watanabe et al. (2020)	RET $n = 24$ (14 males): ~ 73 ± 6 years	Leg extensors: 8 weeks (2 days/week): Isometric contractions of both legs > 80% MVC	VL: MU firing rates and recruitment thresholds recorded during ramp contractions performed to 30% and 70% MVC	No changes in MU firing rates
Maclennan et al. (2021)	RET $n = 9$ males: 12 ± 1 years. CON $n = 5$ males: 13 ± 1 years	Lower-body: 18 weeks (2 days/week): High-intensity barbell deadlifts, back squat, and hang clean	VL: MUs firing rates, action potential amplitudes, and recruitment thresholds at 50% and 80% MVC	No changes in MU firing rates or action potential amplitudes

RET resistance exercise training, *CON* control, *MVC* maximal voluntary contraction, *PIC* persistent inward current, *TA* tibialis anterior, *RM* repetition maximum, *VL* vastus lateralis, *RF* rectus femoris changes in MU firing rate patterns when considering the slope values week-to-week. It also appears that mean MU firing rates did not change either (p. 5, Fig. 3). The authors did not indicate what recruitment thresholds were observed and, thus, is unclear if similar segments of the motoneuron pool were recorded pre- and post-RET or if there was propensity to record more lower- vs higher-threshold MUs as observed with intramuscular electrodes. The firing rates of the higher-threshold MUs are lower and, thus, may have the capacity to increase firing rates more so than the earlier recruited lower-threshold MUs. However, the authors noted that the firing rates of the higher-threshold MUs did not increase to the level comparable to the lower-threshold MUs despite potentially having the capacity to do so.

With the same research design, Beck et al. (2011b) examined the effects of RET on common drive in eight males (21.8 ± 4.2 years). Common drive maintains that active MUs within a muscle are controlled as a pool rather than separately by the central nervous system. Common drive is typically quantified with cross-correlation coefficients of firing rate patterns among MUs. A high correlation suggests that MU firing rates are fluctuating in a similar manner (De Luca et al. 1982). There were no changes in the cross-correlation coefficients among the first recorded MU and each additional MU that was recorded during the contraction. The authors concluded (Beck et al. 2011a, b) that the overall motor control scheme used by the nervous system to regulate MU recruitment and firing rates cannot be changed with RET. However, an increase in the excitatory input and/or decrease the inhibitory input to the muscle may yet be possible.

Far less researched, but persistent inward currents (PIC) may alter firing rates despite no changes in the nervous system's overall regulation of MU activity. Orssatto et al. (2022), examined the effects of 6 weeks (2 days/week) of whole-body "power-orientated" RET in 17 (12 females and 5 males) older individuals (68.5 ± 2.8 years) on MU PICs of the soleus. MU PICs along with peak discharge rates and recruitment thresholds were quantified during isometric triangular-shaped contractions at 20% and 40% MVC along with an isometric trapezoidal contraction at 20% MVC of the plantar flexors. The authors performed data analyses on matched (pre- to post-RET) and unmatched MUs. PICs, peak discharge rates, and recruitment thresholds were greater following the 6 weeks of RET for matched and unmatched MUs. The authors concluded that increases in firing rates following RET in older individuals could be a function of adaptations to intrinsic motoneuron excitability.

Stock and Thompson (2014) examined the effects of 10 weeks (2 days/week) of RET that included barbell deadlifts performed for 5 sets and 5 repetitions in 15 males with 11 males serving as controls ($n = 26$; age = 24 ± 3 years). The load was gradually increased throughout the training. The MU firing rates of the VL and rectus femoris (RF) were examined at recruitment and steady force during the isometric trapezoidal muscle action performed at 50% MVC. The firing rates at recruitment and during steady force were regressed against recruitment thresholds separately for subjects and contractions. The MU relationships were unaltered for both muscles following the RET program. Furthermore, the authors also reported the mean and SDs for the firing rates at recruitment and at steady force without considering recruitment threshold. The authors did not perform statistics on that pooled data, however, no differences are observed (p. 10, Table 2). Similar to other projects discussed, the largest MUs would not be activated during the 50% MVC and, thus, a segment of the motoneuron pool potentially most influenced by RET was not recorded.

