

1 Post-activation potentiation and potentiated motor unit firing patterns in boys and men

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21 Abstract

22 Background: Post-activation potentiation (PAP) describes the enhancement of twitch
23 torque following a conditioning contraction (CC) in skeletal muscle. In adults, PAP may be
24 related to muscle fibre composition and is accompanied by a decrease in motor unit (MU) firing
25 rates (MUFs). Muscle fibre composition and/or activation is different between children and
26 adults. This study examined PAP and MU firing patterns of the potentiated knee extensors in
27 boys and men. Methods: Twenty-three boys (10.5±1.3 years) and 20 men (23.1±3.3 years)
28 completed familiarization and experimental sessions. Maximal isometric evoked-twitch torque
29 and MU firing patterns during submaximal contractions (20% and 70% maximal voluntary
30 isometric contraction, MVIC) were recorded before and after a CC (5s MVIC). PAP was
31 calculated as the percent-increase in evoked-twitch torque after the CC. MU firing patterns were
32 examined during submaximal contractions before and after the CC using Trigno Galileo surface
33 electrodes (Delsys Inc) and decomposition algorithms (NeuroMap, Delsys Inc). MU action
34 potential amplitudes (MUAPamp) and MUFs were calculated for each MU and exponential
35 MUF-MUAPamp relationships were calculated for each participant and trial. Results: PAP was
36 higher in men than in boys (98.3±37.1% vs. 68.8±18.3%, respectively; $p=0.002$). Following
37 potentiation, the rate of decay of the MUF-MUAPamp relationship decreased in both
38 contractions, with a greater decrease among boys during the high-intensity contractions.
39 Conclusion: Lower PAP in the boys did not coincide with smaller changes in potentiated MU
40 firing patterns, as boys had greater reductions in MUFs with potentiation compared with men
41 in high-intensity contractions.

42

43 **Key Words**

44 Adults, Children, EMG decomposition, Maturation, Muscle activation, Skeletal muscle

45 **Abbreviations**

- 46 • CC = Conditioning contraction
- 47 • EMG = Electromyography
- 48 • MU = Motor unit
- 49 • MUAPamp = Motor unit action potential amplitude
- 50 • MUFR = Motor unit firing rate
- 51 • MVIC = Maximal voluntary isometric contraction
- 52 • PAP = Post-activation potentiation
- 53 • PHV = Peak height velocity
- 54 • RMS = Root mean squares
- 55 • RTD_{peak} = Peak rate of torque development
- 56 • sEMG = Surface electromyography

57

58 **Background**

59 During intense exercise, children differ from adults in physiology and performance.
60 Children have better fatigue resistance during high-intensity contractions and faster recovery
61 following high-intensity exercise (Hebestreit et al. 1993; Hatzikotoulas et al. 2014; Ratel et al.
62 2015a; Bontemps et al. 2019; Piponnier et al. 2019). Children's maximal muscle force and
63 anaerobic power are also lower than adults', even after correcting for muscle size (Kanehisa et
64 al. 1995; Armstrong et al. 2001; Falk et al. 2009). These differences may be the result of lower
65 type-II muscle fibre composition in children compared with adults (Lexell et al. 1992;
66 Esbjörnsson et al. 2021), though the specific tension of a muscle, relative to its cross-sectional
67 area, appears to be less affected by its composition (Bottinelli and Reggiani 2000). Another
68 explanation for these differences could be children's suggested lower activation of higher-
69 threshold (presumably type-II) motor units (MUs) compared to adults (Dotan et al. 2012). This
70 notion is supported by indirect evidence demonstrating a later accelerated-rise in surface
71 electromyographic (sEMG) amplitude during progressive exercise (known as the EMG
72 threshold) (Pitt et al. 2015; Long et al. 2017; Woods et al. 2019, 2020) in children, and is in line
73 with their lower maximal volitional muscle activation (Woods et al. 2022). Nevertheless,
74 previous reports of discrete MU activation patterns (using sEMG decomposition) of the knee
75 extensors in boys and men are limited and conflicting. Chalchat et al. (2019) reported no
76 difference in volitional activation and suggested no differences in MU activation patterns
77 between boys and men during contractions of various intensities. On the other hand, Parra et al.
78 (2020) reported lower MU firing rates (MUFs) in boys compared with men during low and
79 moderate intensity contractions. The authors suggested that such low MUFs may be due to
80 boys' lower excitation of the MU pool.

81 Post-activation potentiation (PAP) describes the enhancement of evoked-twitch torque
82 that occurs after a voluntary conditioning contraction (CC) in skeletal muscle. In adults, PAP
83 may occur to a greater extent in muscles with a higher percentage of type-II fibres (Hamada et al.
84 2000b). Since children may be less likely to activate, and subsequently potentiate these type-II
85 fibres during a voluntary CC, it would be expected that children would exhibit lower PAP than
86 adults. However, the current literature on child-adult differences in PAP is limited, inconsistent,
87 and difficult to interpret. The few studies that have attempted to address this knowledge gap have
88 done so in a muscle model that is primarily composed of type-I muscle fibres (i.e., the plantar
89 flexors (Pääsuke et al. 2000), have used relatively small sample sizes (Belanger and McComas
90 1989; Ratel et al. 2015a), or have compared children to adolescents rather than adults (Belanger
91 and McComas 1989). Thus, it is still unknown whether children are characterized by lower PAP
92 than adults.

