# Motor unit firing rates during slow and fast contractions in boys and men

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**Abstract:**

*Background:* Motor unit (MU) activation during maximal contractions is lower in children compared with adults. Among adults, discrete MU activation differs, depending on the rate of contraction. We investigated the effect of contraction rate on discrete MU activation in boys and men.

*Methods:* Following a habituation session, 14 boys and 20 men completed two experimental sessions for knee extension and wrist flexion, in random order. Maximal voluntary isometric torque (MVIC) was determined before completing trapezoidal isometric contractions (70%MVIC) at low (10%MVIC/s) and high (35%MVIC/s) contraction rates. Surface electromyography was captured from the vastus lateralis (VL) and flexor carpi radialis (FCR) and decomposed into individual MU action potential (MUAP) trains.

*Results:* In both groups and muscles the initial MU firing rate (MUFR) was greater ($p<0.05$) at high compared with low contraction rates. The increase in initial MUFR at the fast contraction in the VL was greater in men than boys ($p<0.05$). Mean MUFR was significantly lower during fast contractions only in the FCR ($p<0.05$). In both groups and muscles, the rate of decay of MUFR with increasing MUAP amplitude was less steep ($p<0.05$) during fast compared with slow contractions.

*Conclusion:* In both groups and muscles, initial MUFRs, as well as MUFRs of large MUs were higher during fast compared with slow contractions. However, in the VL, the increase in initial MUFR was greater in men compared with boys. This suggests that in large muscles, men may rely more on increasing MUFR to generate torque at faster rates compared with boys.

**Keywords:** Muscle activation, Children, EMG decomposition, Contraction Rate

**Statement and Declarations**

**Conflict of interest**: The authors declare no conflicts of interest, financial or otherwise

**List of Abbreviations**

ANOVA – Analysis of Variance

ANCOVA – Analysis of Covariance

$EMG_{RMS}$ – Root Mean Square of the Electromyography Signal

FCR – Flexor Carpi Radialis

FDI – First Dorsal Interossei

MU – Motor Unit

MUAP – Motor Unit Action Potential

MUAPamp – Motor Unit Action Potential Amplitude

MUFR – Motor Unit Firing Rates

MVIC – Maximal Voluntary Contraction

P–P – Peak to Peak

RT – Recruitment Threshold

sEMG – Electromyography

STA – Spike Trigger Average

VL – Vastus lateralis

## Introduction

Children's peak rate of torque development is lower compared with adults, even after accounting for differences in body size or maximal strength (Falk et al. 2009b, a; Dotan et al. 2013). These age-related differences in performance are suggested to be associated with children's lower motor unit activation during fast maximal voluntary isometric contractions (MVIC) (Falk et al. 2009a; Dotan et al. 2013). However, differences in discrete motor unit (MU) activation between children and adults have only been examined during submaximal contractions, performed at low contraction rates (Chalchat et al. 2019; Miller et al. 2019b; Parra et al. 2020; Mckiel et al. 2023).

In adults, overall muscle activation, as reflected by the surface electromyographic (sEMG) amplitude has been reported to decrease (Barnes 1980; MacIntosh et al. 2000), increase (Aeles et al. 2022), or not change (Farina et al. 2004; Miller et al. 2019a) with increasing contraction rate. Such inconsistencies have also been demonstrated in children, although to a more limited extent (Seger and Thorstensson 1994, 2000; Gillen et al. 2022). Conflicting results between studies may be related to the examination of different muscles (large vs. small; fast vs slow twitch; pennation angle), contraction intensities (low vs. high) and types (dynamic vs. isometric). For example, among adults, Aeles et al., (2022) reported an increase in the EMG amplitude (as measured by root mean square, $EMG_{RMS}$) of the plantar flexors with increasing contractions rates (from 2 to 20%MVIC/second). On the other hand, Miller et al. (2019a) reported no change in $EMG_{RMS}$ of the vastus lateralis (VL) with increasing contractions rates (from 5 to 20%MVIC/second). Similarly, among children and adolescents, Gillen et al. (2022) reported no change in $EMG_{RMS}$ of the VL during isokinetic maximal contractions at 60-300°/second. Thus, while the neural drive and muscle activation have been shown to increase with increasing isometric contraction intensity (e.g., Bigland-Ritchie, 1981; DeLuca & Erim, 1994; Gillen et al., 2021; Madeleine et al., 2001; Pitt et al., 2015; Woods et al., 2019), the effect that the rate of contraction has on muscle activity is not clear.

While $EMG_{RMS}$ reflects overall muscle activity, discrete MU analysis can provide insight into strategies of force gradation during contractions of different rates. Generally, during slow contractions where the torque or force is produced at low rates (≤10%MVIC/second), MU activation is characterized by a gradual and steady increase in MU recruitment and discharge (DeLuca and Hostage 2010; DeLuca and Contessa 2012), whereas contractions performed fast (≥20%MVIC/second) or explosively, at high rates, are typically characterized by rapid recruitment and discharge of MUs (Desmedt and Godaux 1978; Van Cutsem et al. 1998; Del Vecchio et al. 2019a, b; Emanuele et al. 2023). This change in MU activation in response to differing contraction rates has been observed among young adults in the tibialis anterior (Desmedt and Godaux 1978; Del Vecchio et al. 2019a), masseter (Desmedt and Godaux 1978), soleus (Desmedt and Godaux 1978), gastrocnemius (Aeles et al. 2022) and VL (Emanuele et al. 2023). No such data are available in children or in muscles that move the wrist and hand.

In adults, it has been demonstrated that even small alterations in the contraction rate can influence the MU firing rate (MUFR) at the target torque. Miller et al. (2019a) examined the effect of contraction rate on MU activation patterns at the plateau of trapezoidal knee extensions at 40%MVIC in men and women. Using discrete MU analysis, they found the slopes of the relationships between MU action potential amplitude (MUAPamp) and recruitment threshold (RT) and between MUFR and RT were greater (i.e., steeper) during slow (5%MVIC/second) compared with fast (20%MVIC/second) contractions. The authors suggest that more neural drive and specifically, greater recruitment of larger MUs were required to achieve the target force when performing the contractions at low compared with high rates. Similar conclusions were reported by Aeles et al., (2022), who also argued that recruitment occurs earlier and initial firing rates are higher during fast (20%MVIC/second) compared with slow (2%MVIC/second) contractions. Both studies examined contraction rates only up to 20%MVIC/second, and only in adults. In view of previously-observed age-related differences in MU activation during low contraction rate (10%MVIC/second) (Parra et al. 2020), and children's lower muscle activation during explosive contractions (Falk et al. 2009a; Dotan et al. 2013), it is unclear whether there is an age-related difference in the effect of contraction rate on MU activation pattern, nor whether such a difference is apparent during contractions performed at higher rates.

Therefore, the purpose of this study was to examine age-related differences in MU activation during slow (10%MVIC/second) and fast (35%MVIC/second) trapezoidal contractions at 70%MVIC. To specifically examine whether children activate their type-II MUs to a lesser extent (Dotan et al. 2012), we examined a contraction intensity (70%MVIC), which was likely to involve type-II fibres. Moreover, we aimed to investigate whether age-related differences in the neural adaptations to contraction rate differ between muscles (flexor carpi radialis (FCR) and VL) that have different recruitment ranges. In line with previous studies in adults (Desmedt and Godaux 1978; Del Vecchio et al. 2018, 2019b; Miller et al. 2019a; Aeles et al. 2022), we hypothesized that the initial MUFR (at RT) would be higher during fast compared with slow contractions, in both groups and muscles. Additionally, in line with children's lower explosive muscle strength performance, we hypothesized that these differences in MU activation between contraction rates will be more evident in children compared with adults.