Del Vecchio et al. (2019) examined the effects of 4 weeks (3 days/week) of RET on MU firing rates of the TA in 14 males (age = 23.9 ± 2.9 years) with 14 males (age = 25.1 ± 2.9 years) serving as controls. The training program consisted of three isometric MVCs, 4 sets and 10 repetitions of maximal ballistic contractions, and 30 isometric ramp contractions of the ankle dorsiflexors to 75% MVC. MU firing rates were recorded during isometric trapezoids performed at 35%, 50%, and 70% MVC. The average discharge rate at recruitment (first three interspike intervals), the average discharge rate during the steady force (first nine interspike intervals), and input–output gain of the motoneurons were analyzed. MUs were pooled across subjects for each contraction intensity. The authors also tracked MUs pre- to post-RET based on correlation ($r > 0.7$) analyses of the STA-derived two-dimensional action potential waveforms. The authors reported that the relative recruitment thresholds for MUs decreased and coincided with increases in firing rates at the plateau. The authors also reported that the input–output gain of motoneurons did not change. The authors did not apply linear regressions between MU firing rates and recruitment thresholds, nor did they account for variability in MU firing rates among subjects. It is unclear the viability of tracking MUs with potential increases in muscle cross-sectional area (not measured) and, specifically, the diameters of skeletal muscle fibers increasing pre- to post-RET (Widrick et al. 2002; Fry 2004). Of note, the other studies cited utilizing decomposition methods typically average the firing rates for each MU during the plateau for much longer durations that include > 100 firing times (Beck et al. 2011a; Thompson et al. 2018; Sterczala et al. 2020; MacLennan et al. 2021). Nonetheless, Del Vecchio et al. (2019) provides evidence that increases in strength following short-term RET of the TA may be the result of increases in MU firing rates. The authors suggest increases in net excitatory synaptic input to the motoneuron pool partially explains increases in strength. The authors state that the intrinsic properties of the motoneurons were unaffected as the input–output gain relationship remained constant pre- to post-RET.

Sterczala et al. (2020) examined the effects of 8 weeks (3 days/week) of lower-body high-intensity linear periodization RET on MU firing rates of the VL in 16 males (age = 20.7 ± 1.9 years) with 8 males (age = 19.4 ± 2.5 years) serving as controls. MUs were recorded during isometric trapezoids performed at 70% MVC. The average firing rate was quantified across 8 s during the steady force and peak-to-peak amplitudes of the action potential waveforms were calculated. Firing rates and peak-to-peak amplitudes of the MU action potentials were regressed against recruitment threshold separately for subjects with statistics performed on the calculated y-intercepts and slopes. In addition, authors analyzed the average firing rate for each subject and assessed muscle cross-sectional area of the VL. There were no changes in MU firing rates regardless of analyses methods pre- to post-RET. However, the slopes of the MU action potential amplitudes versus recruitment threshold relationships increased pre- to post-RET and demonstrated a non-uniform change in action potential amplitudes. Specifically, the action potential amplitudes of the higher-threshold MUs increased in size but was unchanged for the lower-threshold MUs. The greater action potential amplitudes may be an indirect marker of muscle fiber diameters and twitch forces of the MU (Milner-Brown et al. 1973; Milner-Brown and Stein 1975; Pucci et al. 2006; Herda et al. 2019; Trevino et al. 2019). The muscle cross-sectional area of VL also increased in size and, therefore, the authors concluded that the increase in muscular strength following 8 weeks of RET was likely primarily mechanical in origin (Fig. 5) and may be a function of the increased strength in muscle fibers housed in the higher-threshold MUs.

Two other studies have reported increases in action potential amplitudes for higher-threshold MUs following RET. The first, Pope et al. (2016) examined the effects of 8 weeks (3 days/week) of high-intensity whole-body RET on MUAP amplitudes and muscle cross-sectional area of the VL in 20 males (age = 22.2 ± 2.6 years). MUs were recorded during an isometric trapezoidal muscle action at 100% MVC. MU action potential amplitudes were regressed against recruitment threshold separately for each subject. The MU action potential amplitudes increased for the higher-threshold MUs and correlated with the increases in muscle cross-sectional area. Jenkins et al. (2020) examined the effects 8 weeks (4 days/week) whole-body progressive resistance (2 days) and aerobic interval exercise (2 days) training on MU action potential amplitudes and muscle cross-sectional area of the VL in 9 females with 18 females serving as controls (2 control groups) (age = 20.8 ± 3 years). MUs were recorded during isometric trapezoidal muscle actions at 70% MVC. Similar to Pope et al. (2016) and Sterczala et al. (2020), there were increases in MU action potential amplitudes for