93 In adults, the augmented contractility from PAP is offset through changes in MU firing
94 patterns. Specifically, PAP can induce MUFRR reductions (Klein et al. 2001; Inglis et al. 2011;
95 Miller et al. 2017; Zero et al. 2022). Among adults, individuals with greater potentiation-related
96 changes in MUFRRs during contractions at 50% of maximal voluntary isometric contraction
97 (MVIC) force of the first dorsal interosseous muscle are more likely to have greater twitch
98 torque potentiation (Miller et al. 2017). Such changes in MU firing patterns in the potentiated
99 state have not been examined in children. Therefore, the first purpose of this study was to
100 compare PAP of the knee extensors, a mixed-fibre composition muscle, between boys and men.
101 Secondly, we aimed to address the gap in the literature regarding the effect of potentiation on
102 MU firing pattern in children. Therefore, we aimed to examine whether possible child-adult
103 (specifically boy-man) differences in PAP coincide with differences in potentiated MUFRRs,

104 during both low- and high-intensity submaximal contractions. Since children may have lower
105 type-II fibre composition and potentially lower ability to activate their high-threshold MUs, it
106 was hypothesized that boys would display lower PAP than men, and a lower reduction in
107 MUFrs during volitional potentiated submaximal contractions.

108

109 **Methods**

110 *Participants*

111 In line with our first objective, an *a priori* power analysis of PAP following a 5s maximal
112 CC was completed for the pilot data of 4 boys (PAP=52.8±10.1%) and 4 men
113 (PAP=86.0±26.2%) to determine the desired sample size for the present study. Using an α error
114 probability of 0.05 and a power of 0.80 (GPower 3.1), this analysis indicated that 7 participants
115 would be needed in each group for the comparison of PAP. We did not have previous data of
116 MU patterns during PAP. However, based on a previous study in our lab (not published), we
117 expected large inter-individual variance in MU firing pattern in both boys and men. Therefore,
118 we estimated that more participants in each group would be needed for the comparison of MU
119 firing pattern and aimed to include 20 participants in each group.

120 In total, twenty-nine boys and 24 men volunteered to participate in this study.

121 Participants were healthy and recreationally active. Four boys and 2 men discontinued their
122 participation after familiarization and were therefore excluded from analysis. Further, the
123 electromyograph (EMG) files of an additional 2 boys and 2 men had unrectifiable technical
124 issues, which also excluded them from analysis. Consequently, data from 23 boys and 20 men
125 were analyzed. The basic participant characteristics are shown in Table 1.

126 Of the 23 boys included, the self-assessed pubertal stage (Tanner 1962) ranged from 1 to
 127 3. While the boys were smaller (height, mass) than the men, there was no difference between
 128 groups in body composition or in subcutaneous fat thickness at the surface EMG (sEMG) sensor
 129 placement site (see experimental setup for location). The boys habitually participated in
 130 significantly more physical activity than the men (Godin and Shephard 1985). Many of the boys
 131 participated in competitive sports (e.g., lacrosse, hockey, basketball, soccer etc.), and many of
 132 the men had participated in competitive sports in the past. At the time of testing, none of the men
 133 were still competing in their respective sports. However, most were participating in recreational,
 134 unstructured resistance training. Prior to participating in the study, written and verbal
 135 consent/assent were obtained from the participants and their parents (for children only). The
 136 study received clearance by the Brock University Research Ethics Board (file #21-003).

	Boys	Men
n	23	20
Age (years)**	10.5±1.3	23.1±3.3
Years from PHV (years)	-2.7±1.1	N/A
Pubertal stage (1,2,3,4,5)#	9,8,5,0,0	N/A
Height (cm)**	146.3±9.4	180.4±7.4
Mass (kg)**	37.8±8.4	79.7±10.8
Body fat percentage (%)	13.6±5.8	17.4±6.6
Vastus lateralis subcutaneous fat depth (mm)	5.4±2.0	4.6±2.0
Physical activity (score)*^	84.9±29.9	55.3±24.8

Data shown as mean ± standard deviation. PHV = peak height velocity.

Differences between groups: $p < 0.05$ are indicated by: *

Differences between groups: $p < 0.001$ are indicated by: **

Number of boys in each stage. One boy did not feel comfortable completing the questionnaire

^ Physical activity assessed using the Godin-Shephard leisure-time exercise questionnaire, appendix B.

137

138 *Table 1. Participants' characteristics.*

139

140 *Experimental procedure*

141 Participants made 2 visits to the Applied Physiology Laboratory at Brock University,
142 separated by a minimum of 24 hours. The first visit involved anthropometric measurements and
143 familiarization with the muscle contraction procedures that were performed in visit 2. The
144 second visit served as the experimental session (see Experimental protocol below). Participants
145 were asked to refrain from strenuous exercise, and caffeine consumption for 24 and 12 hours,
146 respectively, prior to all testing sessions.

147 *Anthropometric measurements*

148 Anthropometric measures included standing and seated (boys only) height to the nearest
149 0.1 cm (Ellard Instrumentation Ltd. Stadiometer, Monroe, WA, USA), and body mass and body
150 fat percentage to the nearest 0.1 kg and 0.1%, respectively, by bioelectrical impedance analysis
151 (InBody 520, Biospace CO., Ltd., S. Korea). Years to age of peak height velocity (PHV) was
152 estimated for the boys according to the equations described by (Mirwald et al. 2002). Participants
153 were asked to refrain from eating or drinking 4 hours before their first laboratory visit, they were
154 then hydrated upon arrival and asked to void their bladder prior to measurements.