# Methods

## Participants

Participants included in the study were involved in a larger study examining child–adult differences in neuromuscular function. Some of the results, specifically aspects relating to the slow contractions, have been recently published (Woods et al. 2024b, a). Thirty-four boys (7–12 years old) and twenty-two men (18–30 years old) volunteered to participate in the study. Participants were healthy and recreationally active, not participating in any structured training program >5 hours per week. Both boys and men reported they participated in regular sessions of vigorous, moderate and mild exercise on a weekly basis. Due to COVID-19 restrictions, fitness centres were closed and sports programs were on hold at the time of the data collection. Before participating in the study and signing informed consent and assent forms, a thorough explanation of the study's purpose, measurement procedures, benefits and potential risks or discomforts were provided to all participants and the boys' parents/guardians. The participant's physical characteristics appear in Table 1.

Participants' data were included in the final analysis if the following criteria were met: 1) participants were not regularly taking medications which may alter neurological function, 2) participants were able to execute and sustain the 70%MVIC trapezoidal contractions performed at slow and fast rates for at least one of two trials (see contraction protocols, below) and 3) the MU data met all the validation criteria (see data processing, below). In addition, only boys who self-assessed themselves to be pre- or early-pubertal (Tanner 1962) were included in the study. Data from one man were excluded as their MVIC could not be accurately calculated (technical malfunction). Overall, data from 14 boys and 20 men were included in the final analysis, with data from 9 boys and 14 men included in the analysis of the FCR and 10 boys and 16 men included in the analysis of the VL. All participants included in the analysis were right-handed and right-footed except for one man who reported being ambidextrous.

[Table 1]

**Experimental Procedures**

Participants made three visits to the laboratory, completing a habituation and two experimental sessions (one for knee extension, and one for wrist flexion). Participants were asked to refrain from strenuous exercise, and caffeine consumption for 24, and 12 hours, respectively before all testing sessions. During the first visit anthropometric measures, including height, seated height (boys only), mass, and body composition (see anthropometric measurements section, below) were obtained. The dynamometers were then fitted to each participant prior to performing maximal strength tests and submaximal contraction protocols (see exercise protocols, below) for knee extension and wrist flexion. Participants then completed the experimental sessions (visits 2 and 3) for knee and wrist assessments in a random order. Fifty percent (17/34) of boys and 52% (12/23) of men performed the knee extension assessments in visit 2, while 50% of the boys and 48% of the men performed the wrist flexion in visit 2. During these visits, fat thickness underlying the surface electrodes was determined using ultrasound (see anthropometric measurements section, below), before the MVIC assessment of the flexor and extensor muscle groups. Following a 2-minute rest, participants then performed 70%MVIC submaximal contractions at low (10%MVIC/s) and then at high (35%MVIC/s) rates. Trapezoidal contractions were each performed two times with at least 2-minutes rest between trials.

**Anthropometric Measurements**

Standing and sitting (boys only) height were measured to the nearest 0.1 cm (Ellard Instrumentation Ltd. Stadiometer). Body mass and fat percentage were measured to the nearest 0.1 kg and 0.1%, respectively, by bioelectrical impedance analysis (InBody 520, Biospace CO., Ltd., S. Korea). Participants were hydrated upon arrival to the laboratory and asked to void their bladder before measurements. In boys, standing height, seated height, body mass and chronological age were used to estimate the years from the age of peak height velocity (Mirwald et al. 2002).

Ultrasound (B-Mode; Vivid-q; General Electric Healthcare, USA) was used to assess the thickness of fat tissue underlying the electrode sites (see below), as measured from the deepest aspect of the dermis to the deepest aspect of the subcutaneous tissue layer. During measurement, the probe was placed on the forearm or thigh with as little pressure as possible so that the underlying tissues would not be compressed. The median of three measurements was used to characterize subcutaneous fat tissue thickness at each site.

Pubertal status was self-assessed, based on secondary sex characteristics of pubertal hair, using drawings, as outlined by Tanner (1962).

Habitual physical activity levels were assessed using the Godin-Shephard Leisure Time Physical Activity questionnaire (Godin and Shephard 1985).

**Contraction Protocols**

Contraction protocols for knee extension were performed using the right leg on a Biodex System III Isokinetic dynamometer (Biodex, Shirley, NY). Contractions were performed with the knee and hip positioned at 90° and 60°, respectively. Participants were secured to the seat of the Biodex with straps placed across the hips and chest. Contraction protocols for wrist flexion were performed using the right arm on a custom, purpose-built dynamometer placed adjacent to the Biodex seat (Figure 1). The participant's right forearm and hand were secured to the purpose-built dynamometer using custom-made clamps. During all contractions, the wrist was placed in a neutral position and the elbow between ~90 to 100° of flexion (Figure 1). Special care was taken to ensure that contractions were performed only with the wrist flexors, with no movement of the fingers or shoulder. To minimize the use of other muscles during the wrist flexion task, participants were secured to the seat using straps, with hips at 60° of flexion.

[insert Figure 1]

Before performing the MVIC assessments (agonist and antagonists), participants were guided through a warm-up consisting of three, 5–10-second isometric contractions at progressing intensity from ~50–80% of maximal perceived effort. Participants then completed 3 MVICs for agonist and antagonist muscle groups, separated by 2 minutes of rest. MVIC was then determined using MATLAB (v.2020b, MathWorks Inc., Natick MA) as the highest 500ms of torque achieved during one of the MVIC trials. For each MVIC trial, participants were provided visual feedback and verbal encouragement to ensure a maximal performance was achieved.

To assess age-related differences in the neuromotor strategy used to modulate torque, 70%MVIC isometric trapezoidal contractions were performed at 10%MVIC/second (*slow/low rate*) and 35%MVIC/second (*fast/high rate*). Based on pilot data, 35%MVIC/second was the fastest rate that could be accurately traced with no torque overshoot. The 10%MVIC/second rate was chosen as it is the commonly used in the assessment of discrete MU data (e.g., DeLuca and Hostage 2010; DeLuca and Contessa 2012; Martinez-Valdes et al. 2018; Chalchat et al. 2019; Parra et al. 2020). Trapezoidal contractions comprised a steady progression of torque development at a rate of 10%MVIC/second (total of 7 seconds) or 35%MVIC/second (total of 2 seconds) to the 70%MVIC, an isometric hold at 70%MVIC lasting 12 seconds and then a steady release of torque back to baseline. Two trials of each contraction type were performed with at least 2-min rest between trials.

**Data Acquisition**

Neuromuscular activity was recorded by Delsys Inc. Trigno Galileo Sensors at 2222Hz. The sensors comprised four silver electrode pins arranged in a diamond configuration, with an inter-electrode distance of 5mm. EMG signals were digitized and filtered at 20-450Hz using a 16-bit A/D converter before being transmitted using Bluetooth to a base station (Delsys Inc., Natick, MA, USA). Before placing the sensor on the skin, it was thoroughly prepared by shaving, then performing a series of tape pulls to remove dead skin cells and cleaning the area using rubbing alcohol. Following the SENIAM guidelines, the electrode for the VL was placed at

2/3 the distance between the anterior superior iliac spine and the superior aspect of the patella. The electrode over the FCR was placed using palpation of the muscles during repeated wrist flexions and extensions. The reference for each sensor was placed adjacent to the recording site, i.e., on the medial quadriceps and belly of the biceps brachii for VL and FCR, respectively. All sensors were secured to the skin surface using double-sided adhesives, and taping over the head of the sensor.

Wrist flexion and extension forces were measured via a load cell (micro1401, Cambridge Electronics Design, Cambridge, UK) attached in series to where participants applied force on the purpose-built dynamometer. Knee extension and flexion torque were captured from the Biodex III. All Force and torque signals were digitized (16-bit A/D) then Bluetooth transmitted by a Delsys Inc.Wireless Trigno Analog Adapter at a rate of 2222 Hz (Delsys Inc., Natick, MA, USA), to a base station and filtered at DC-100Hz. All force and torque signals were captured in volts and converted to torque during the initial phases of data processing (see below). Torque and sEMG signals were synchronized and transmitted simultaneously.

