### Sex Differences in Motor Unit Discharge Rates at Maximal and Submaximal Levels of Force Output

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| Novelty bullets: points that summarize the key findings in the work: | • Females had higher MUDRs, and greater percentage of motor unit trains with doublets across submax force outputs (20-80%MVC). • Differences were even greater for a strength matched sub-set. • Differences in motor unit behaviour may arise from musculoskeletal differences requiring greater neural drive in females. |
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Sex Differences in Motor Unit Discharge Rates at Maximal and Submaximal Levels of Force Output

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Abstract

This study evaluated potential sex differences in motor unit (MU) behaviour at maximal and submaximal force outputs. Forty-eight, 24 females and 24 males, performed isometric dorsiflexion contractions at 20, 40, 60, 80, and 100% of a maximum voluntary contraction (MVC). Tibialis anterior electromyography was recorded both by surface and intramuscular electrodes. Compared to males, females had a greater MU discharge rate (MUDR) averaged across all submaximal intensities (Δ 0.45 pps, 2.56%). Males exhibited greater increases in MUDR above 40% MVC, surpassing females at 100% MVC (p’s<0.01). Averaged across all force outputs, females had a greater incidence of doublet and rapid discharges and a greater percentage of MU trains with doublet and rapid (5-10ms) discharges (Δ 75.55% and 61.48% respectively, p’s<0.01). A sub-set of males (n=8) and females (n=8), matched for maximum force output, revealed that females had even greater MUDR (Δ 1.38 pps, 7.47%) and percentage of MU trains with doublet and rapid discharges (Δ 51.62%, 56.68% respectively, p’s<0.01) compared to males at each force output, including 100% MVC. Analysis of the sub-set of strength matched males and females suggest that sex differences in MU behaviour may be a result of females needing to generate greater neural drive to achieve fused tetanus.

Novelty bullets:

• Females had higher MUDRs, and greater percentage of motor unit trains with doublets across submax force outputs (20-80%MVC).
• Differences were even greater for a strength matched sub-set.
• Differences in motor unit behaviour may arise from musculoskeletal differences requiring greater neural drive in females.

Key words: Motor unit discharge rate; doublet discharges; rapid discharges; tibialis anterior; isometric contraction, strength matched, sex differences
Introduction

Alterations in the amount of force produced by skeletal muscle can be modulated by alterations in rate coding, motor unit recruitment and other motor unit behaviours (i.e. doublet discharges, synchronization) (Adrian and Bronk 1929; Enoka and Fuglevand 2001; Farina et al. 2010). Earlier work on sex differences in maximal strength suggested that males had greater muscle activation, which was inferred from the surface electromyographic (sEMG) signal, without reference to a specific type of motor unit behavior (Häkkinen and Pakarinen 1994; Cioni et al. 1994; Pincivero et al. 2001). However, Hannah and associates (2012) reported following normalization for maximal voluntary contraction (MVC) that in the knee extensors during both voluntary and evoked explosive force production that males were similar to females in their ability to utilize the available force-generating capacity. The amount of force a motor unit (MU) produces is heavily influenced by the rate at which they discharge, termed the force-frequency relationship (Rack and Westbury 1969). Increases in discharge rate result in increases in force output, particularly at the initial portion of the force-frequency curve (Bigland-Ritchie et al. 1983). The literature focusing on sex differences in motor unit discharge rate (MUDR) is even more sparse than the literature involving sex differences in sEMG (Christie and Kamen 2010; Harwood et al. 2014; Peng et al. 2018).

Recent work by Krishnan and Williams (2009a) showed that females had higher sEMG magnitudes in the vastus medialis during submaximal (<30% MVC) isometric knee extension. These findings are consistent with the earlier observations of Cioni and associates (1994) (15 healthy males ~35.4 yrs and 15 healthy females ~28.3 yrs) who investigated the tibialis anterior at various torque outputs from 10 to 100% MVC and Visser and de Rijke (1974) (15 ‘normal’ males ~31.5 yrs and 10 ‘normal’ females ~26.8 yrs) who studied the adductor pollicis with
tensions at 2,000 g, 4,000 g, and half of MVC. Both groups suggested that sex differences in the sEMG-force relationship maybe due to the recruitment of a larger number of motor units at each contraction intensity in females, prior to substantial increases in MUDR. While females may recruit more motor units at a given contraction intensity, there is no evidence to suggest that muscles in the extremities of females have more motor units (Yerdelen et al. 2006).

Doublet discharges (inter-pulse intervals between 2 and 5 ms) occur at the onset of isometric contractions, fatiguing contractions and during the plateau portion of sustained contractions (Calvin and Schwindt 1972; Kudina 1974; Bawa and Calancie 1983; Griffin et al. 1998; Christie and Kamen 2006). The incidence of doublet discharges are believed to take advantage of the muscles ‘catch-like’ properties to enhance force production (Binder-Macleod and Barrish 1992). Similar to MUDRs, doublet discharges can also increase sEMG amplitude (Griffin et al. 1998; Van Cutsem et al. 1998) and may be another possible mechanism underlying sex differences inferred from the sEMG signal. While doublets may not be a primary means for enhancing static force, their presence may reflect greater levels of excitation. This excitation may be a result of increased neural drive to the muscle resulting in greater discharge rates and incidents of rapid and doublet discharges (Van Cutsem et al. 1998).

The majority of studies on sex difference in force gradation have inferred MU activity based on sEMG (Visser and de Rijke 1974; Bilodeau et al. 1992, 2003; Cioni et al. 1994; Merletti et al. 1999; Shultz and Perrin 1999; Pincivero et al. 2000, 2003; Farina et al. 2004; Clark et al. 2005; Christie et al. 2009; Bolgla et al. 2014; Nishikawa et al. 2017), and it is becoming increasingly apparent that such interpretations are problematic (Farina et al. 2004). Nevertheless, Lawrence and DeLuca (1983) hypothesized that differences in MU activity patterns could be detected through the sEMG-force relationship.
Lenhardt and colleagues (2009) investigated the sEMG-force relationship using both the amplitude and frequency domains (root-mean square (RMS) amplitude and mean power frequency (MNF)) at various force outputs in the TA. Since the pattern of change in both RMS amplitude and MNF activity were the same for males and females, it was concluded that there were no sex differences in the gradation of muscle force. Unfortunately, it has now been established that MNF and RMS of the sEMG signal can no-longer be used to make inferences about MU behavior (Farina et al. 2004). This is partially due to both waveform cancellation and source-distance effects (skinfold thickness) masking changes in MU recruitment and discharge rate in the sEMG signal (Yao et al. 2000; Day and Hulliger 2001; Dimitrova and Dimitrov 2003; Keenan et al. 2005). This may lead to an underestimation of changes in peripheral neural drive (Day and Hulliger 2001; Dimitrova and Dimitrov 2003; Farina et al. 2004; Keenan et al. 2005). As a result, a lack of sex differences in the study by Lenhardt and colleagues (2009) may be due to conclusions based solely on sEMG measures. The use of intramuscular recording electrodes eliminates the limitations of sEMG by directly measuring MU activity patterns, such as recruitment and discharge rate (De Luca et al. 1982; McGill et al. 2005).