155 Subcutaneous fat tissue depth at the electrode placement site on the vastus lateralis (see
156 Instrumentation and experimental setup for location) and knee extensor muscle depth were
157 measured using a real-time B-mode ultrasound system (Vivid-q; General Electric Healthcare,
158 Chicago, IL, USA). Sonograms were taken with the participant in a relaxed supine position, with
159 the probe held perpendicular to the direction of the muscle fibres. Vastus lateralis subcutaneous
160 fat depth was determined as the distance from the dermis to the superficial aspect of the muscle
161 fascia. Quadriceps muscle depth was determined as the distance from the superficial muscle fascia

162 to the femur at half the distance between the anterior superior iliac spine and the superior border
163 of the patella. Fat and muscle depth were both measured 3 times to the nearest 0.1 mm, and the
164 median values were used for analysis.

165 *Instrumentation and experimental Setup*

166 All contractions were performed isometrically on a Biodex System 3 Dynamometer
167 (Biodex Medical Systems, Shirley, NY, USA). Participants were seated with their knees and hips
168 positioned at 90° and 70° of flexion, respectively. A pad was positioned at the distal portion of
169 the right leg, just above the malleoli. Participants were securely strapped to the dynamometer at
170 the pad, as well as over their hips and across their chest, to assist with isolating the knee
171 extensors (reducing upper body movement). Real time torque signals were shown on a monitor
172 in front of the participants.

173 A Trigno Galileo sEMG sensor (Delsys Inc., Boston, MA, USA) was used for capturing
174 the myoelectric data. The sensor was placed according to the guidelines of the Surface
175 Electromyography for Non-Invasive Assessment of Muscles (SENIAM; (Hermens et al. 1999),
176 for the vastus lateralis. Specifically, the sensor was placed 2/3 (66.67%) the distance between the
177 anterior superior iliac spine and the superior border of the patella. The on-board stabilizing
178 reference for the sensor was placed parallel to the electrode, approximately 5-10 cm away on the
179 anterior aspect of the thigh. Before placement of the electrode, the skin was prepared by shaving
180 any hairs, removing dead skin with Transpore medical tape, and cleaning the surface with
181 rubbing alcohol. The sensor was secured to the skin using double-sided tape and Transpore tape
182 over the casing to minimize movement artifacts during the test. Both the torque and the sEMG
183 signals were captured at 2222 Hz and digitized using a 16-bit A/D converter. The torque signal
184 was filtered at DC-100 Hz and the sEMG signal was band-pass filtered at 20-450 Hz. Both

185 signals were transmitted via bluetooth to a base station and were recorded using EMGworks
186 Acquisition software (Delsys Inc., Boston, MA, USA).

187 Evoked twitches were stimulated using custom-made electrode pads (single use), placed
188 over the quadriceps, which indirectly stimulate muscle fibres. The pads were made of aluminum
189 foil wrapped in paper towel with a thin layer of conductive gel on the side of the pad in contact
190 with the skin (Signa Gel, Parker Laboratories Inc., Fairfield, NJ, USA), and applied transversely
191 to the thigh with medical Transpore tape. Palpation and visual assessment were used to
192 determine the sites of the electrodes. One electrode was placed on the distal thigh, and the other
193 electrode was placed just distal to the crease of the hip. Electrodes were custom-made to cover
194 the width of the quadriceps muscle group at the proximal and distal sites for each participant.
195 The size of the electrodes for children was approximately 6-10 cm X 8-14 cm. The size of the
196 adult electrodes was approximately 8-12 cm X 14-20 cm. A ground electrode was placed over
197 the spinous process located on the seventh cervical vertebrae. A Digitimer stimulator, model
198 DS7AH (Digitimer Ltd., Welwyn Garden City, UK), was used to deliver electrical stimulation
199 aimed at eliciting maximal muscular twitches. The Digitimer stimulator delivered a single
200 square-wave pulse, with a maximal voltage of 400V and duration of 0.2ms, as has been used in
201 previous work with a similar experimental setup (Dalton et al. 2015).

202 ***Experimental protocols***

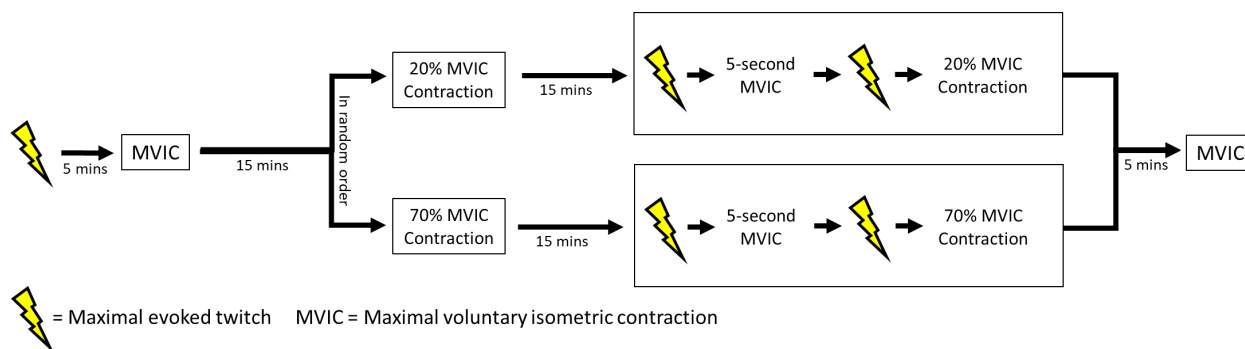
203 A schematic of the experimental protocol can be found in Figure 1. Once participants
204 were secured to the dynamometer, the stimulation intensity required to evoke a maximal twitch
205 was determined. This was achieved by performing a series of stimulations with progressively
206 increased current. The final current reached, as determined by no further increase in twitch
207 torque, was then increased by 10% to account for variability under all possible test conditions

208 (Dalton et al. 2010). This supramaximal intensity was used for all evoked twitches throughout
209 the experimental session. Approximately 30s of rest was provided between stimulations. The
210 maximal current ranged from 120mA-250mA in the boys, and 250mA-400mA in the men.