**Data Processing**

Force and torque signals were imported into MatLab (v.2020b, MathWorth, Natick, MA, USA) to calculate MVIC and ramp speed, and into LabView (National Instruments, Austin, TX, USA) to determine torque produced during the submaximal contraction tasks. For wrist flexion, all force signals were converted to torque (Nm) by multiplying the measured force by the dynamometer's moment-arm length (0.059m fixed distance). MVIC was calculated as the highest 500ms of torque collected during the 3 trials. In LabView, the mean submaximal torque was then calculated during the most stable 3-s period (lowest standard deviation) of the trapezoid contraction. The mean submaximal torque was then expressed as a percentage of MVIC.

Overall muscle activation and antagonist coactivation were assessed from the sEMG signal collected in the first of the four sEMG channels. Using MATLAB (v.2020b, MathWorks Inc., Natick MA), $EMG_{RMS}$ amplitude was calculated for the MVIC and 70%MVIC trials during the highest 500ms and most stable 3-s of force (lowest standard deviation), respectively. FCR and VL $EMG_{RMS}$ at 70%MVIC were expressed as a percentage of $EMG_{RMS}$ calculated during the MVIC. Antagonist coactivation was calculated as the antagonist muscle $EMG_{RMS}$, expressed as a percentage of its maximal $EMG_{RMS}$ amplitude when acting as an agonist (Kellis and Unnithan 1999; Falk et al. 2009b). Antagonist muscle activity was captured from the extensor carpi radialis and semitendinosus for wrist flexion and knee extension, respectively.

Once collected, sEMG data were decomposed into individual motor unit action potential (MUAP) trains by Delsys Neuromap software V.4.7.3, using the newest version of precision decomposition software (EMGworks 4.7.6, Natick, MA, USA; De Luca & Contessa, 2012; De Luca & Hostage, 2010). Following decomposition, all MU data were exported from NeuroMap and validated using spike trigger averaging (STA) procedures in LabView (Herda et al., 2020; National Instruments Corp. Austin, TX, USA). These procedures were used to "double-check" the data produced by the Delsys NeuroMap algorithm. Specifically, the validation procedures also ensured that only the MU trains with the lowest MUAP amplitude (MUAPamp) variability are included and that the firing times identified are truly associated with MU firing rather than erroneous noise. NeuroMap-derived MUAP templates and firing times were used to perform the STA analysis on each EMG channel. Based on recommendations by Hu et al., (2013b) MUs were included in the final analysis if the coefficient of variation of the STA MUAPamp was <0.3 across all 4 channels and if the correlation coefficient between the P–P amplitude of NeuroMap-derived templates and the STA-determined amplitude was >0.7. To ensure that the STA-determined MUAPamp corresponded with the NeuroMap-derived firing times we also added

Gaussian noise set to shift firing times by 0.5 and 1.5% for each MU and then assessed whether the MUAPamp could still be detected. Indeed, after the addition of small amounts of Gaussian noise (shifting firing times by <2ms), no defined action potential waveforms could be detected (Figure 2). In addition to these validation procedures, participants' data were included in the analysis if the recruitment threshold (RT) range was >1/3 of the contraction intensity, and 5 MUs met all the above criteria. Only data from one of the two trials were included in the final analysis. The trial with the best performance, largest RT range, and highest number of MUs was selected.

[Figure 2]

For each MU, RT (%MVIC), average MUAPamp (mV), MUFR at recruitment, and average MUFR (pps) at the plateau phase were computed externally, using LabView (Sterczala et al. 2018; Miller et al. 2019a; Herda et al. 2019). RT was determined as the average 0.1-ms epoch of torque (average of 4 samples) associated with the first firing time (i.e., discharge) for the MU. The average MUAP amplitude was calculated as the average of the P–P amplitudes in the 4 channels for each unique MU. Initial MUFR (i.e., at recruitment onset) was calculated as the reciprocal of the first 3 inter-spike intervals (rate of first 4 pulses) for each MU. Average MUFR at the plateau was assessed during the 3-s period during which the torque signal was most stable (lowest standard deviation) and was calculated as the reciprocal of the average inter-spike interval for each MU. Group differences in discrete MU activation were assessed by comparing the mean MUAPamp, initial MUFR and MUFR at the plateau. Additionally, for each participant and contraction, the MUFR were expressed relative to their MUAPamp and fit with an exponential function [$\mathrm{MUFR} = \mathrm{A}e^{\mathrm{B(MUAPamp)}}$](Chalchat et al. 2019; Miller et al. 2019b). A- and B-terms were extracted to characterize differences in MUFR between groups and contraction rates independent of differences in MU RT (See Figure 3 for example). The A-term represents the theoretical MUAPamp for a MU recruited at 0%MVIC. The B-term represents the rate of MUFR decay with one unit increase in MUAPamp.

[Figure 3]

**Statistical Analysis**

All assumptions and statistical analyses were performed using IBM SPSS 28.0 (IBM Corp., Armonk, NY, USA). Normality was assessed by visual examination of the frequency distributions and determined when skewness or kurtosis was less than ±3. The assumption of normality was met for all measures. Not all participants had valid data for both the wrist flexors and knee extensors. Therefore, data from wrist flexion and knee extension were assessed separately. This strategy was chosen to maximize the number of participants in each analysis. Statistical differences were indicated when $p<0.05$. When appropriate, follow-up analyses included pairwise comparisions, with Bonferroni correction. The effect size was assessed using d and $\eta^2$, as recommended by (Cohen 1988). Data are presented as means and standard deviations unless otherwise stated.

T-tests were used to assess group differences in physical characteristics, MVIC and normalized MVIC (Nm per kg lean body mass). Differences between groups and contraction rates in muscle performance, MU parameters, and A- and B-term of the MUFR-MUAPamp relationship were assessed using Repeated Measures (RM) ANOVAs, with Group as the between-subject factor and contraction rate as the within-subject factor. A RM ANCOVA was used to assess differences in minimum and maximum MUAPamp while accounting for differences in subcutaneous fat thickness underlying the electrode (covariate). MU parameters included MU recruitment range, the number of MUs identified from decomposition, average MUFR, average MUAPamp, initial MUFR and normalized EMG RMS.

## Results

### Anthropometrics

Group means and standard deviations of the anthropometric measures are presented in Table 1. As expected, men were significantly older, taller and heavier compared with boys ($p<0.001$). While body fat percentage was not different between groups ($p=0.24$), fat thickness at the VL electrode site was significantly greater in boys compared with men [$t(24) = 2.54$, $p=0.02$, $d = 1.03$]. There were no significant differences in the fat thickness at the FCR electrode site between boys and men ($p=0.16$).

### Muscle Performance & Surface Electromyography

Group means and standard deviations of the MVIC are presented in Table 1, and muscle performance assessments during the submaximal contraction are presented in Table 2. Wrist flexor and knee extensor MVICs were significantly higher in men compared with boys (Wrist: [$t(21) = -8.10$, $p<0.001$, $d=-3.46$]; Knee: [$t(24) = -8.64$, $p<0.001$, $d= -3.48$]). Lean body mass-normalized MVIC was significantly greater in men compared with boys during knee extension [$t(24) = -5.14$, $p<0.001$, $d=-2.07$], but not wrist flexion ($p = 0.06$). For wrist flexion, the ramp speed and relative torque sustained were not different between groups nor contraction rates ($p>0.05$). For knee extension, the relative torque sustained (%MVIC) was not different between contraction rates ($p = 0.62$) but was statistically greater in men compared with boys [$F(1,24) = 5.50$, $p=0.03$, $\eta^2=0.17$]. Note that although this difference was statistically significant, the differences between groups were <1%MVIC. Normalized $EMG_{RMS}$ during the trapezoidal contractions were not different between groups nor contraction rates in both FCR and VL muscles ($p>0.05$). For both knee extension and wrist flexion, antagonist coactivation was not different between boys and men, nor between contraction rates ($p>0.05$).