Recent intramuscular EMG research by Peng and colleagues (2018) and Harwood and associates (2014) reported that females had either greater or lower MUDRs than males, respectively. Further to this, Christie and Kamen (2010) reported males had greater MUDR compared to females at maximum force output. However, they only examined MUDRs at maximum force output. Therefore, it is not known if the differences in MUDRs exist throughout a large range of force output, or if there is a different MU behavior (doublet and rapid discharges) involving rate coding as might be suggested by either Peng and colleagues (2018) or Harwood and associates (2014). Therefore, we hypothesized that based on the work by both
Christie and Kamen (2010) who found that males MUDR were greater at MVC in the TA and Harwood and associates (2014) who reported females having lower submaximal MUDR in the biceps brachii, that the females in our group would also have lower MUDR through the force gradation process in the TA.

We chose to test this hypothesis on the TA for the following reasons. Specific strength and tension in the TA of males and females are similar (Kent-Braun and Ng 1999; Kent-Braun et al. 2000). There are also sex-related similarities in TA fibre type distribution (Holmbäck et al. 2003; Souron et al. 2016) and proportion (Henriksson-Larsén et al. 1983; Helliwell et al. 1987; Jakobsson et al. 1990). Further, there is no evidence of any sex differences in the recruitment range for the TA, which has been reported up to 90% MVC (Desmedt and Godaux 1977; Van Cutsem et al. 1997). Given the similarities in maximal isometric dorsiflexion strength and TA contractile characteristics, this specific action at the ankle is an ideal model to examine potential sex differences in the neural control of maximal efforts. The purpose of this study was, therefore, to evaluate potential differences in MUDR and in the incidence of doublet discharges between males and females at 20, 40, 60, 80 and 100% of MVC, in balanced order of presentation.

**Methods**

**Participants**

Forty-eight (24 males and 24 females) college aged (18-25 yrs) students were recruited to participate in the study. All participants were right leg dominant (preferred kicking leg) and free of any neuromuscular or orthopedic disorders. Written informed consent in accordance with the Brock University Research Ethics Board guidelines (REB-12-027) was provided prior to participation in the study. Prior to testing, participants reported their history of physical activity
and weight training as well as the duration (hours per week and per day) and the percentage of weight training focusing on upper body or lower body.

**Experimental Setup**

All testing was completed within a grounded Faraday cage. Participants were seated in a testing chair used to isolate the ankle joint during dorsiflexion contractions. The hip and knee joints were secured at 90° with the ankle joint fixed at 20° of plantarflexion (Inglis et al. 2011). A padded bar was secured to a foot plate across the distal metatarsal to allow the recording of isometric dorsiflexion contractions. Force output was recorded from a load cell (JR3 Inc., Woodland, CA) secured to the foot plate below the distal metatarsals (Christie and Kamen 2009).

Auditory feedback was provided (Advent, 1002, Lake Mary, FL) to ensure indwelling EMG signal quality, as well as visual feedback from an oscilloscope (Tetronix, TDS 460A, Beaverton, OR) (Spitzer et al. 1992; Okajima et al. 2000; Daube and Rubin 2009). Visual and auditory feedback were utilized to locate areas of maximal motor unit activity inside the muscle. Adjustments of the intramuscular electrode were made to maximize the indwelling EMG signal quality (Stashuk 2001). A second oscilloscope (Hitachi, VC-6525, Woodbury, NY) provided real-time force feedback to the participants with error bars set at ± 2.5% of the desired level of contraction.

**Subject Information and Anthropometric Measurements**

Participants provided demographic information including age, weight, height, training, and physical activity background. All subjects lower leg anthropometric measurements were collected with a tape measure as follows: lower leg length (fibular head to lateral malleolus),
lower leg circumference (mid-calf), whole foot length (calcaneus to distal first digit), lateral malleolus to bottom of foot length, lateral malleolus to metatarsals length, and calcaneus to metatarsals length.

**Surface Electromyography**

The most proximal electrically identified TA motor point was located by using a low intensity electrical stimulus applied to the TA through an anode adhered to the midpoint of the posterior aspect of the lower leg, and a hand-held probe cathode on the belly of the TA (Grass Telefactor S88; Astro-Med, Warwick, RI, USA). The motor point was identified as the area where the lowest voltage of stimulation was able to produce a muscle twitch (Inglis et al. 2011). A large portion of the TA and patellar tendon was then shaved, mildly abraded (NuPrep®; Weaver and Company, Aurora, CO, USA), and cleansed with alcohol. Electrolyte gel (Signal Gel®; Parker Laboratories, Fairfield, NJ, USA) was applied to Ag/AgCl electrodes (Grass F-E9, Astro-Med Inc., West Warwick, RI), and placed in a monopolar configuration on the TA with the recording electrode placed over the motor point and a reference electrode placed over the distal tibial tendon. The monopolar electrode configuration with the recording electrode placed on the TA motor point was chosen as this configuration is sensitive to changes in muscle activity with increases in isometric force output (Gabriel 2011). A ground electrode (CF5000; Axelgaard Manufacturing CO., LTD, Fallbrook, CA) was placed on the lateral malleolus. Skin impedance was measured both prior to and following each session with an impedance meter (Grass EZM5; Astro-Med Inc., West Warwick, RI) to ensure the impedance remained below 10 kΩ.
**Intramuscular Electromyography**

An approximately five cm area of skin distal to the surface recording electrode was shaved and sterilized with ChloraPrep® One-Step (Chlorhexidine Gluconate 2% w/v and isopropyl 70% v/v solution). An intramuscular 1.5-inch, 25-gauge quadrifilar needle recording electrode (Viasys Healthcare UK; Surrey, England) was inserted approximately one cm distal to the surface recording electrode. The ground electrode for intramuscular recordings was placed on the patella. The intramuscular needle electrode was inserted while participants performed and held a 20% MVC. Auditory feedback during the low-level contraction was used to determine when the electrode passed through the fascia and into the active muscle. The needle cannula contained four 50 μm diameter platinum-iridium wires that were exposed through a side port, which allowed for the detection of individual MUs. The electrode remained in the muscle for the duration of the testing protocol. The connecting wires (needle to amplifier) were adhered to the testing jig to limit movement but allow for minor adjustments as needed to ensure signal recording quality.