211 Participants were then guided through a warm-up consisting of 3-5 isometric knee
212 extension contractions, beginning at 50% of perceived maximal effort and progressively
213 increased to 85-90% of the participant's perceived maximal effort. The warm-up was followed
214 by the determination of knee extension MVIC torque. Participants were asked to "kick as hard as
215 possible" over a 3-5s interval. Visual feedback of the torque produced was provided to the
216 participant in real-time. Each participant completed a series of 3 maximal contractions with
217 ≥ 120 s of rest between trials. The highest torque value of the 3 MVIC trials was used for the
218 determination of submaximal loads.

219 After a 15-minute rest, to ensure that potentiation from the MVICs had dissipated
220 (Baudry and Duchateau 2004), participants performed a series of submaximal and maximal
221 contractions (interspaced with 15-minute rest intervals), accompanied by supramaximal evoked
222 twitches for the determination of PAP (see Figure 1). The contractions were performed in the
223 following order: submaximal contraction (20 or 70%MVIC), 15-minute rest, supramaximal
224 evoked twitch, 5s maximal CC, supramaximal evoked twitch, submaximal contraction (20 or
225 70%MVIC). The unpotentiated evoked twitches were performed in a 3s window immediately
226 before the onset of the CC, and the potentiated evoked twitches were performed immediately
227 following relaxation (i.e., within 1s) from the CC. The series of contractions was then repeated
228 after 15 minutes of rest using the other submaximal contraction intensity (i.e., the submaximal
229 intensity not used during the first series of contractions). At the end of the experimental session,
230 a final MVIC was performed to assess cumulated fatigue.

231



232

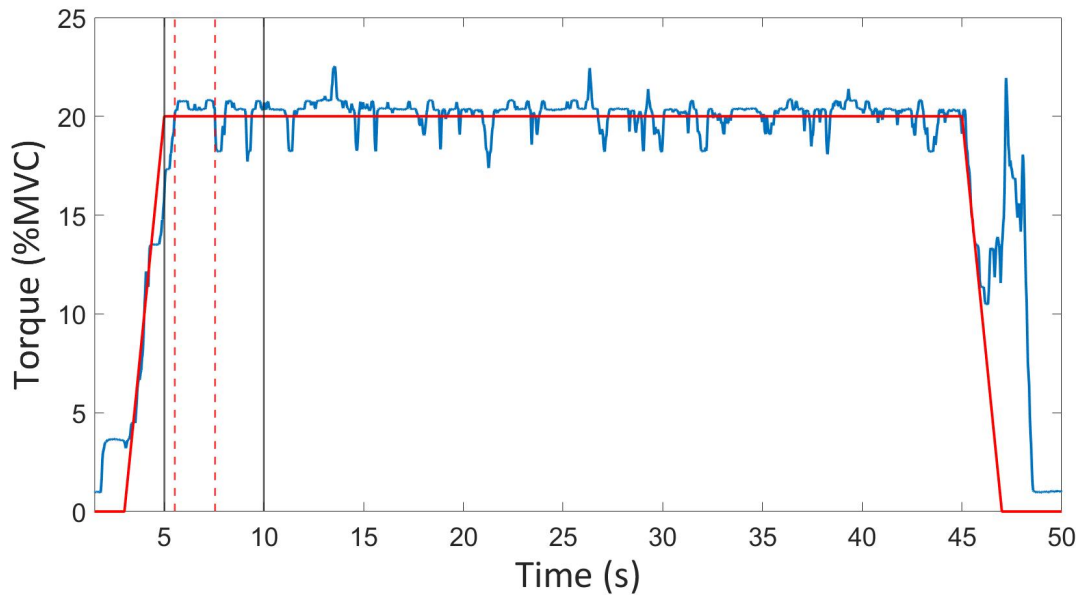
233 *Figure 1: Schematic representation of the experimental session.*

234

235 The submaximal contractions were performed at a low (20%MVIC) and high
 236 (70%MVIC) intensity for the assessment of MU activation in the unpotentiated and potentiated
 237 states. To perform the submaximal contractions, participants followed real-time torque traces on
 238 a monitor in front of them that ramped up at 10%MVIC/s to the desired relative intensity (Figure
 239 2). For the low-intensity contractions, participants ramped to the target torque (2s) and then
 240 maintained torque at 20%MVIC for 40s. For the high-intensity contractions, participants ramped
 241 to the target torque (7s) and then maintained torque at 70%MVIC for 7s, after which the torque
 242 trace was maintained at 40%MVIC for an additional 15s. For both intensities, only the first 5s of
 243 the torque plateau at the desired intensity was used for MU analysis to exclude from the analysis
 244 any possible effects of fatigue and potentiation in the later part of the submaximal contractions.
 245 The remaining 35s of the low-intensity contractions and 17s of the high-intensity contractions
 246 were used to improve the yield and accuracy of the MUs detected during signal decomposition
 247 but were not used for analysis (see Data reduction and analysis, below). The windows in which