[Table 2]

**Motor-Unit Decomposition**

Table 3 describes the MU characteristics for each group during the slow and fast contractions. Overall, the number of MUs identified per participant was not different between boys and men in either, the FCR nor VL ($p>0.05$). The main effect of contraction rate on MU number did not reach statistical significance in the FCR ($p=0.11$), nor the VL ($p=0.05$). For FCR, the highest RT was statistically greater in men compared with boys [$F(1,21) = 12.82$, $p=0.002$, $\eta^2=0.38$], and during fast compared with slow contractions [$F(1,21) = 4.20$, $p=0.05$, $\eta^2=0.17$]. Thus, in the FCR the RT range was greater in men compared with boys, and in fast compared with slow contractions.

**Initial Motor-Unit Firing Rates (at Recruitment Onset)**

Figure 4 displays the initial MUFR in the FCR and VL for boys and men during contractions performed at slow and fast rates. In both muscles, initial MUFR was significantly greater in fast compared with slow contraction (main-effect - Rate)(FCR: [$F(1,21) = 108.71$, $p<0.001$, $\eta^2=0.84$]) VL: [$F(1,24) = 92.16$, $p<0.001$, $\eta^2=0.79$]). In the VL, there was a significant group-by-contraction rate interaction [$F(1,24) = 5.15$, $p=0.03$, $\eta^2=0.18$]), indicating that in the VL, the initial MUFR was higher in men compared with boys in the fast, but not the slow contraction rate. There was no significant group-by-contraction rate interaction ($p = 0.77$), nor effect of group (0.10) in the FCR.

[Figure 4, Table 3]

**MUAPamp and MUFR at Target Torque**

The mean MUAPamp and MUFR for each group and contraction appear in Table 3. After accounting for group differences in fat thickness, there was no difference in mean MUAPamp between boys and men nor between slow and fast contractions in the VL ($p=0.19$; $p=0.27$, respectively) and FCR ($p=0.63$; $p=0.14$, respectively) muscles. There was also no group-by-intensity interaction for mean MUAPamp in VL (p=0.74) and FCR (p=0.68) muscles. In the FCR and VL, there was no effect of rate or group-by-rate interaction on the lowest nor highest MUAPamp (p>0.05). In the VL, there was a significant effect of group on the highest MUAPamp [Group effect: $F(1,23) = 4.28$, p=0.05, $\eta^2=0.16$], indicating that the largest MUAPamp detected in men was greater compared with boys. This difference was present even when accounting for group differences in fat thickness. No group effects were observed in the FCR (p>0.05).

There was a main effect of group on mean MUFR in the VL [$F(1, 24) = 5.06$, $p<0.05$, $\eta^2=0.17$], but not the FCR (p = 0.92), indicating that overall, the mean VL MUFR was significantly greater in men compared with boys. Mean MUFR was significantly lower in the fast compared with the slow contractions in the FCR [$F(1, 21) = 4.91$, p=0.04, $\eta^2=0.19$], but not in the VL (p = 0.20). There were no significant group-by-rate interactions on mean MUFR in the VL (p=0.77) nor FCR (p=0.86).

Figure 5 displays the mean exponential decay relationship between MUFR and MUAPamp in boys and men during the 70%MVIC trapezoidal contractions performed at slow and fast rates. Table 4 provides the results of the RM ANOVA examining group and rate differences in the MUFR-MUAPamp relationship. In both the VL and FCR, there were no group-by-rate interactions for the A- nor B-terms of the MUFR–MUAPamp relationship, reflecting that the effect that contraction rate on the MUFR-MUAPamp relationship is not different between groups. In the VL only, the MUFR-MUAPamp B-term was significantly lower (more negative) in boys compared with men [$F(1, 24) = 6.11$, p=0.02, $\eta^2=0.20$]. The VL A-term was also lower in boys compared with men, however, differences did not reach statistical significance [$F(1, 24) = 4.28$, p=0.05, $\eta^2=0.15$]. Overall, this indicates that during slow and fast contractions, MUFRs were lower in boys, especially among larger (presumably higher-threshold)

MUs. In both groups and muscles there was a significant effect of rate on the B-terms of the MUFR-MUAPamp relationship (FCR: [$F(1, 21) = 5.62$, $p=0.03$, $\eta^2=0.21$]; VL: [$F(1, 24) = 12.95$, $p=0.001$, $\eta^2=0.35$]. Specifically, the B-term was less negative during fast compared with slow contractions, reflecting a smaller decrease in MUFR with increasing MUAPamp during fast contractions. In the VL, there was also a significant effect of rate on the A-term [$F(1, 24) = 5.50$, $p=0.03$, $\eta^2=0.19$]. Specifically, the MUFR-MUAPamp A-term was significantly lower during fast compared with slow contractions, in both boys and men.

[Table 4, Figure 5]

## Discussion

This is the first study to investigate age-related differences in the discrete MU activation strategy used to modulate torque during slow and fast contractions. The main finding of our investigation is that the general strategy utilized to increase the rate of torque production (from 10%MVIC/s to 35%MVIC/s) was similar in boys and men. Namely, both boys and men had a greater initial MUFR during fast compared with slow contractions. In the VL, the increase in initial MUFR with increasing rate was greater in the men compared with the boys. We also observed that the contraction rate similarly affected the MUFR at the plateau in both groups and muscles. Specifically, the rate of decay in MUFR with increasing MUAPamp was less steep in the fast compared with slow contractions, reflecting higher MUFRs, especially in the larger MUs during fast contractions (Figure 5). Overall, these findings suggest that, in order to achieve a moderate intensity torque at faster contraction rates, both boys and men increase the MUFR at the beginning as well as at the target torque.

Greater initial MUFR in response to an increase in contraction rate has previously been observed by Aeles et al. (2022), who reported greater initial MUFR in adults performing plantar flexion at higher (20%MVIC/second) compared with lower (2%MVIC/second) rates. DeLuca & Contessa (2012) also observed an increase in initial MUFR with increasing contraction rate in the VL and first dorsal interosseous. In the present study, boys and men demonstrated similar increases in initial MUFR in response to increased contraction rates in the FCR, whereas in the VL, the increase in initial MUFR in the high contraction rate was greater in men compared with boys (Figure 4). These findings suggest that during knee extension, while both boys and men relied on increasing initial firing rates to produce torque at a faster rate, the increase in initial firing rate may have played a lesser role in the boys. It is possible that different muscle activation patterns between groups may be due to boys' lower neural drive during the initial phases of the contraction. However, this suggestion should be viewed with caution. Although the increase in initial MUFR in the VL was statistically greater in men compared with boys, the difference between groups was quite small (0.81pps greater in men). This small difference in initial MUFR may be related to the small deviations in ramp performance between groups. Namely, while the mean ramp rate was not statistically different between groups, the increase in mean ramp rate from low to high was slightly greater (by 1.64%MVIC/second) in men compared with boys. Thus, despite the statistically greater initial MUFR in the men, the realistic neural strategy of increasing the contraction rate in the FCR and VL appears to be similar in boys and men.