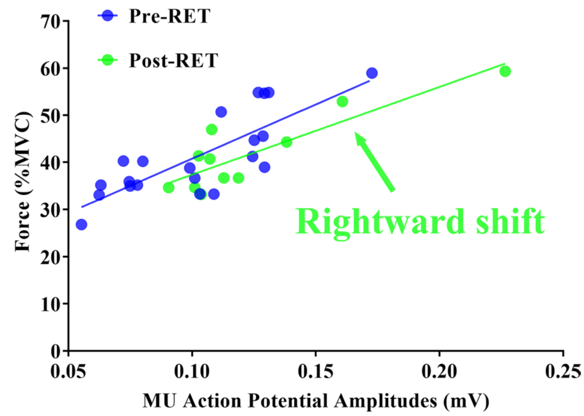

Fig. 5 Plotted is the MU recruitment thresholds relative to percent maximal voluntary contraction (%MVC) and the corresponding action potential amplitudes (mV) of the vastus lateralis from an isometric muscle action performed at 70% MVC pre- and post-resistance exercise training (RET) for the subject presented in Fig. 2 from Sterczala et al. (2020). There was a shift in the force-action potential amplitude relationships unlike for the firing rates, which may indirectly indicate that increases in muscle fiber diameters and twitch forces were the primary contributor to increases in strength

the higher-threshold MUs that correlated with increases in VL cross-sectional area. Pope et al. (2016) and Jenkins et al. (2020) did not report MU firing rates. Nonetheless, the results would suggest non-uniform changes in MU properties can occur with action potential amplitudes increasing for the higher-threshold MUs.

Watanabe et al. (2018, 2020) conducted two studies that examined supplementation and RET on MU firing rates in older adults. Watanabe et al. (2018) examined the effects of 6 weeks of RET (2 days/week) and fish protein on MU firing rates of the VL in older males and females (age = 61–83 years). Twenty-five males and females completed the RET while consuming either the fish protein (n = 12; males = 6) or placebo (n = 13; males = 6) and 25 (males = 12) performing the study without RET but either in the supplementation or control group. RET included three sets of ten repetitions of bilateral leg press at 70% of maximal strength. MUs were recorded during ramp contractions performed from 0 to 90% MVC. The ramp contractions were completed at the same absolute force obtained at pre-RET. The mean firing rates for each MU were calculated every 10% MVC and placed into three categories based on recruitment thresholds: < 20%, 20–40%, and 40–60% MVC. Therefore, the MU firing rates were pooled across subjects. Unlike previous studies discussed, there were no significant increases in isometric and leg press strength or muscle size. There were increases in firing rates for MUs recruited < 20% for the RET (no supplementation) with different responses (increases and decreases) among recruitment thresholds reported for the RET group that consumed the supplementation. The authors suggested that lower-threshold MUs might be more plastic to the effect of RET in older individuals. This is the first instance where it is suggested that non-uniform changes in MU firing rate patterns may occur following RET.

Watanabe et al. (2020) examined the effects of 8 weeks (2 days/week) of isometric leg extension RET and milk fat globule membrane supplementation on MU firing rates of the VL in older (age = 63–84 years) males and females. Twenty-four individuals were equally randomized into the RET with (males = 7) and RET without supplementation (males = 7). RET consisted of three sets of five isometric contractions > 80% MVC during unilateral leg extension for the left and right legs. MUs were recorded during isometric ramp contractions from 0 to 30% and 70% MVC. Similar to Watanabe et al. (2018), the isometric ramps were performed at the absolute force obtained at pre-RET. The mean firing rates were calculated every 5% or 10% MVC (30% or 70% MVC ramp) with the MUs grouped based on recruitment threshold in a similar manner to the authors previous RET supplementation study. Of note, isometric strength increased for the RET without supplementation group, but not for the RET + supplementation group with no changes in muscle thickness for either group. There were no significant changes in MU firing rates for either group, however, the authors suggested there was a trend for firing rates to increase during RET + supplementation group and decrease during the RET without supplementation. Watanabe et al. (2018, 2020) reports non-uniform changes in firing rates across recruitment thresholds. However, regressing the firing rates across recruitment thresholds for each subject to account for inter-individual variability should be the preferred approach for interpretations since it is very likely that not all subjects are represented equally in each MU recruitment threshold bin. Overall, adaptations to MU firing rates in older individuals to maintain the same task post-RET may depend on recruitment threshold.