**Signal Collection Equipment**

The gains of the surface and an intramuscular EMG activity were adjusted using a Grass P511 amplifier (Astro-Med Inc., West Warwick, RI), to maximize the resolution on a 16-bit analogue-to-digital converter (NI PCI-6052E; National Instruments, Austin, TX, USA), for offline analysis (Dell; Round Rock, TX, USA). Surface EMG was band-pass filtered between 3 and 1000 Hz, while the intramuscular EMG was band-pass filtered between 1 and 10 kHz (Brownell and Bromberg 2009; Brown et al. 2010). All signals were sampled at 25,600 Hz using
a computer-based data acquisition system (DASYLab; DASYTEC National Instruments, Amherst, NH, USA).

**Experimental Protocol**

Participants visited the Electromyography and Kinesiology Laboratory for two sessions separated by a minimum of 24 hours. The first session was a familiarization session and the second involved the testing protocol.

**Familiarization Day**

On the first visit participants, read the information letter outlining study requirements, and provided written informed consent. This was followed by completing a physical activity readiness questionnaire (PAR-Q) and activity journal. Anthropometric measurements (Table 1) were taken, and task familiarization was performed. During task familiarization, the participants were seated in the testing chair and performed five-second contractions at 20, 40, 60, 80, and 100% MVC. The contractions were used to ensure the participants were able to both achieve and hold both maximal and submaximal contractions at the targeted level of force output. Great care was taken to ensure that they were not using their toe extensor muscles. Participants held the contraction at the desired force level until instructed to completely relax.

**Test Day**

Once the surface and intramuscular electrodes were placed and the participant was in the test position, they were instructed to perform three eight-second MVCs, each separated by three minutes of rest. To establish the maximum value, each participant was instructed to contract “as hard and as fast as possible” with an emphasis on the “hard” (Sahaly et al. 2001). Following the
initial maximal attempt, a target line was placed at 110% of the previously achieved peak value maximal contraction. This was completed three times. If the participant was able to reach the target line an additional contraction was added to ensure maximum was achieved (Lenhardt et al. 2009). The maximum which could be held was used as the MVC value (Inglis et al. 2011).

Each participant performed three maximal isometric voluntary dorsiflexion contractions prior to and following the submaximal bouts. The pre and post MVCs were used to test for the presence of fatigue. Following the first set of MVCs, each participant performed three consecutive submaximal contractions at 20, 40, 60, and 80% MVC. Each of the ‘Test Day’ contractions were also eight-seconds in duration with three minutes of rest in-between and performed “as hard and as fast as possible up to the target without overshooting it”. If the submaximal bout had a greater than five percent ‘overshoot’ of the target line the bout was stopped and re-preformed. Desired force outputs were displayed on the oscilloscope for real-time feedback, with two horizontal error bars positioned at ± 2.5% of the target level of force.

**Data Reduction and Analysis**

All criterion measures were extracted from a two-second epoch taken from the most stable portion of the force output which needed to be within ± 2.5% of the desired level of contraction, which was the target presented to the participants. Force output at each percent of MVC was the mean value of the force output in the same data window. The relative values are reported in Tables 2 and 3. Peak rate of force development (RFD) was calculated as seen previously in Andersen and Aagaard (2006) and Inglis and colleagues (2013, 2017). Briefly, this involves calculating the slope ($\Delta f/\Delta t$) over, successive 20 ms, non-overlapping intervals starting from the onset of the torque-time curve. Force onset was determined when the force output increase from
baseline surpassed 1%. The peak RFD was then the maximum slope (Folland et al. 2014). Time to peak RFD was the time from force onset to peak RFD. Representative force, surface and indwelling EMG signals recorded during 100% MVC are depicted in Figure 1, as well as shimmer plots, which depict the MUAPTs associated with each discharge for that particular train.

The intramuscular interference patterns were decomposed and then the decompositions were checked a second time in EMGlab by a single operator (GI) who had intraclass correlation coefficients of 0.95 and 0.98 for agreement with two other expert users (JP, LG) (Inglis et al. 2012). Decomposition followed the protocol outlined by McGill and associates (2005). EMGlab (McGill et al. 2005) was used to decompose intramuscular EMG interference patterns from multiple channels into their component MUAPT. The program includes algorithms for template matching and superposition resolution. Following the automated portion of MU identification, the operator (GI) inspected each train to identify any missed, misidentified or resolve any superpositions that may have occurred during the trial. Amplitude, duration and discharge statistics of the MUAP was used to determine if it was part of a particular train.

The reciprocal of the inter-pulse interval (IPI) for the MUAPT was used to calculate the instantaneous MUDR (Lefever and De Luca 1982; Kamen and De Luca 1989), based on a point-by-point moving window of five consecutive action potentials (four inter-pulse intervals) for the duration of the train (Graham et al. 2016). Inter-pulse intervals less than 10 ms or greater than 200 ms were not used in the calculation of MUDR (Christie et al. 2009; Christie and Kamen 2010). Motor unit discharge rate for the contraction was calculated by averaging the instantaneous MUDRs across all MUs that discharged continuously within the two-second epoch and had a coefficient of variation of less than or equal to 30% to reduce inter-individual
variability (Stashuk 2001). Additionally, MUDRs were calculated from five trains with the highest discharge rate with a coefficient of variation of less than or equal to 30% at each force output (MUDR Top Five) for each subject. This was done to confirm that the MUDR results were not driven by comparing a different number of MUs between subjects and sexes (see Tables 2 and 3).

Measurement of doublet discharges within the two-second epoch and during force development was based on an inter-pulse interval between 2 and 5 ms while discharges between 5 and 10 ms were considered rapid discharges (Kamen et al. 1995; Van Cutsem et al. 1998; Christie and Kamen 2006). The larger interval of 5 to 10 ms was studied in case there were sex differences for the inter-pulse intervals over which doublet discharges have previously been shown to occur (Van Cutsem et al. 1998). The number of MUs detected and studied at each level of force output were also calculated. The number detected represents all of the identified and decomposed MUAPTs, whereas the number studied were MUAPTs that met the inclusion criteria for analysis (which was a coefficient of variation of less than or equal to 30 percent).