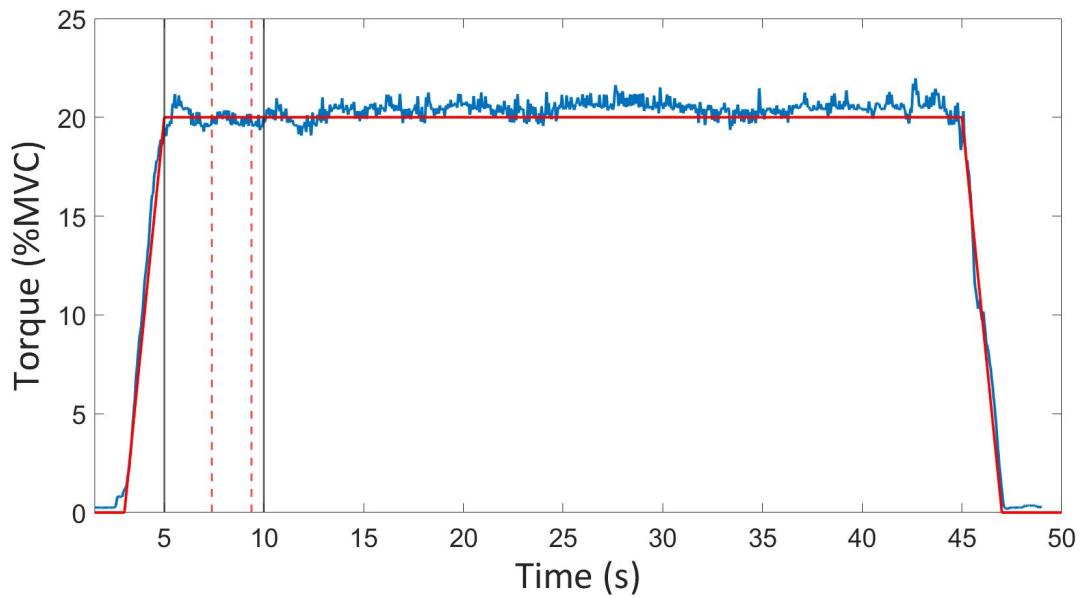
248 data were analyzed are shown in Figure 2. The order of the submaximal contraction intensities
249 was counterbalanced to ensure there was no order effect.

250 **A.**



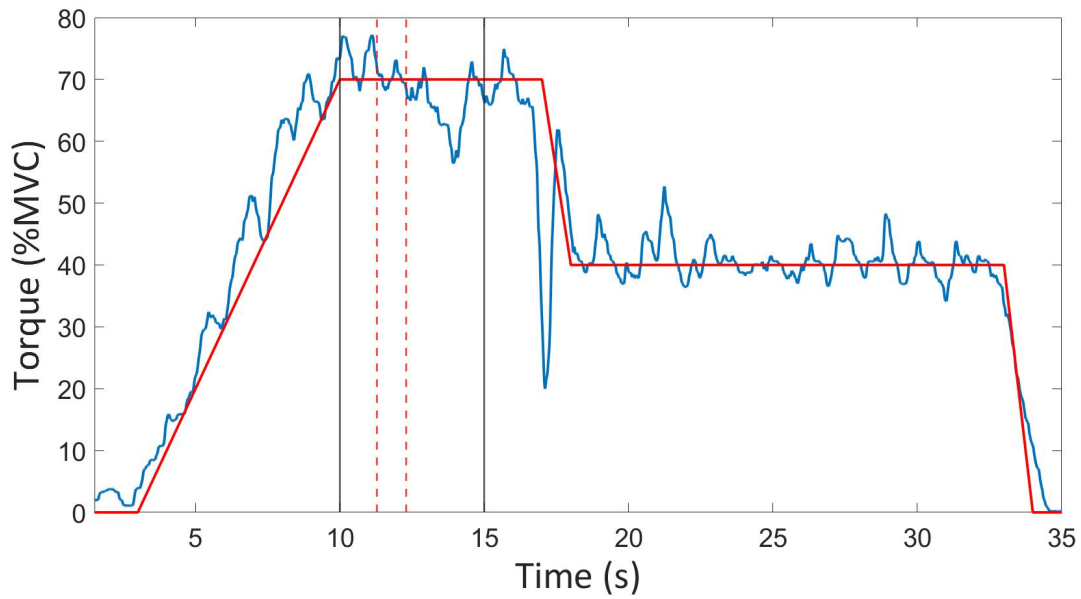
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252 **B.**