MacLennan et al. (2021) is the only study to date to examine potential changes in MU firing rates and AP amplitudes following RET in adolescent youth. The authors examined the effects of 16 weeks (2 days/week) of RET in nine males (age = 12 ± 1 years) while five males (age = 13 ± 1 years) served as controls. Lower-body RET (Romanian deadlift, back squat, and hang clean) was performed for three sets of five repetitions. Loads were progressively increased throughout the duration of the study. The subjects also completed short-duration balance training, plyometrics, speed work, and agility drills during each session. MUs were recorded from the VL during isometric trapezoidal muscle actions at the force levels of 50% and 80% MVC that corresponded to pre- and post-RET strength. MU firing rates and action potential amplitudes were regressed against recruitment thresholds separately for subjects and contractions with the calculated slopes and y-intercepts used for statistical purposes. There were no increases in isometric leg extensor strength with no changes in MU firing rates, however, there were increases that were moderate magnitude for strength at faster isokinetic velocities (300° s^{-1}). Similar to the majority of projects discussed, recording MU firing rates during movements used during RET may provide better insight on the involvement of MU firing rates on increases in strength.

Summary of physiological interpretations

There could be a learning effect that leads to increases in strength accompanied with increases in firing rates during maximal isometric efforts from an initial baseline test to the next experimental visit in absence of a familiarization session (Patten and Kamen 2000; Kamen and Knight 2004). This learning effect might only be evident during maximal contractions. The simplest explanation is that voluntary effort of the participants increases as they become more familiar and comfortable with the isometric strength testing. Therefore, the increase in firing rates and strength could be due to greater voluntary effort resulting in changes in net excitatory synaptic input. The other RET studies incorporate familiarization sessions to minimize the learning effect on potential changes to MU properties.

The findings regarding the effects of RET on MU firing rates lacks consistency and, therefore, physiological interpretations are limited. There is a consensus that increases in net excitatory synaptic input to the MU pool or, potentially, changes to the intrinsic properties of motoneurons could occur. However, the overall scheme used by the nervous system to regulate MU recruitment and firing rates are less likely to be altered by RET.

The majority of studies that investigate the effects of RET on MU properties focus on firing rates. Interestingly, the most consistent results in the literature are the non-uniform changes in action potential amplitudes of the MUs following RET in adults. Three studies utilizing surface EMG decomposition report increases in the action potential amplitudes of the higher-threshold MUs. Action potential amplitudes of the higher-threshold MUs associates with a marker of muscle fiber type area and size (Colquhoun et al. 2018a; Herda et al. 2019; Trevino et al. 2019), whole muscle cross-sectional area (Pope et al. 2016; Trevino et al. 2019), and muscular strength (Trevino et al. 2019). Therefore, it is speculated that action potential amplitudes may be an indirect marker of muscle fiber diameters and, thus, strength of those MUs were increasing pre- to post-RET. A study utilizing intramuscular electrodes supports these conclusions drawn by the more recent works as the MU twitch forces were increasing following RET with a greater change occurring for the higher-threshold MUs (Van Cutsem et al.

1998). Together, these studies regressed MU action potential amplitudes and twitch forces against recruitment thresholds and demonstrate non-uniform changes to the MU pool following RET. Importantly, quantifying MU action potential amplitudes may be a more sensitive measurement to detect changes as a waveform for a given MU likely does not vary greatly as a function of contraction intensity (i.e., level of excitation) unlike its firing rate.

Factors that confound physiological interpretations

There are a number of variables that make it difficult to isolate changes in MU properties as a function of RET, especially firing rates. The primary reason for the lack of clarity on potential changes in firing rates is that a small percentage of MUs are recorded during each contraction despite decomposition techniques allowing for a greater MU yield. For example, there might be up to 40 recorded out of roughly 550 active MUs for the vastus lateralis during a 70% MVC (De Luca and Contessa 2015). The use of coefficients (y-intercepts and slopes) from linear regression applied to MU data for each subject does help with interpreting firing rates and action potential amplitudes that are not directly recorded (De Luca and Hostage 2010), but interpretations may be limited for MUs not within the recorded recruitment threshold ranges (Parra et al. 2021). The slopes from the relationships indicate a considerable amount of variability in the firing rates among active MUs at a given level of excitation that is explained by recruitment threshold. Failure to account for recognize the variability among MU properties at a given excitation level as a function of recruitment threshold renders most interpretations limited. Furthermore, research utilizing decomposition methods provides information indicating great variability of MU properties between individuals as a function of sex (Trevino et al. 2019; Parra et al. 2020b), muscle cross-sectional area (Herda et al. 2019; Trevino et al. 2019), and markers of fiber type (Trevino et al. 2016, 2019; Colquhoun et al. 2018a), yet the majority of RET does not account for inter-individual differences.