Calculation of the intramuscular EMG measures and the signal-to-noise ratio (SNR) of the recordings were completed in MATLAB (Mathworks, Natick, MA) 
\[
\text{SNR (dB)} = 10 \log \left( \frac{\text{Signal Power}}{\text{Noise Power}} \right)
\]

Statistics

Demographic differences were evaluated using unpaired t-tests, while pre and post-testing of impedance and temperature measures were analyzed using a paired t-test to observe any changes over the course of the protocol. Similarly, mean maximum force, RMS, and MNF of the
sEMG signal for the pre versus post set of 100% MVCs, were analyzed using a paired \( t \)-test to detect the presence of fatigue (Bigland-Ritchie 1981; Moritani et al. 1986; Merletti et al. 1990).

Preliminary analysis showed that there was no significant difference between trials, so they were averaged for each submaximal and maximal force output. Males and females (Sex), across levels of MVC, and their interaction (Sex × MVC) were evaluated using a two-factor, mixed model repeated-measures analysis of variance. Different levels of force output were used to identify potential sex differences in the following key variables: (1) motor unit discharge rate; (2) number of motor units detected and studied; (3) the percent of motor unit trains with doublet and rapid discharges; and (4) the incidence of doublet and rapid discharges (counts). The SNR was evaluated using the same ANOVA model to ensure that the signal quality was similar between the sexes.

Post-hoc analyses were accomplished with orthogonal polynomials trend analysis of means while orthogonal contrasts were used for specific comparisons between means when necessary. Finally, a sub-set of the subjects were matched for strength (8 males, 8 females) within 5% of their maximal force exerted. Participants with similar maximal force outputs were then paired based on their reported physical activity levels (Hunter et al. 2004). The sub-set of data were analyzed to determine if potential sex differences in MU behaviour were due to strength differences. All statistical procedures were performed in SAS® (SAS Institute Inc.; Cary, NC, USA) with alpha set at the 0.05 probability level.

**Results**

**Methodological Controls**
The skin impedance averaged across the first and last three MVC trials decreased by 0.83 kΩ (Δ11%). No practical significance can be placed on small changes in impedance below 10 kΩ, which is well within the accepted range for sEMG (Hewson et al. 2003). The average skin temperature increased 0.31 degrees Celsius (Δ1%). While it was statistically significant (t = 1.98; p = 0.04), far greater changes (±15°C) are required to alter the sEMG signal (Winkel and Jørgensen 1991; Rutkove 2001).

The data were also analyzed for the presence of fatigue from beginning to end of the testing protocol. Force output was averaged for the three pre-submaximal MVC trials and the three post-submaximal MVC trials. There was a 6.4 N (Δ3.8%, Pre: 167.9 ± 58.7, Post: 161.5 ± 54.8, t = 2.22; p = 0.03) decrease in MVC force while RMS (Δ5%, t = 1.39; p = 0.17) and MNF (Δ2%, t = -1.33; p = 0.19) for surface EMG remained unchanged. The small magnitude of the observed changes are considered trivial, which is consistent with previous findings wherein a similar number of isometric contractions at different percentages of MVC are present within the same test session in balanced order, with similar rest periods (Gabriel et al. 2007). Overall, EMG data did not exhibit the classic signs of muscle fatigue: a decrease in MNF and an increase in RMS amplitude (Moritani et al. 1986; Merletti et al. 1990).

**Participants and Rate of Force Development**

The means, standard deviations, and t-ratios for the physical and demographic characteristics of the participants are presented in Table 1. As might be expected, there were significant anthropometric differences. There were significant differences between the sexes for height and weight (p’s < 0.01), but not BMI (p = 0.09). Lower leg length and lower leg girth were similar between the sexes (p < 0.01 and p = 0.18, respectively). Males and females were
significantly different from each other for two out of the three anthropometric measures of foot dimensions. There was no significant difference between males and females with respect to the total amount of physical activity per week \((p = 0.32)\). Males engaged in more weightlifting hours per week \((p < 0.01)\), but both sexes were similar in the percentage of total weightlift time focused on the lower limb \((p = 0.28)\).

Sex differences in the peak rate of force development (RFD) were observed from 20 to 100\% MVC. On average males were \(197.22 \pm 118.11\) N/sec greater than females \((\Delta = 33.6\% \text{ difference}, p = 0.003)\). Yet, there was not a significant sex by force output interaction term \((p = 0.83)\). Interestingly, there were no sex differences in time to peak RFD \((p = 0.87)\). However, there was an increase in the time to peak RFD as the percent of MVC increased \((11.66 \text{ ms}, \Delta = 89.1\%, p < 0.01)\). When MVC was used as a covariate, the peak RFD sex differences disappeared \((p = 0.92)\).

**Sex Differences in Motor Unit Variables**

The means, standard deviations and \(F\)-ratios for the criterion measures are presented in Table 2. It was important to determine that both sexes were comparable with respect to the percent MVC targeted force across submaximal conditions, so that differences in relative force did not confound the results. The means and standard deviations for percent force across the 20 to 80\% MVC conditions show that both sexes were similar \((p = 0.35)\). Both sexes had similar “grand mean” MUDRs. However, males and females exhibited different patterns of change across force levels \((p < 0.01)\). Orthogonal contrast testing confirmed that females had greater MUDRs than males below 80\% MVC \((\Delta 3.75\%; p = 0.03)\). Motor unit discharge rate for females plateaued between 80 and 100\% MVC \((p = 0.36)\), while males exhibited a dramatic increase.
between these force levels ($p < 0.01$). As a result, males had a significantly higher MUDR than females at 100% MVC ($\Delta 6.8\%; p = 0.0004$).

Overall, the percentage of MUAPTs exhibiting doublet discharges was 75.55% greater for females than males ($p = 0.03$). Orthogonal contrast testing for means below 100% MVC revealed that females had a greater percentage of trains with doublet and rapid discharges compared to males ($p's < 0.01$). Similar to MUDR, between 80 and 100% MVC, males exhibited an increase in the incidence of doublet and rapid discharges, but were still lower than the females (respectively, $p = 0.0003$ and $p = 0.01$). A sub-set of strength matched participants (female = 8; male = 8) had no significant difference in maximal force output ($\Delta 1.29\%; p = 0.90$). The strength matched participants showed that females were still greater than males with respect to MUDR whether it was calculated from all the analyzed MUs ($\Delta 7.45\%, p = 0.18$, see Figure 2) or those with the five highest discharge rates ($\Delta 9.25\%, p = 0.19$). The same was true for the percentage of doublet and rapid discharges at all levels of force output ($p's < 0.01$) (Table 3). However, when expressed as raw incidence, males and females alternated which of the two groups had a greater mean value at a particular submaximal force condition.