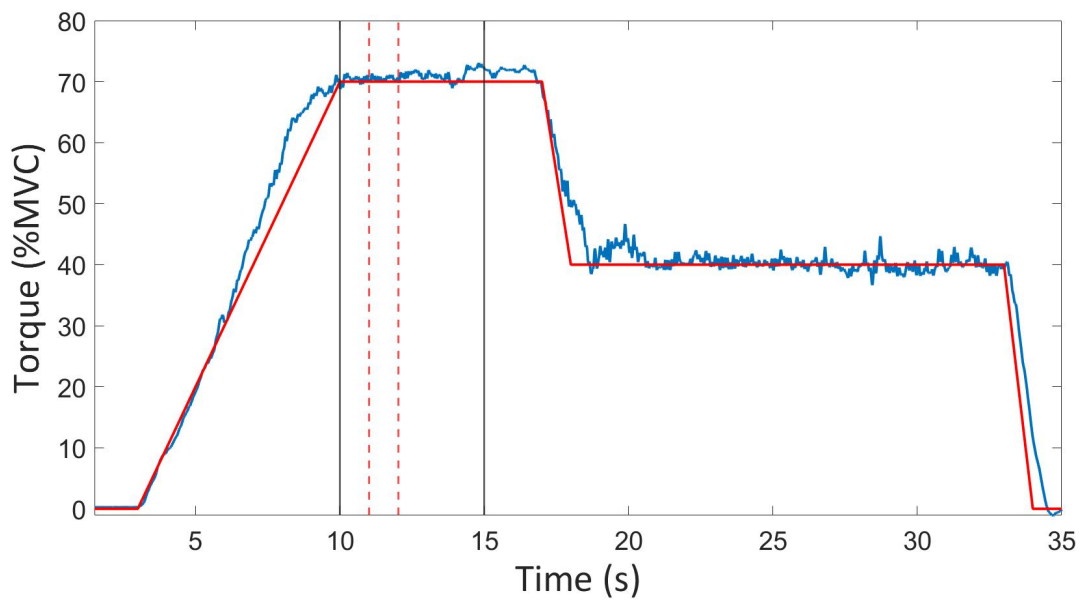
253

254 C.



255

256 D.



257

258 *Figure 2: Example of a torque trace for one child (a & c) and one adult (b & d) participant*259 *during a low-intensity (a & b) and high-intensity (c & d) contraction. The grey shaded areas*

260 *represent the 5s windows at the beginning of the torque trace plateaus in which motor units*
261 *(MUs) could be extracted. The red shaded areas represent the 2s and 1s windows in which*
262 *torque was the most stable in the low- and high-intensity contractions, respectively. The*
263 *remaining trace to the right of the grey areas was only used to maximize MU yield from the*
264 *decomposition algorithms. The MU firing patterns were not analyzed outside of the grey shaded*
265 *area. In the high-intensity contraction (c & d), the torque trace dropped to 40%MVC because*
266 *70% could not be held for a sufficient duration to maximize MU yield.*

267

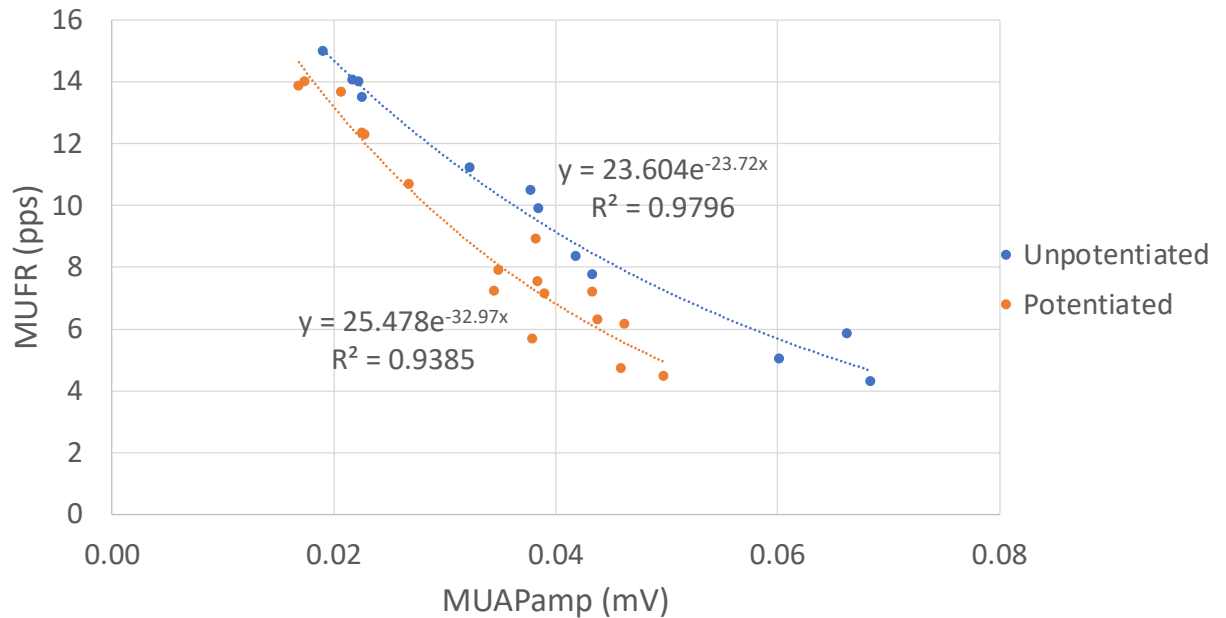
268 ***Data reduction and analysis***

269 Data reduction for all torque and global sEMG outcomes were performed using custom
270 scripts in MATLAB (v.2020a; Mathworks, Natick, MA, USA). The MVIC torque of each
271 participant was determined as the greatest 0.5s of torque produced. The root mean square (RMS)
272 of the sEMG signal for each participant's MVIC was also determined during this 0.5s interval.
273 The twitch torque signals were low-pass filtered with a 20 Hz cutoff, zero-phase, fourth-order
274 Butterworth filter. Maximal isometric twitch torque and peak rate of torque development
275 (RTDpeak) were compared before and immediately after the 5s CCs. RTDpeak for each twitch
276 was calculated as the peak of the first derivative for the torque signal of each twitch. PAP for
277 each outcome (torque and RTDpeak) were determined as the percent increase after a CC relative
278 to the unpotentiated state. The greatest twitch torque and RTDpeak PAP values for each
279 participant were used for statistical analyses.

280 Despite extensive familiarization with task procedures, some participants still had
281 difficulty maintaining a stable target torque. This was especially apparent among some of the

282 boys (Figure 2). Therefore, prior to decomposing the sEMG signals, the most stable 2s period
283 within the first 5s of the torque trace plateau of the low-intensity contractions and the most stable
284 1s period within the first 5s of the torque trace plateau of the high-intensity (70%MVIC)
285 contractions were determined. These periods were determined based on the lowest standard
286 deviation of the torque signal and were used as the intervals from which MUFRs were extracted.
287 Submaximal contractions were excluded from further analysis if the torque was $\geq \pm 2\%$ of the
288 relative intensity for low-intensity contractions (i.e., < 18 or $> 22\%$ MVIC), and $\geq \pm 5\%$ of the
289 relative intensity for high-intensity contractions (i.e., < 65 or $> 75\%$ MVIC). These criteria
290 eliminated the high-intensity contractions of 6 boys from MU analysis.