Organization of the MU pool

Failure to recognize the organizational structure of the MU pool during isometric contractions limits potential physiological interpretations. The firing rates, action potential amplitudes, and recruitment thresholds of MUs are strongly associated with each other during isometric muscle actions (Hu et al. 2013). Action potential amplitudes have a strong relationship with recruitment threshold, however, muscle fiber diameters and action potential amplitudes of MUs can get larger following RET (Fry 2004; Pope et al. 2016; Sterczala et al. 2020; Jenkins et al. 2020). Therefore, utilizing MU action potential amplitudes to gauge changes in firing rates can be misleading as the firing rates for a relatively larger MU action potential amplitude would appear to increase post-RET. This gives the impression that larger MUs with the capacity to increase firing rates are, indeed, increasing firing rates post-RET. However, it is possible that the firing rates are not changing, but rather action potential amplitudes are increasing in size as previously demonstrated (Pope et al. 2016; Sterczala et al. 2020; Jenkins et al. 2020). It also remains unclear how non-uniform changes in action potential amplitudes would affect the MU tracking utilized by Del Vecchio et al. (2019). Albeit, it is unclear if muscle cross-sectional area or fiber diameters changed following RET as it was not reported for Del Vecchio et al. (2019).

The best marker to account for variability among MU firing rates is recruitment thresholds. The strong relationships between firing rates and recruitment thresholds on a subject-by-subject basis allows for comparing firing rates pre- to post-RET for a given recruitment threshold. To date, there is no research that demonstrates RET changes MU firing rates when recruitment position for MUs is accounted for on a subject-by-subject basis rather than pooled across subjects. Of note, our laboratory has reported changes in MU firing rates with this analytical approach that includes examining MU firing rates as a function of recruitment thresholds on a subject-by-subject basis following endurance cycling training (Trevino et al. 2022). Therefore, this analytical approach is sensitive to changes in firing rates following an exercise intervention.

There are a few studies that did record recruitment thresholds without accounting for inter-individual variability where changes in firing rates occurred. Two of the studies reported decreases in recruitment thresholds of recorded MUs that coincided with increases in the firing rates (Van Cutsem et al. 1998; Del Vecchio et al. 2019) with another study reporting greater firing rates and recruitment thresholds following RET (Orssatto et al. 2022). Recording a greater propensity of MUs with lower recruitment thresholds will result in higher mean firing rates in absence of a change in firing rates for a given recruitment threshold as we have reported previously (Dimmick et al. 2022) and illustrate in Fig. 1. Quantifying MU properties in relation to recruitment position separately for each subject should be the preferred method of analyses.

The findings of Watanabe et al. (2018, 2020) suggested that there could be non-uniform changes in firing rates post-RET, but for the lower-threshold MUs in contrast to the findings for action potential amplitudes where changes occurred for the higher-threshold MUs. Vila-Chã et al. (2010) also reported changes in firing rates during lower intensity contractions that would isolate lower-threshold MUs, but did not perform higher-intensity contractions to examine potential non-uniform changes across the motoneuron pool. Sterczala et al. (2020) and Beck et al. (2011a) performed higher intensity contractions that results in the recording of very few MUs with lower recruitment thresholds. It is unclear if Stock and Thompson (2014) and MacLennan et al. (2021) recorded MUs within the recruitment threshold ranges during the 50% MVC similar to Watanabe et al. (2018, 2020). It is possible that these studies would report non-uniform MU firing rates when regressed against recruitment threshold relationships on a subject-by-subject basis if contractions ranging from low- to higher-intensity were included. However, the findings of Watanabe et al. (2018, 2020) might be a function of the population tested (older individuals) or changes in firing rates may not be observed if different analytical approaches were utilized.