The numbers of MUs detected and analyzed increased across force levels for both groups ($p's < 0.01$). On average the number of MUs analyzed for females was 8.38% greater than that for males at each force level below 80% MVC ($p < 0.05$), after which, males exhibited a significantly greater number ($\Delta 5.96\%$) up to 100% MVC ($p < 0.01$). The SNR increased 23.31% across force levels as the signal increased relative to baseline ($p < 0.01$). However, there were no significant sex differences in intramuscular EMG SNR ($p = 0.38$). Moreover, when only five MUs with the highest MUDRs were analyzed for each participant, similar statistical results were observed as when all MUs were analyzed for both the entire sample and strength matched sub-
set (see Table 2 and 3). Sex differences in MUDR, doublet and rapid discharges were present for the strength matched sub-set, despite being similar in percent force across submaximal conditions ($p = 0.98$). There were no sex differences for the inter-pulse intervals over which doublet discharges are thought to occur. Both doublet (2-5ms) and rapid discharges (5-10ms) were greater for females than males.

Discussion

The purpose of this study was to explore sex-related differences in MUDR and doublet discharges at both maximal and submaximal levels of force output. There were several unique findings. Females had higher submaximal MUDRs as compared with males, but not during maximal contractions. Females also had a greater incidence of doublet and rapid discharges across all levels of force output, including 100% MVC. The sex-related difference persisted when expressed as a percentage of the MUAPTs exhibiting the behavior of either doublet or rapid discharges.

The sub-set analysis of strength matched participants (N=16) supported the overall findings. Not only were the MU variables in females still greater than males across all submaximal force levels, but when matched for strength, sex differences were even greater and included the 100% MVC condition. Thus, sex differences observed in the larger sample of participants (N=48) in regard to MU variables were not due to differences in maximum strength, number of MUs analyzed, or in the percent level of submaximal MVC performed by the two groups.
**Force Output**

The percent difference in maximum strength of the lower limb between males and females observed in the present work (Table 2, males 36% greater) is comparable to other studies in the literature. Lenhardt and colleagues (2009) reported maximum dorsiflexion force was 29% greater in males than females. The 36% and 29% greater strength in males are slightly lower than Brown and colleagues (2009) who reported males’ maximal dorsiflexion force being on average 39% greater compared to females’. It has been suggested that females may exhibit a higher degree of coactivation (Solomonow et al. 1988; Krishnan and Williams 2009b, 2010), which would lower overall force output at the joint. By placing the ankle joint in 20° of plantar-flexion during testing, the triceps surae complex was in passive insufficiency for both sexes, subsequently minimizing the role of coactivation plays in force production (Marsh et al. 1981; McNeil et al. 2005; Manal et al. 2006). Additionally, males and females were similar with respect to both RFD (when MVC was used as a covariate) and time to peak RFD. Ultimately, the demographic data suggest that strength differences observed in the present study may be explained by differences in the males greater muscle size (males: body mass 20.4% greater; leg length 8.0% greater; leg girth 2.6% greater) but not the level of physical activity or amount of resistance training in the lower limb, which is consistent with the findings of Hannah and colleagues (2012).

**Motor Unit Variables and Muscle Force**

In agreement with Peng and colleagues (2018), the present work showed that females had greater MUDRs than males at submaximal contraction intensities. The present work extends those findings for isometric contraction intensities across a larger spectrum of force levels. Although not investigated in the present work, we suggest that the greater MUDRs and rapid
discharges observed in females may be a way in which the nervous system compensates for biomechanical sex differences with respect to muscle length and pennation angle. Biomechanical compensation has been seen previously by both Manal and colleagues (2006) and Mela and associates (2001) it is possible that the female’s TA pennation angle and muscle length were less optimal in the test position. Manal and colleagues (2006) reported sex differences in the TA pennation angle. Although small (Δ15%), this difference is significant in regard to the production of tension. While a larger than optimal pennation angle can result in a lesser transmission of tension to the tension-generating axis. Muscle fibers rotate during force development allowing tensile force to be transmitted more efficiently down the tendon, even though the pennation angle may not be optimal for force output (Fukunaga et al. 1997). Therefore, a larger pennation angle that allows for a greater physiological cross-sectional area in the active muscle will arrange more contractile fibers in parallel, contributing to greater force production (Maganaris and Baltzopoulos 1999; Manal et al. 2008).

Changes in muscle length can result in either increases or decreases in MUDR (Gandevia and McKenzie 1988; Bigland-Ritchie et al. 1992; Mela et al. 2001). Mela and associates (2001) suggest that based on the observation of a leftward shift of the normalized moment/frequency curve when moving from a shortened (9° dorsiflexion) to lengthened (16° and 44° plantar-flexion) muscle length. This movement towards an optimal muscle length requires a lower stimulation frequency to achieve the same moment output. Perhaps the differences in submaximal MU behaviour may have arisen as a compensation mechanism to overcome a less optimal ankle joint angle due to sex differences from both musculoskeletal and biomechanical factors, that may not be seen at maximum.
In the current study, females had a significantly greater percentage of MUAPTs with doublet and rapid discharges (61.33% and 48.09%, respectively) during the rate of force development, similar to the remaining portion of the contraction. Sex differences in MU behaviour may reflect a compensation mechanism of the nervous system due to greater joint laxity or tendon compliance in females (Granata et al. 2002b, 2002a; Onambélé et al. 2006, 2007; Gabriel et al. 2008; Komi and Karlsson 2008; Inglis et al. 2017; Jakobi et al. 2018; Smart et al. 2018). The incidence of doublet and rapid discharges would facilitate the uptake of slack in the musculoskeletal-tendon unit and a more efficient transmission of force (Mayfield et al. 2016).

It could be argued that, if females have longer twitch contraction times, they would require lower MUDRs to achieve fused tetanus (Grimby et al. 1979). Belanger and associates (1983) and Davies and colleagues (1985) reported that females have significantly longer twitch contraction times. However, in our previous work (Inglis et al. 2017) when testing the same muscle group in a similar population to the current study, there were no sex differences in contraction time (Δ0.01%). Thus, we expect that contraction times between the sexes in the current study would be also similar and not a factor affecting MUDR. However, biomechanical sex differences were not measured in the current study and therefore pause must be taken when interpreting these findings. Future work should investigate the biomechanics of sex differences simultaneously with potential changes in motor unit behaviour and neural drive.