In both slow and fast contractions participants sustained their torque at 70%MVIC. Therefore, it was expected that the MUFR at the plateau would not differ between slow and fast contractions when expressed relative to their MUAPamp. Nevertheless, in both muscles and groups, we observed a significantly lower rate of MUFR decay with increasing MUAPamp during fast contractions. This reflects that MUFR, especially among the larger MUs was higher during fast compared with slow contractions. To our knowledge, DeLuca & Contessa (2012) is the only other study to examine MUFR during contractions at differing rates in a small muscle

(FDI). However, they did not examine the MUFR-MUAPamp relationship, nor was target torque constant between contraction rates (2%MVIC/second to 50%MVIC; 4%MVIC/second to 80%MVIC; 10%MVIC/second to 100%MVIC), which makes it difficult to determine whether changes in MUFR at the target torque were due to differences in contraction intensity or ramp rates. Our findings are in contrast with Miller et al., (2019), who reported no differences in the B-term of MUFR-MUAPamp relationship during moderate intensity (40%MVIC) isometric knee extensions performed at higher compared with lower rates (20 vs. 5%MVIC/s). This apparent inconsistency may be related to the different contraction rates and intensities in the two studies. That is, we examined a much higher contraction intensity (70%MVIC vs. 40%MVIC) and a higher contraction rate (35%MVIC/second vs. 20%MVIC/second). Although speculative, it is possible, that MUFR was elevated during the fast compared with slow contraction due to faciliatory feedback from muscle afferents (Ia and II). Alternatively, because the fast contractions were much shorter than the slow contractions (26 vs. 16 seconds), it is possible that during the former, the withdrawal of afferent signalling leading to a decrease in MUFR had not yet occurred (De Luca 1985). Higher MUFRs during fast contractions may also be related to our study design, in which slow contractions were performed before fast contractions. Sufficient rest was provided between trials, as all trials were successfully performed. However, it is also possible that there was cumulative peripheral fatigue over the experimental session, which would be apparent, especially in the large MUs. Similar decreases in the B-term of the MUFR-MUAPamp relationship have been observed during repeated knee extensions at 30%MVIC and contractions of the FDI at 50%MVIC (Contessa et al. 2016, 2018). Nevertheless, in those studies, an increase in the $EMG_{RMS}$ and MUFR-MUAPamp A-term was also observed (Contessa et al. 2016, 2018), which we did not see in the present study.

We observed no effect of contraction rate on mean MUFR in the large VL muscle, but a lower mean MUFR during the fast contraction in the FCR. These differential findings are along the lines of those reported by Del Vecchio et al., (2018) who observed that the decrease in mean MUFR with increasing contraction rate was greater in the FDI (small muscle) than in the tibialis anterior (larger muscle) during low-intensity cyclical contractions. As suggested by the authors, it is possible that the effect of contraction rate on mean MUFR was different between smaller vs larger muscles (FCR vs. VL, or FDI vs. TA) due to their differing recruitment ranges. That is, at any given contraction intensity, and specifically at higher intensities, as used in the current study, relatively larger (and faster) MUs are recruited in the smaller muscle (FCR), due to its narrower recruitment range. Specifically, these alterations in MU recruitment during the ramp phase, ultimately change the interplay of torque developed by MU recruitment vs. MUFR. Therefore, if relatively larger MUs are recruited during contractions performed at high rates, MUFRs would be lower, so that the target force generated is similar to that attained during a low contraction rate. Although the effect of contraction rate on mean FCR MUAPamp did not reach statistical significance the effect size for this comparison was moderate to large ($\eta^2 = 0.11$). This observation supports the idea that relatively larger MUs were recruited during fast compared with slow contraction in the FCR.

Although we observed contraction rate to affect the discrete MU activation patterns, there was no effect of contraction rate on overall VL or FCR muscle activation ($EMG_{RMS}$), or antagonist coactivation. These findings suggest that the contraction rate did not affect the overall neural drive required to achieve the target torque (70%MVIC). This is in line with findings from Miller et al., (2019a) and Gillen et al., (2022), who reported no differences in VL $EMG_{RMS}$ during low and maximal contraction intensities, performed at low and high contraction rates in adults and children. On the other hand, Aeles et al., (2020) reported greater gastrocnemius

$EMG_{RMS}$ during plantar flexion at high compared with low rates among 9 adults. It should be noted, however, that the authors also demonstrated variable individual responses of the $EMG_{RMS}$ (increases and decreases) and that the reported higher mean values appear to be driven by two individuals with very large increases (Aeles et al., 2020, Figure 4).

Although the effect of contraction rate on MU activation was not different between groups, in the VL, the boys presented a different pattern of MUFR compared with men. Boys demonstrated generally lower overall MUFR compared with men, as reflected in their lower mean MUFR. Additionally, in the VL, boys demonstrated a greater rate of MUFR decline with increasing MUAPamp (more negative B-term), reflecting that the lower MUFR in boys is especially apparent among the larger MUs. These observations are similar to Chalchat et al., (2019), who reported lower (more negative) VL MUFR-MUAPamp B-term in boys compared with men during isometric knee extensions at 20-80%MVIC. Disparities in the age-related differences in MUFR between muscles may be related to muscle-specific variations in MU recruitment range and size. Overall, lower MUFR in boys can partially explain their lower normalized knee extension strength compared with men.

A previously reported effect of a high contraction rate on MU activation pattern is recruitment compression (Desmedt and Godaux 1978; Del Vecchio et al. 2018; Aeles et al. 2022). Recruitment compression is thought to be a beneficial adaptation that may allow for more efficient mechanical summation of force (Desmedt and Godaux 1977). For example, during maximal explosive dorsi flexions, Del Vecchio et al. (2019b) observed a strong negative association between MU recruitment time and rate of torque development. In the present study, we observed that the highest RT was not different between contraction rates during knee extension and was significantly higher in the fast compared with slow contractions during wrist flexion (Table 3). Additionally, the largest MUAPamp identified was not different contraction rates for both VL and FCR. Overall, these findings suggest that recruitment compression was not observed. Miller et al. (2019a), also observed that the highest RT was higher during fast (20%MVIC/s) compared with slow (5%MVIC/s) submaximal knee extensions. They suggest that this observation may be a function of muscle spindle activity.

**Limitations**

Due to spatial effects on sEMG, we acknowledge that MUAPamp is affected by many factors (e.g., subcutaneous tissue thickness, MU depth) which impact the conduction volume. Thus, it has been argued that MUAPamp may not be a good indicator of MU size (Del Vecchio et al. 2020). In the present study, we choose to relate MUFR to MUAPamp as the purpose of this study was to examine the effect of contraction rate on MUFR, independent of changes in MU recruitment. Importantly, it should be noted that comparisons between rates were performed within individuals. Therefore, any inaccuracy in the MUAPamp would be consistent within individuals and would not affect the comparison between contraction rates.

Compared with previous studies, we observed lower initial MUFR (Monster and Chan 1977; Aeles et al. 2022). The lower initial MUFRs in the present study may be related to the use of the new NeuroMap decomposition algorithm. While the new algorithm is based on the previous precision decomposition (PD) III, there are some differences in its output. Potentially, a missed firing event during the initial recruitment would result in lower initial MUFR values. Of note, a propensity for missed firings during the steady force likely has minimal impact on our results since the mean MUFR is an average spanning across several seconds (Hernandez-Sarabia et al. 2020). We suspect that missed firings at recruitment may have resulted in lower initial MUFRs. Nevertheless, it should be noted that it is consistent across all participants and trials. Therefore, the observed differences between groups and contraction rates would likely not be impacted.

On average, each participant had ~11-13 MUs verified for each contraction. Other studies using similar technology have identified more MUs per individual (e.g., In the VL and FDI, De Luca & Hostage et al., (2010) report up to 35 MU per individual; In the VL, Parra et al., (2020) report up to 30 MUs per individual). On the other hand, recent studies examining MU activation in the VL in children and adults, using HD-EMG technology, reported lower number of identified valid MUs (average of 6 MUs per participant, range 3-15; Yoshimura et al. 2022; Okudaira et al. 2023). While, we identified less MUs than some, we still captured a large sample of MUs per individals. More importantly, we were able to capture a similar number of valid MUs in both groups, across a wide spectrum of sizes and RTs.

Finally, it should be noted that the slow contractions were performed prior to the fast contractions, rather than in random order. Therefore, we cannot ascertain that there was no order effect. Nevertheless, we provided participants with sufficient rest between contractions.

## Conclusions

In summary, we observed that when the contraction rate was increased during moderate intensity contraction, both boys and men increased their initial MUFR and MUFR of large MUs at target torque. These adaptations were apparent in both the FCR and VL muscles. While the increase in the initial MUFR was greater in men compared with boys, specifically in the VL, the difference between groups was quite small and may be related to the minor differences in the ramp performance of the contraction. Increasing contraction rate had a similar effect on the MUFR-MUAPamp relationship in boys and men, demonstrating a smaller decrease in MUFR with increasing MUAPamp in both muscles. While the pattern of adaptations of MU activation to increasing contraction rate is similar in boys and men, mean MUFR and MUAP are consistently lower in the boys in the VL, but not the FCR.