Muscle tested

The structure and functional roles of skeletal muscle vary greatly along with variability in MU properties within skeletal muscle. To add complexity, skeletal muscles are plastic and respond to physical activity levels with adaptations dependent on the functional role (Trappe et al. 2009). The mixed results among studies regarding the changes in MU properties might be dependent on the muscle tested and the contraction intensity to record MUs. The TA might be more prone for increases in MU firing rates because of its functional role that does not typically include explosive or maximal efforts and shorter recruitment range in comparison to the VL (De Luca and Kline 2012). To date, no study has measured the effects of whole-body resistance exercise training program on MU properties from skeletal muscles with differing function roles and MU behavior, such as a leg extensors vs. plantar flexors vs. dorsiflexors. For the VL, MU firing rates were higher during lower intensity contractions or for the lower-threshold MUs in older individuals. There were no changes in MU firing rates for the VL during RET at higher intensity contractions regardless of recording method. Changes in MU firing rates for a given recruitment threshold might be best observed at certain levels of excitation in the motoneuron pool. The majority of studies do not test changes in MU firing rates at various levels of excitation nor do they account for potential changes in firing rates for a given MU at various levels of excitation in their analytical approaches. For example, changes in firing rates for lower-threshold MUs might be evident at lower contraction intensities or vice versa for higher-threshold MUs.

Total torque output of the limb is dependent on the combination of agonist and antagonist muscle activation. Lower antagonist MU activation is routinely proposed to partially explain rapid increases in agonist muscle strength. Antagonist MU firing rates can be recorded with decomposition techniques and is influenced by the type of contraction and level of excitation to the motoneuron pool (Reece and Herda 2021; Reece et al. 2021). Lower MU activity of the antagonist would, in theory, raise whole limb torque if the activation of the agonist MU pool remains the same. The activity of antagonist MUs and the subsequent effects on torque output of the limb has yet to be researched in RET studies.

Types of contractions used to record MUs

Proposed by several authors, the isometric contractions used to record MUs might not be revealing neural adaptations occurring during RET that primarily includes isotonic contractions. Recent advancements in surface EMG decomposition methods (De Luca et al. 2015; Oliveira and Negro 2021) that allows for recording of MUs during isotonic contractions will improve our understanding of neural adaptations during RET. Furthermore, recording MUs during isotonic muscle actions used during the RET might better isolate potential changes in firing rates and potentially other neural adaptations.

Population tested

A major limitation is the rather small total sample size in RET research that includes recording of MUs. These studies only included a total of 148 and 20 young adult males and females, respectively and 46 and 31 older adult males and females, respectively. For the most part, physical activity levels were not assessed, but the subjects were classified as untrained or recreationally active. Levels of physical activity associates with skeletal muscle mass (Westerterp 2018) and physical performance (Barnekow-Bergkvist et al. 1998) and may be a confounding variably when monitoring changes in MU properties pre- to post-RET. While there is only one study who examined children (nine adolescent males). Of note, no research has examined the effects of RET on prepubescent children who possess lower MU firing rates of the VL in comparison to adults (Herda et al. 2018; Parra et al. 2020a). This population may be of interest as they may possess a greater capacity to increase MU firing rates pre- to post-RET. Overall, theories developed from this work perpetuated in the literature comes from a small sample.

Future directions

There is lack of clarity on potential RET-related neural adaptations that involve MU firing rates and recruitment patterns. A limitation of most research is that the potential for non-uniform changes could be occurring for firing rates and variability in the properties of MUs and between individuals is not considered in analytical approaches. The only consistent finding is that MU action potential amplitudes undergo non-uniform increases that may coincide with increases in the diameters of those skeletal muscle fibers following high intensity RET. Future research should confirm the link between MU action potential amplitudes and skeletal muscle fiber diameters pre- and post-RET.

There is much work needed to confirm potential changes in MU firing rates. Future research should consider the following to better understand potential changes in MU firing rates: (1) accounting for variability among MU properties with the use of recruitment thresholds and between subjects should be the preferred analytical approach; (2) contractions performed at discrete levels from lower to higher intensities might allow for a better understanding if non-uniform changes in MU firing rates is occurring similar to action potential amplitudes; (3) the inclusion of testing on multiple muscles with different functional roles; (4) measure MU firing rates of the antagonist muscle; and (5) recording MUs during isotonic contractions might better isolate the effects of RET on firing rates.

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Author contributions TJH developed the manuscript and created tables and figures.

Declarations

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