In summary, females had greater MUDR below 100% MVC. Males then surpassed females at 100% MVC. When matched for strength females had greater MUDRs up to and including 100% MVC. Additionally, the females had a greater percentage of MUAPTs with doublet and rapid discharges at all force outputs for the full sample (N=48) and strength matched sub-set
(N=16). We suggest sex differences at various submaximal and maximal voluntary contraction intensities arise from musculoskeletal differences that required greater neural drive in the females to achieve fused tetanus during submaximal contractions.

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**Conflict of interest statement**
There are no conflicts of interest
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Table 1. Subject demographics, anthropometrics and physical activity.

|                                | Females ($N=24$) | Males ($N=24$) | Percent Difference | $t$-ratios and $p$-values |
|--------------------------------|-----------------|----------------|-------------------|---------------------------|
| Age (years)                    | $21.54 \pm 1.69$ | $22.00 \pm 2.06$ | $2.1$             | $t = -0.84; p = 0.40$     |
| Height (m)                     | $1.68 \pm 0.05$  | $1.82 \pm 0.06$  | $7.7^*$           | $t = -9.99; p < 0.01$     |
| Mass (kg)                      | $64.86 \pm 6.97$ | $81.45 \pm 11.46$ | $20.4^*$          | $t = -6.16; p < 0.01$     |
| Body Mass Index (kg/m$^2$)     | $23.31 \pm 2.31$ | $24.59 \pm 2.85$ | $5.2$             | $t = -1.73; p = 0.09$     |
| Leg Length (cm)                | $36.33 \pm 2.24$ | $39.50 \pm 2.10$ | $8.0^*$           | $t = -5.06; p < 0.01$     |
| Leg Girth (cm)                 | $36.92 \pm 2.09$ | $37.92 \pm 2.98$ | $2.6$             | $t = -1.35; p = 0.18$     |
| Foot Length (cm)               | $23.73 \pm 0.93$ | $26.44 \pm 1.21$ | $10.2^*$          | $t = -8.69; p < 0.01$     |
| Lateral malleolus to bottom of the foot length (cm) | $7.27 \pm 0.74$ | $8.00 \pm 1.12$ | $9.1^*$           | $t = -9.50; p < 0.01$     |
| Lateral malleolus to metatarsals length (cm) | $12.02 \pm 1.71$ | $12.50 \pm 1.78$ | $3.8$             | $t = -0.95; p = 0.34$     |
| Calcaneus to metatarsals length | $15.25 \pm 1.51$ | $17.04 \pm 2.14$ | $10.5^*$          | $t = -3.35; p = 0.01$     |
| Physical activity (hours/week) | $4.52 \pm 1.36$  | $4.02 \pm 2.05$  | $11.1$            | $t = 1.00; p = 0.32$      |
| Weight-lifting (hours/week)    | $2.67 \pm 2.46$  | $5.24 \pm 3.13$  | $49.0^*$          | $t = -3.16; p < 0.01$     |
| Ratio of lower body weight-lifting (%) | $48.82 \pm 14.53$ | $43.50 \pm 14.61$ | $10.9$           | $t = 1.11; p = 0.28$      |

*Significant at the $p < 0.01$ probability level. All values are means ± standard deviation (M ± SD).

\[
\text{Percent Difference} = \left( 1 - \frac{\text{Smaller Value}}{\text{Larger Value}} \right) \times 100
\]
Table 2. Criterion measures for the complete population at all force outputs.