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**Figure Legends:**

Figure 1. Experimental instrumentation/setup. (A) Wrist (B) Knee.

Figure 2. sEMG signal from all four channels from the FCR of one boy (A). The firing times from a single motor unit determined by NeuroMap (lines) and with the addition of Gaussian noise to the firing times (STA+G)(circles and crosses)(B). Using the firing times, four unique motor unit action potential waveforms of a single motor unit were calculated by NeuroMap, spike trigger averaging procedure (STA) and with the STA with the addition of Gaussian noise to the firing times (STA+G)(C).

Figure 3. One subject's (man) MUFR-MUAPamp with a line of best fit for slow (squares) and fast (triangles) contractions

Figure 4. Mean MUFR at RT for boys (blue) and men (red) during slow (light bars) and fast (dark bars) trapezoidal contractions at 70%MVIC

Figure 5. Mean MUFR-MUAPamp relationship for boys (blue) and men (red) during slow (dashed) and fast (solid) trapezoidal contractions at 70%MVIC. Left panel: FCR; Right panel: VL. Mean MUFR-MUAPamp relationships were derived using the mean exponential equations developed from the mean A- and B-terms extracted from the individual MUFR-MUAPamp relationships

Table 1. Participants' Characteristics

| | **Boys** | **Men** |
|---|---|---|

| | | |
|---|---|---|
| **n** | 14 | 20 |
| **Age** (years) | 10.1±1.8 | 25.3±2.9* |
| **Height** (cm) | 141.6±10.4 | 177.6±7.5* |
| **Weight** (kg) | 36.4±11.4 | 77.1±10.8* |
| **Body Fat** (%) | 14.5±9.1 | 17.9±6.1 |
| **Pubertal Stage** (1,2,3,4,5)# | 6,8,0,0,0 | N/A |
| **Years from Age at PHV** | -2.96±1.07 | N/A |
| **Physical Activity** (Score) | 117.9±83.4 | 56.4±16.5* |
| **FCR Fat thickness** (cm) | 0.40±0.20 | 0.29±0.08 |
| **VL Fat thickness** (cm) | 0.70±0.20 | 0.51±0.17* |
| **Absolute MVIC** (Nm) | | |
| **Wrist flexion** | 4.3±1.6 | 10.0±1.7* |
| **Knee extension** | 66.7±25.6 | 230.5±56.1* |
| **Relative MVIC** (Nm/LBM) | | |
| **Wrist flexion** | 0.14±0.03 | 0.16±0.03 |
| **Knee extension** | 2.23±0.52 | 3.60±0.73* |

PHV = Peak height velocity; FCR Fat Thickness = Subcutaneous tissue thickness underlying flexor carpi radialis electrode site; VL Fat Thickness = Subcutaneous tissue thickness underlying vastus lateralis electrode site. MVIC = Maximal voluntary isometric contraction; LBM = Lean body mass

*Significantly different from Boys

# number of participants in stage 1,2,3,4, and 5

Table 2. Muscle Performance in submaximal contractions

| | **Boys** | | **Men** | |
|---|---|---|---|---|
| | ***Slow*** | ***Fast*** | ***Slow*** | ***Fast*** |
| ***Wrist Flexion*** | | | | |
| **Torque Achieved** (%MVIC) | 70.6±2.7 | 70.3±1.9 | 70.1±1.3 | 69.9±1.2 |
| **Ramp Speed** (%MVIC/s)† | 10.6±1.9 | 32.0±4.5 | 9.6±0.5 | 30.7±2.6 |
| **Normalized** $\mathbf{EMG_{RMS}}$ (%RMS during MVIC) | 80.5±22.6 | 76.1±25.5 | 73.5±19.5 | 74.9±18.7 |
| **Coactivation** (%) | 11.3±2.2 | 11.6±2.7 | 11.5±8.1 | 11.0±6.8 |
| ***Knee Extension*** | | | | |
| **Torque Achieved** (%MVIC)* | 69.1±1.7 | 68.7±1.8 | 69.8±0.9 | 69.9±0.9 |
| **Ramp Speed** (%MVIC/s)† | 10.1±0.7 | 30.2±2.6 | 9.7±0.5 | 31.3±2.7 |
| **Normalized** $\mathbf{EMG_{RMS}}$ (%RMS during MVIC) | 84.7±18.4 | 85.6±18.2 | 80.6±19.7 | 80.2±20.3 |
| **Coactivation** (%) | 5.9±5.5 | 5.4±2.8 | 6.1±3.8 | 5.6±3.1 |

MVIC = maximal volitional contraction; $EMG_{RMS}$ = root mean squared

*Statistically significant difference between boys and men (Group effect)

†Statistically significant difference between slow and fast contractions (Rate effect)

Table 3. Characteristics of the identified motor units in the FCR and VL during slow and fast contractions

| | Boys | | Men | |
|---|---|---|---|---|
| | ***Slow*** | ***Fast*** | ***Slow*** | ***Fast*** |
| ***Wrist Flexion (FCR)*** | | | | |
| **MUs per participant** | 12±3 | 11±2 | 13±2 | 12±2 |
| **RT – lowest** (%MVIC) | 2.2±3.5 | 3.0±5.7 | 1.5±2.4 | 7.8±8.3 |
| **RT– highest** (%MVIC)†* | 38.3±9.5 | 43.3±9.7 | 48.7±7.0 | 52.9±8.0 |
| **MUAPamp – lowest (mV)** # | 0.07±0.05 | 0.09±0.05 | 0.07±0.04 | 0.08±0.05 |
| **MUAPamp – highest (mV)** # | 0.25±0.14 | 0.27±0.15 | 0.24±0.13 | 0.31±0.15 |
| **Mean MUAP** (mV)# | 0.14±0.10 | 0.15±0.08 | 0.15±0.07 | 0.17±0.08 |
| **Mean MUFR** (pps)† | 17.8±2.5 | 16.2±4.9 | 17.6±2.8 | 16.2±2.1 |
| ***Knee Extension (VL)*** | | | | |
| **MUs per participant** | 13±2 | 11±3 | 14±4 | 13±4 |
| **RT – lowest** (%MVIC) | 9.2±6.6 | 11.4±6.9 | 8.8±6.6 | 10.9±9.5 |
| **RT– highest** (%MVIC) | 48.6±7.8 | 53.3±13.7 | 53.2±10.8 | 56.8±9.0 |
| **MUAPamp – lowest (mV)** # | 0.024±0.02 | 0.03±0.01 | 0.028±0.02 | 0.03±0.01 |
| **MUAPamp – highest (mV)** #* | 0.11±0.07 | 0.10±0.06 | 0.13±0.06 | 0.15±0.06 |
| **Mean MUAP** (mV)# | 0.049±0.03 | 0.051±0.03 | 0.061±0.02 | 0.066±0.03 |
| **Mean MUFR** (pps)* | 15.8±1.9 | 15.2±2.6 | 17.9±2.4 | 16.9±3.1 |