291 The firings of individual MUs were extracted from the sEMG signals using NeuroMap
292 decomposition software (v1.2.2; Delsys Inc., Boston, MA, USA). This software uses the most
293 updated version of the PDIII algorithm described by De Luca et al. (De Luca et al. 2006). Only
294 MUs with a reported accuracy above 90% were included in the analysis. For each MU, the mean
295 MUFR and mean MUAPamp were extracted. The MUFR-MUAPamp relationship was then
296 plotted for each contraction. As has previously been used, the exponential trend line: $MUFR =$
297 $Ae^{B(MUAPamp)}$, was fit to the MUFR-MUAPamp relationships, where A is the theoretical MUFR
298 of a MU with a MUAPamp of 0V, and B is the decay coefficient of the MUFRs with increments
299 in MUAPamp (Miller et al. 2019a) (see Figure 3 for example).



300

301 *Figure 3. Examples of the motor unit firing rate (MUFR) vs. motor unit action potential*
 302 *amplitude (MUAPamp) relationships for a participant's low-intensity contractions.*

303

304 The MUFR-MUAPamp relationships from a set of contractions (i.e., pre-, and post-CC)
 305 were included for analysis if the following criteria were met: 1) both contractions included ≥ 5
 306 MUs, 2) the recruitment range of both contractions were at least 1/3 of the contraction intensity
 307 (i.e., 6.67% for the low-intensity contractions and 23.33% for the high-intensity contractions),
 308 and 3) the R^2 value of the relationships for both contractions were ≥ 0.4 . The low-intensity
 309 contractions of 12 boys and 6 men, and the high-intensity contractions of 4 boys and 3 men were
 310 excluded from analysis based on these criteria. Therefore, the low-intensity MU firing patterns
 311 from 11 boys and 14 men, and the high-intensity MU firing patterns from 13 boys and 17 men
 312 were included for the final statistical analyses.

313 ***Statistical analysis***

314 All statistical analyses were performed using IBM SPSS software (v.28; SPSS Inc.,
315 Chicago, IL, USA). Independent t-tests were used to assess differences between groups in
316 anthropometric measures, physical activity level, and PAP. The mean A and B terms for each
317 group (boys and men) from the MUFR-MUAPamp relationships, and the volitional and evoked
318 contraction characteristics were each analyzed using 2-way mixed-model ANOVAs. The within-
319 subject (i.e., repeated measures) factor for each ANOVA was state/time of session
320 (unpotentiated/potentiated state or beginning/end of session) and the between-subject factor was
321 age group (boys or men). MU firing patterns in the low- and high-intensity contractions were
322 analyzed separately. Post-hoc tests were done for significant interactions with Bonferroni
323 corrections. The assumptions of normality and homogeneity of variance were confirmed using
324 the Kolmogorov-Smirnov test and Levene Statistic, respectively, as appropriate. Sphericity was
325 confirmed using Mauchly's test, and the Greenhouse-Geisser correction was applied where
326 appropriate. Data are presented as means and standard deviations. For all analyses, statistical
327 significance was set at $p < 0.05$.

328

329 **Results**

330 ***Volitional Contraction Characteristics***

331 A summary of the results for the maximal and submaximal volitional contractions characteristics
332 are described below and can be found in Table 2.

333

	Boys	Men
MVIC (Nm)**†¥		
Start of session	87.1±32.8	272.1±44.0
End of session	88.9±33.3	256.1±42.1
MVIC EMG RMS (mV)**		
Start of session	0.067±0.027	0.167±0.127
End of session	0.072±0.027	0.160±0.118
CC torque (%MVIC)	96.2±8.3	98.1±4.9
Low-intensity contraction torque (%MVIC)		
Pre-CC	20.4±1.1	20.0±0.4
Post-CC	19.9±0.7	20.1±0.6
High-intensity contraction torque (%MVIC)		
Pre-CC	70.4±2.2	69.8±1.5
Post-CC	69.6±1.8	69.4±1.7

Data shown as mean ± standard deviation. CC = conditioning contraction; MVIC = maximal volitional isometric contraction; RMS = root mean square.

Group effect: $p < 0.001$ is indicated by: **

State/time effects: $p < 0.05$ are indicated by: †

Group-by-time interaction: $p < 0.05$ is indicated by: ¥, reflecting a decrease in MVIC in men but not boys.

334 Table 2. Volitional contractions characteristics.

335

336 Maximal volitional contractions

337 As expected, MVIC torque and sEMG RMS were greater in men compared with boys.

338 MVIC torque was also greater in men after accounting for differences in body mass (boys=

339 2.3±0.5 Nm/kg, men= 3.4±0.6 Nm/kg; $t(41)=-7.49$, $p < .001$, power=1.00), and when quadriceps

340 muscle depth was used as a covariate ($F(1, 42)=29.16$, $p < .001$, power=1.00). There was a

341 significant overall reduction in MVIC torque at the end of the experimental protocol compared to

342 the beginning (time effect: $F(1, 41)=7.77$, $p=.008$, power=.777), with a significant interaction

343 between groups (boys vs. men) and time (beginning vs. end of session) ($F(1, 41)=12.52$, $p=.001$,

344 power=.932), reflecting a reduction in the men's end-of-session MVIC ($p < .001$), but not in the

345 boys ($p=.585$). The decrease in MVIC torque was not accompanied by changes in sEMG RMS,

346 (time effect: $F(1, 41)=.03, p=.872, \text{power}=.053$), with no significant interaction ($F(1, 41)=1.19,$
347 $p=.281, \text{power}=.187$).