| N = 48 | Female = 24 | Male = 24 |
|-------|-------------|-----------|

| Percent MVC (M ± SD) | ANOVA F-ratio [df] |
|----------------------|---------------------|
|                      | Sex [1, 46] | Force [3, 184] | Sex × Force [3, 184] |
| 20                   |            |              |                      |
| 40                   |            |              |                      |
| 60                   |            |              |                      |
| 80                   |            |              |                      |
| 100                  |            |              |                      |
| Force (Newtons)      |            |              |                      |
| Females             | 28.74 ± 7.55 | 54.30 ± 14.16 | 78.29 ± 20.43 | 103.59 ± 27.17 | 123.75 ± 32.77 | 8.34 | 123.75 ± 45.62 |
| Males                | 43.32 ± 10.89 | 83.68 ± 18.82 | 125.35 ± 27.40 | 162.78 ± 38.97 | 199.32 ± 45.62 | 123.75 ± 32.77 |
| Force (percent)      |            |              |                      |
| Females             | 23.69 ± 4.39 | 44.41 ± 6.18 | 63.82 ± 9.00 | 84.66 ± 11.90 | 100 | 9.30 | 12.52 |
| Males                | 21.84 ± 10.89 | 42.37 ± 4.73 | 63.45 ± 6.15 | 82.05 ± 8.90 | 100 | 9.30 |
| MUDR (pulses/sec)   |            |              |                      |
| Females             | 14.78 ± 1.91 | 17.16 ± 2.44 | 18.71 ± 1.82 | 19.69 ± 1.50 | 20.20 ± 2.33 | 148.07* |
| Males                | 13.55 ± 1.80 | 16.41 ± 1.96 | 18.82 ± 2.18 | 19.76 ± 1.80 | 21.68 ± 3.06 | 148.07* |
| MUDR Top Five (pulses/sec) |        |              |                      |
| Females             | 17.30 ± 3.22 | 20.50 ± 4.70 | 22.62 ± 3.78 | 24.52 ± 3.90 | 26.11 ± 4.84 | 148.07* |
| Males                | 15.36 ± 2.99 | 18.98 ± 3.01 | 21.94 ± 3.61 | 23.66 ± 2.82 | 27.68 ± 4.47 | 148.07* |
| Doublets (percent)  |            |              |                      |
| Females             | 10.22 ± 11.51 | 14.72 ± 16.34 | 13.48 ± 15.45 | 15.75 ± 18.48 | 12.52 ± 12.12 | 103.59 ± 27.17 |
| Males                | 1.78 ± 4.01 | 3.30 ± 7.20 | 5.04 ± 9.23 | 3.19 ± 4.58 | 6.06 ± 7.94 | 103.59 ± 27.17 |
| Doublets (incidence) |            |              |                      |
| Females             | 4.36 ± 5.73 | 7.85 ± 10.24 | 7.62 ± 9.49 | 11.01 ± 17.18 | 6.80 ± 7.40 | 21.51* |
| Males                | 1.96 ± 7.80 | 2.71 ± 6.11 | 4.33 ± 12.52 | 2.58 ± 3.99 | 5.28 ± 7.77 | 21.51* |
| Rapid (percent)     |            |              |                      |
| Females             | 13.88 ± 15.88 | 18.40 ± 18.56 | 21.32 ± 22.27 | 25.34 ± 24.43 | 20.36 ± 17.15 | 103.59 ± 27.17 |
| Males                | 3.51 ± 7.15 | 5.61 ± 9.71 | 8.33 ± 14.54 | 7.54 ± 8.38 | 13.26 ± 13.84 | 103.59 ± 27.17 |
| Rapid (incidence)   |            |              |                      |
| Females             | 8.00 ± 13.23 | 15.15 ± 26.40 | 15.43 ± 20.24 | 21.90 ± 26.94 | 15.04 ± 16.48 | 103.59 ± 27.17 |
| Males                | 5.57 ± 21.31 | 5.43 ± 12.32 | 7.71 ± 19.79 | 5.10 ± 6.06 | 11.39 ± 15.72 | 103.59 ± 27.17 |
| Motor Unit Trains Detected (counts) |        |              |                      |
| Females             | 17.25 ± 6.54 | 20.53 ± 5.50 | 24.67 ± 4.44 | 24.63 ± 4.11 | 27.96 ± 6.18 | 78.29 ± 20.43 |
| Males                | 15.07 ± 3.69 | 20.07 ± 4.98 | 23.36 ± 4.63 | 28.22 ± 4.91 | 30.21 ± 4.45 | 78.29 ± 20.43 |
| Motor Unit Trains Detected (range) |        |              |                      |
| Females             | 5.33 - 32.33 | 11.00 - 30.33 | 17.00 - 34.67 | 15.67 - 31.00 | 16.33 - 47.00 | 6.34 - 20.43 |
| Males                | 7.67 - 23.33 | 12.33 - 31.00 | 16.67 - 35.67 | 18.33 - 36.00 | 21.33 - 40.67 | 6.34 - 20.43 |
| Motor Unit Trains Studied (counts) |        |              |                      |
| Females             | 13.88 ± 5.49 | 16.57 ± 4.58 | 19.91 ± 4.50 | 20.56 ± 4.34 | 22.82 ± 4.70 | 15.45 ± 4.98 |
| Males                | 11.36 ± 3.36 | 15.90 ± 4.56 | 18.86 ± 3.96 | 22.50 ± 4.84 | 23.62 ± 4.66 | 15.45 ± 4.98 |
| Motor Unit Trains Studied (range) |        |              |                      |
| Females             | 5.33 - 25.00 | 8.33 - 24.33 | 12.00 - 30.00 | 12.33 - 27.33 | 13.67 - 34.67 | 8.34 - 20.43 |
| Males                | 5.00 - 18.00 | 9.00 - 25.00 | 11.33 - 26.00 | 10.67 - 31.67 | 14.33 - 31.67 | 8.34 - 20.43 |
| SNR (Db)            |            |              |                      |
| Females             | 7.50 ± 1.26 | 7.88 ± 1.79 | 8.72 ± 2.02 | 9.30 ± 1.34 | 9.43 ± 1.55 | 15.45 ± 4.98 |
| Males                | 6.94 ± 1.85 | 7.91 ± 1.60 | 8.34 ± 1.74 | 8.69 ± 2.27 | 9.31 ± 2.30 | 15.45 ± 4.98 |

LEFT: All values are means ± standard deviation (M ± SD). Criterion measures. Right: ANOVA F-ratios and df (degrees of freedom) for Sex, Force and the Sex by Force interaction. † F-ratios df for Force (percent): Sex [1, 46], Force [3, 138], Sex × Force [3, 138]. *Significant at the p < 0.05 probability level.
**Table 3.** Strength matched criterion measures for the sub-population at all force outputs.