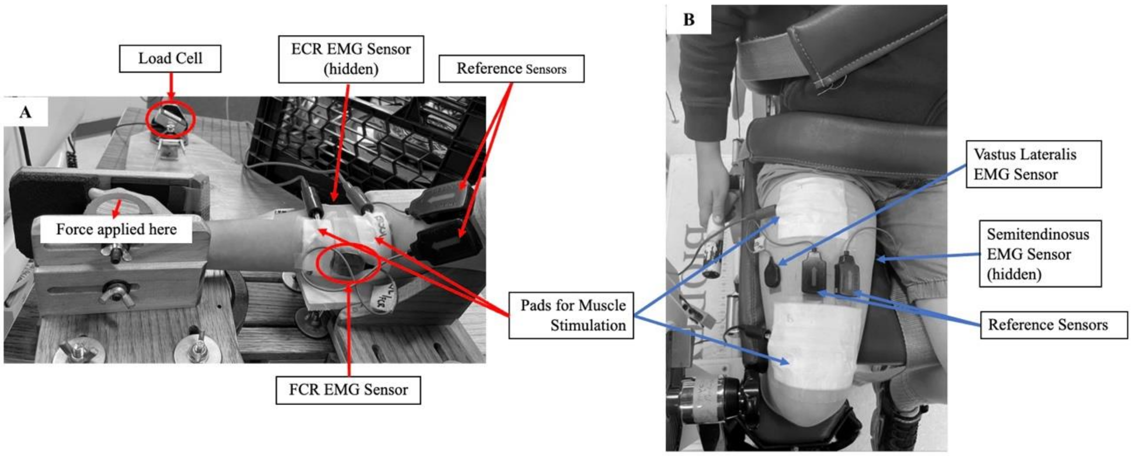
MU = motor unit, RT = recruitment threshold, MVIC = maximal volitional contraction, MUAPamp = motor unit action potential amplitude; MUFR = motor unit firing rate
*Statistically significant difference between boys and men (Group effect)
†Statistically significant difference between slow and fast contractions (Rate effect)
# Values adjusted for group differences in subcutaneous fat thickness

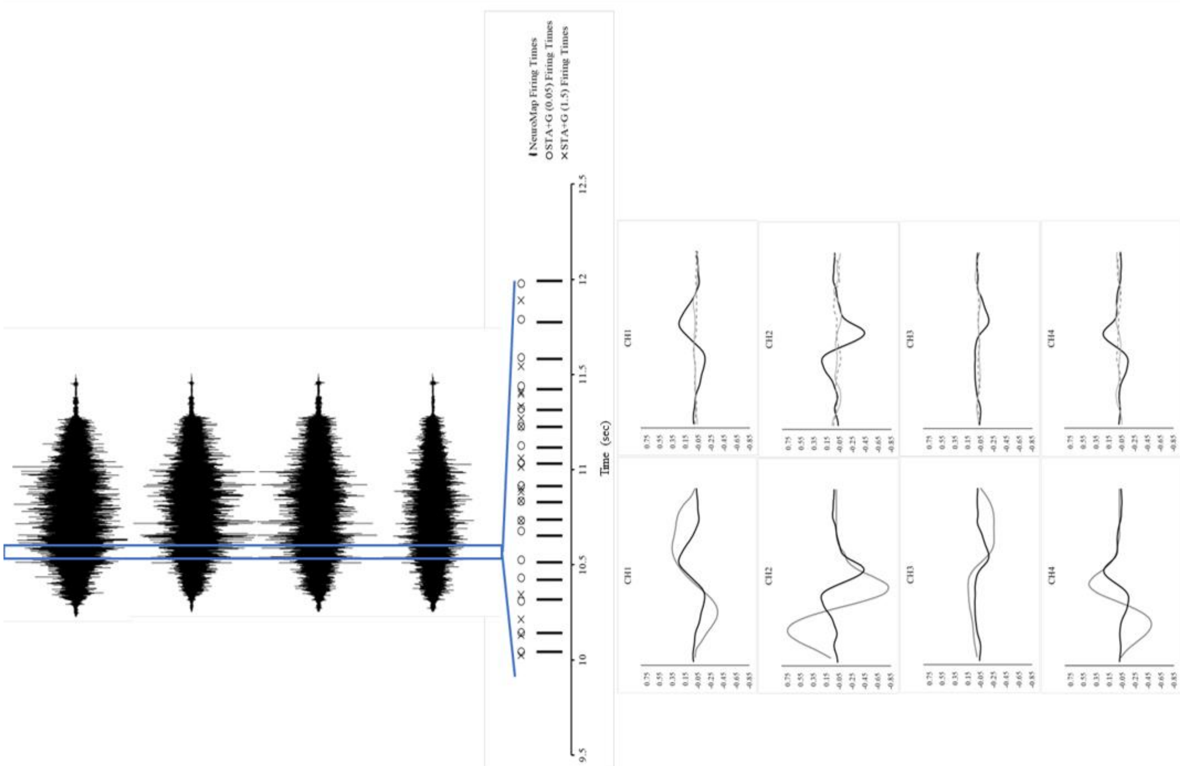
Table 4 A- and B-terms of the MUFR-MUAPamp relationship in boys and men during slow and fast contractions

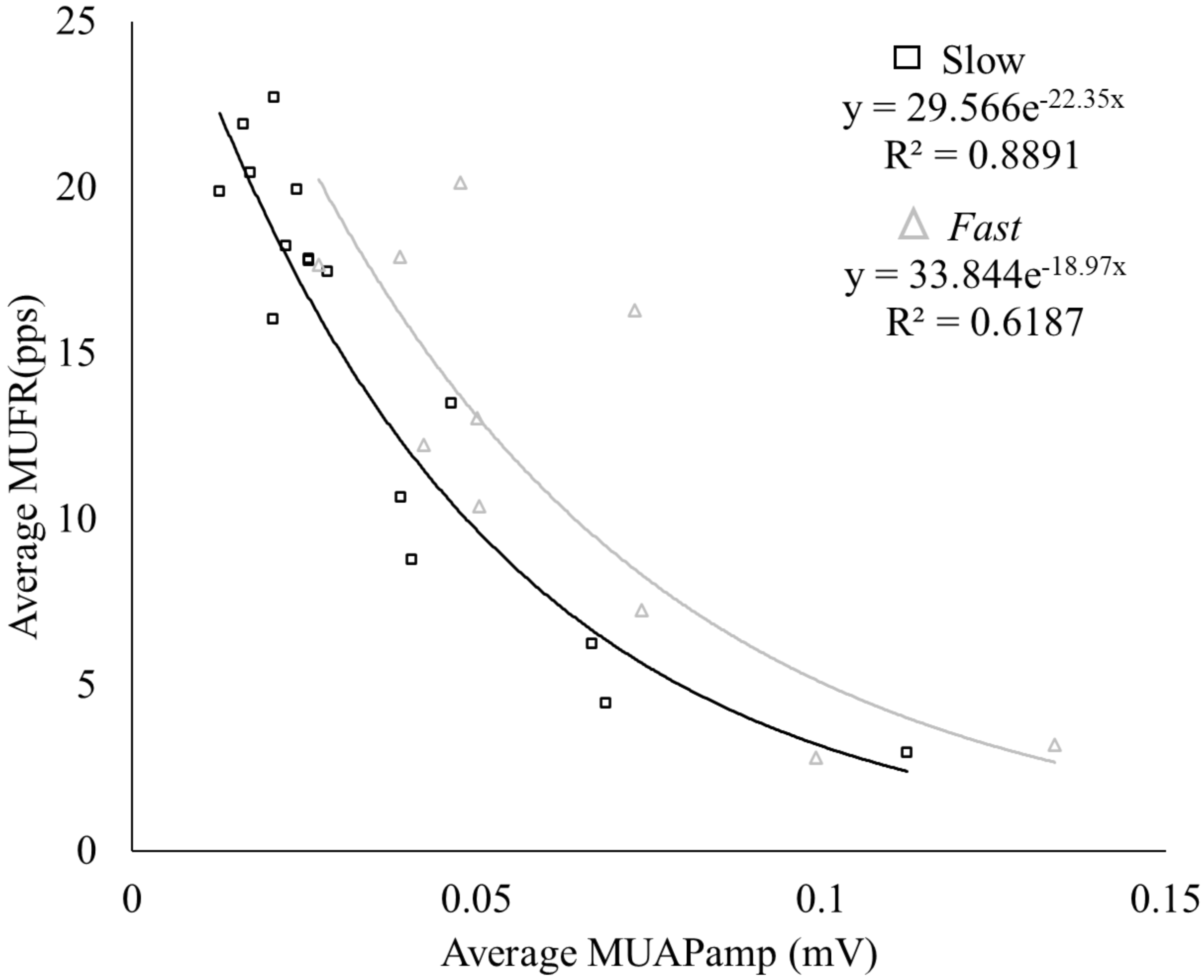
| | Boys | | Men | |
|---|---|---|---|---|
| | ***Slow*** | ***Fast*** | ***Slow*** | ***Fast*** |
| ***Wrist Flexion (FCR)*** | | | | |
| **A-term (pps)** | 54.93±22.88 | 38.71±11.84 | 46.12±15.82 | 46.06±12.84 |
| **B-term (pps/mV)†** | -11.70±5.11 | -8.40±4.44 | -7.85±4.88 | -7.54±4.19 |
| ***Knee Extension (VL)*** | | | | |
| **A-term (pps) †** | 31.65±9.04 | 27.41±4.87 | 40.00±13.65 | 31.59±8.61 |

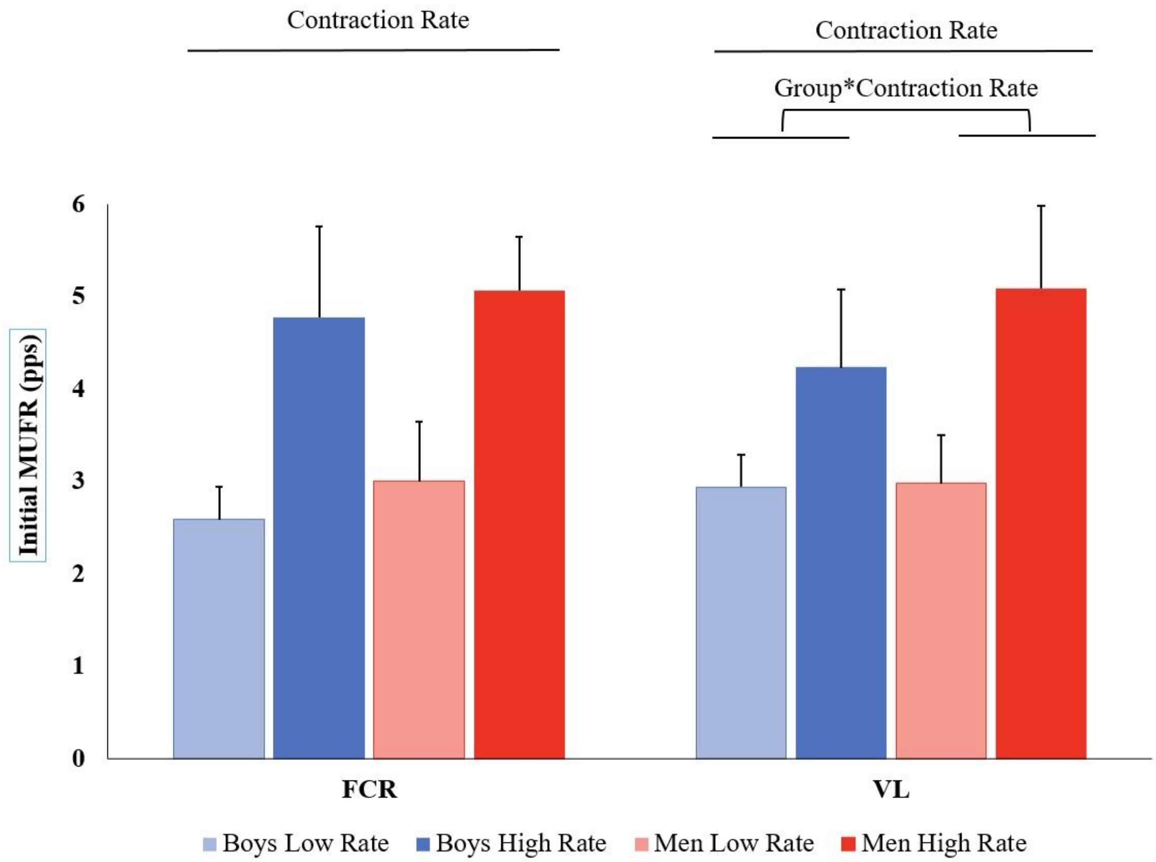
| | | | | |
|---|---|---|---|---|
| **B-term (pps/mV)** *† | -21.14±7.88 | -15.20±7.42 | -14.97±6.7 | -10.13±5.47 |

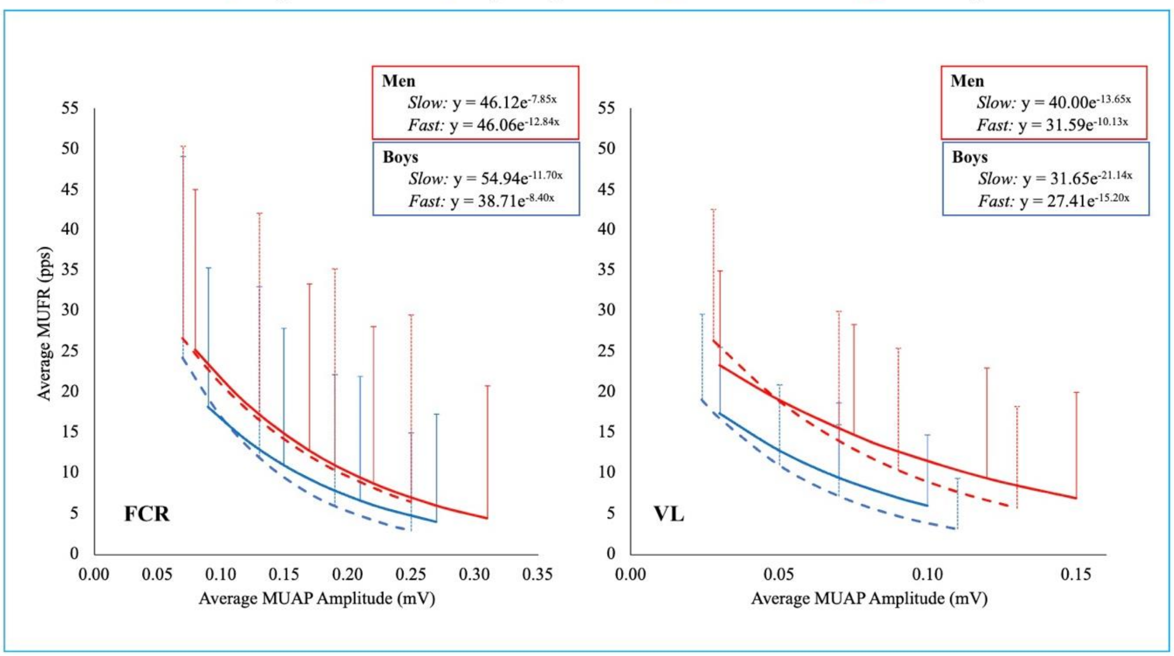
*Significantly different between boys and men (Group effect)
†Significantly different between slow and fast contractions (Rate effect)




Slow
y = 29.566e-22.35x
R² = 0.8891
Fast
y = 33.844e-18.97x
R² = 0.6187
Average MUFR(pps)
Average MUAPamp (mV)
0
5
10
15
20
25
0
0.05
0.1
0.15


Contraction Rate
Contraction Rate
Group*Contraction Rate
Initial MUFR (pps)
0
1
2
3
4
5
6
FCR
VL
Boys Low Rate
Boys High Rate
Men Low Rate
Men High Rate


Men
Slow: $y = 46.12e^{-7.85x}$
Fast: $y = 46.06e^{-12.84x}$
Boys
Slow: $y = 54.94e^{-11.70x}$
Fast: $y = 38.71e^{-8.40x}$
Average MUFR (pps)
FCR
Average MUAP Amplitude (mV)
Men
Slow: $y = 40.00e^{-13.65x}$
Fast: $y = 31.59e^{-10.13x}$
Boys
Slow: $y = 31.65e^{-21.14x}$
Fast: $y = 27.41e^{-15.20x}$
VL
Average MUAP Amplitude (mV)