|                  | Percent MVC (M ± SD) | ANOVA F-ratio [df] |
|------------------|----------------------|---------------------|
|                  | 20                   | 40                  | 60                  | 80                  | 100                  | Sex [1, 14] | Force [4, 56] | Sex x Force [4, 56] |
|                  |                      |                     |                     |                     |                     |              |                |                    |
| Force (Newtons)  |                      |                     |                     |                     |                     |              |                |                    |
| Females          | 31.67 ± 8.72         | 61.60 ± 14.75       | 91.20 ± 17.50       | 122.64 ± 26.14      | 144.97 ± 27.19      | 0.03        | 281.47*       | 0.27               |
| Males            | 32.71 ± 7.65         | 64.42 ± 13.36       | 95.61 ± 17.52       | 119.53 ± 22.10      | 146.94 ± 31.76      |              |                |                    |
| Force (percent)  |                      |                     |                     |                     |                     |              |                |                    |
| Females          | 21.59 ± 3.67         | 42.40 ± 5.97        | 63.19 ± 7.11        | 84.85 ± 11.23       | 100                  | † 0.07      | 463.29*       | 0.74               |
| Males            | 22.52 ± 3.75         | 44.34 ± 5.85        | 65.92 ± 7.71        | 82.74 ± 13.21       | 100                  |              |                |                    |
| MUDR (pulses/sec)|                      |                     |                     |                     |                     |              |                |                    |
| Females          | 15.03 ± 0.78         | 17.32 ± 1.99        | 18.71 ± 1.50        | 20.09 ± 1.09        | 20.98 ± 1.62        | 1.99        | 93.98*        | 0.97               |
| Males            | 13.27 ± 2.41         | 15.74 ± 2.57        | 18.10 ± 3.05        | 18.32 ± 1.71        | 19.84 ± 3.28        |              |                |                    |
| MUDR Top Five    |                      |                     |                     |                     |                     |              |                |                    |
| Females          | 17.91 ± 1.77         | 20.88 ± 3.25        | 22.32 ± 3.31        | 25.61 ± 3.31        | 28.03 ± 3.74        | 1.81        | 51.65*        | 1.87               |
| Males            | 15.59 ± 4.30         | 19.34 ± 3.83        | 22.23 ± 4.93        | 21.70 ± 1.95        | 25.29 ± 4.84        |              |                |                    |
| Doublets (percent) |                   |                     |                     |                     |                     |              |                |                    |
| Females          | 12.03 ± 12.35        | 13.80 ± 17.20       | 13.35 ± 12.44       | 17.28 + 15.89       | 18.26 ± 15.21       | 1.84        | 2.01          | 1.22               |
| Males            | 4.04 ± 6.05          | 7.83 ± 11.46        | 9.68 ± 11.91        | 5.22 ± 6.00         | 9.20 ± 11.66        |              |                |                    |
| Doublets (incidence) |               |                     |                     |                     |                     |              |                |                    |
| Females          | 4.79 ± 4.97          | 8.50 ± 12.66        | 5.96 ± 5.60         | 9.62 ± 8.47         | 9.33 ± 8.21         | 0.35        | 1.73          | 0.56               |
| Males            | 5.46 ± 13.35         | 6.33 ± 9.12         | 10.58 ± 20.71       | 4.04 ± 5.48         | 8.08 ± 10.36        |              |                |                    |
| Rapid (percent)  |                      |                     |                     |                     |                     |              |                |                    |
| Females          | 17.48 ± 18.22        | 18.76 ± 18.81       | 25.90 ± 23.62       | 30.13 ± 20.54       | 29.32 ± 20.54       | 2.31        | 4.42*         | 1.83               |
| Males            | 7.79 ± 10.84         | 10.60 ± 15.63       | 14.40 ± 17.32       | 8.68 ± 9.42         | 15.49 ± 17.19       |              |                |                    |
| Rapid (incidence)|                      |                     |                     |                     |                     |              |                |                    |
| Females          | 10.17 ± 10.93        | 15.92 ± 20.44       | 13.62 ± 12.93       | 24.25 ± 22.68       | 20.54 ± 17.78       | 0.45        | 2.38          | 1.55               |
| Males            | 15.04 ± 36.38        | 12.58 ± 18.92       | 17.33 ± 31.70       | 6.21 ± 7.33         | 17.17 ± 22.73       |              |                |                    |
| Motor Unit Trains Detected (counts) |         |                     |                     |                     |                     |              |                |                    |
| Females          | 19.38 ± 5.22         | 21.67 ± 6.60        | 24.75 ± 4.57        | 25.88 ± 3.32        | 28.21 ± 3.85        | 0.38        | 26.15*        | 1.79               |
| Males            | 14.25 ± 2.47         | 20.54 ± 5.21        | 23.83 ± 4.62        | 26.21 ± 6.67        | 29.37 ± 4.80        |              |                |                    |
| Motor Unit Trains Detected (range) |          |                     |                     |                     |                     |              |                |                    |
| Females          | 14.33 - 29.00        | 13.67 - 30.00       | 18.33 - 32.67       | 20.33 - 30.33       | 23.33 - 34.67       |              |                |                    |
| Males            | 11.00 - 18.00        | 14.33 - 31.00       | 19.00 - 33.67       | 18.33 - 36.00       | 21.33 - 37.00       |              |                |                    |
| Motor Unit Trains Studied (counts) |           |                     |                     |                     |                     |              |                |                    |
| Females          | 15.96 ± 3.82         | 17.75 ± 5.21        | 20.04 ± 4.61        | 21.17 ± 4.00        | 23.29 ± 3.77        | 2.43        | 18.97*        | 1.54               |
| Males            | 9.50 ± 3.17          | 15.29 ± 4.76        | 18.38 ± 4.29        | 20.08 ± 6.73        | 21.04 ± 5.61        |              |                |                    |
| Motor Unit Trains Studied (range) |           |                     |                     |                     |                     |              |                |                    |
| Females          | 12.33 - 24.00        | 11.00 - 24.33       | 12.67 - 26.67       | 12.67 - 25.67       | 18.00 - 29.67       |              |                |                    |
| Males            | 5.00 - 15.67         | 9.67 - 25.00        | 11.67 - 26.00       | 10.67 - 31.67       | 14.33 - 30.00       |              |                |                    |
| SNR (Db)         |                      |                     |                     |                     |                     |              |                |                    |
| Females          | 7.26 ± 0.77          | 7.62 ± 1.38         | 8.77 ± 1.32         | 9.89 ± 1.08         | 9.45 ± 1.10         | 4.59        | 6.22*         | 2.83*              |
| Males            | 6.31 ± 1.78          | 7.30 ± 1.55         | 7.32 ± 2.09         | 6.94 ± 2.84         | 7.36 ± 2.52         |              |                |                    |

LEFT: All values are means ± standard deviation (M ± SD). Criterion measures. Right: ANOVA F-ratios and df (degrees of freedom) for Sex, Force and the Sex by Force interaction. † F-ratios df for Force (percent): Sex [1, 14], Force [3, 42], Sex x Force [3, 42]. *Significant at the p < 0.05 probability level.
**Figure 1:** Representative trial at 100% MVC. UPPER LEFT: Black line represents the force output, vertical lines represent each identified discharge from each motor unit (N=22). Blue lines are the motor units used in the analyses (n=13), grey lines were identified but did not make the inclusion criteria (n=9). The grey box represents the trials two second epoch. LOWER LEFT: top red trace is the surface interference pattern and the three red traces below are the intramuscular interference pattern recorded from each channel. Pooled motor unit discharge rates were calculated across the two second epoch based on the most stable portion of the force trace. RIGHT: Four sampled motor units (rows) identified across all three channels (columns). Greyed portion is the shimmer of each motor unit discharge throughout the entire trial. Black line is the average of all of the motor unit discharges.

**Figure 2:** Motor unit discharge rates across all force outputs. ABOVE: Total population. BELOW: Strength matched group.
Figure 1. Representative trial at 100% MVC. UPPER LEFT: Black line represents the force output, vertical lines represent each identified discharge from each motor unit (N=22). Blue lines are the motor units used in the analyses (n=13), grey lines were identified but did not make the inclusion criteria (n=9). The grey box represents the trials two second epoch. LOWER LEFT: top red trace is the surface interference pattern and the three red traces below are the intramuscular interference pattern recorded from each channel. Pooled motor unit discharge rates were calculated across the two second epoch based on the most stable portion of the force trace. RIGHT: Four sampled motor units (rows) identified across all three channels (columns). Greyed portion is the shimmer of each motor unit discharge throughout the entire trial. Black line is the average of all of the motor unit discharges.
Figure 2: Motor unit discharge rates across all force outputs. ABOVE: Total population. BELOW: Strength matched group.

Motor Unit Discharge Rates (N = 48)

Motor Unit Discharge Rates - Strength Matched (N = 16)