348 *Submaximal sustained contractions*

349 Relative knee extensor torque (%MVIC) was not different between groups during the
350 low-intensity sustained contractions in the unpotentiated (pre-CC) and potentiated (post-CC)
351 states, (state effect: $F(1, 23)=.93, p=.334, \text{power}=.153$), with no significant interaction ($F(1,$
352 $23)=1.98, p=.173, \text{power}=.271$). Likewise, relative knee extensor torque was also not different
353 between groups during the high-intensity sustained contractions in the unpotentiated and
354 potentiated states, (state effect: $F(1, 28)=2.59, p=.119, \text{power}=.343$), with no significant
355 interaction ($F(1, 28)=.18, p=.673, \text{power}=.070$).

356 *Twitch Characteristics and Post-Activation Potentiation*

357 A summary of twitch characteristics can be found in Table 3. The unpotentiated and
358 potentiated twitch torques were significantly lower in boys compared with men ($F(1,$
359 $41)=197.00, p<.001, \text{power}=1.00$), with a significant increase with potentiation ($F(1,$
360 $41)=311.65, p<.001, \text{power}=1.00$), and a significant group-by-state interaction ($F(1, 41)=134.90,$
361 $p<.001, \text{power}=1.00$), indicating greater potentiation in the men. Likewise, unpotentiated and
362 potentiated twitch RTD_{peak} were significantly lower in boys compared with men ($F(1,$
363 $41)=219.77, p<.001, \text{power}=1.00$), with a significant increase with potentiation ($F(1,$
364 $41)=351.72, p<.001, \text{power}=1.00$), and a significant group-by-state interaction ($F(1, 41)=146.58,$
365 $p<.001, \text{power}=1.00$), indicating greater potentiation in the men.

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	Boys	Men
Twitch torque (Nm)**††¥¥		
Pre-CC	10.5±4.4	34.5±9.2
Post-CC	17.3±7.5	65.7±14.0
Twitch RTDpeak (Nm/s)**††¥¥		
Pre-CC	202.6±115.6	712.9±167.4
Post-CC	375.9±197.8	1517.2±292.9

Data shown as mean ± standard deviation. CC = conditioning contraction; RTDpeak = peak rate of torque development.

Group effect: $p < 0.001$ is indicated by: **

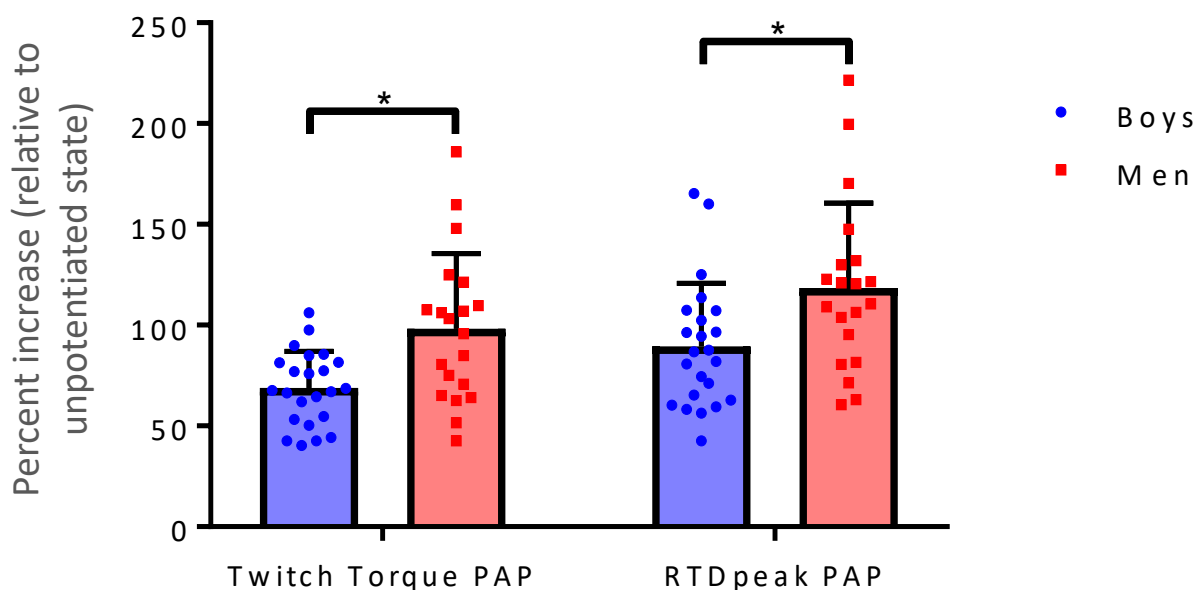
State effect: $p < 0.001$ is indicated by: ††

Group-by-state interaction: $p < 0.001$ is indicated by: ¥¥, reflecting a greater increase in men than in boys.

368 *Table 3. Twitch characteristics.*

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370 The percent increase in twitch torque with potentiation (i.e., twitch torque PAP) was
371 98.3±37.1% and 68.8±18.3% in the men and boys, respectively. The percent increase in
372 RTDpeak with potentiation (i.e., RTDpeak PAP) was 118.4±42.0% and 89.4±31.3% in the men
373 and boys, respectively (Figure 4). Both twitch torque PAP ($t(41)=3.38$, $p=.002$, power=.898),
374 and RTDpeak PAP ($t(41)=2.59$, $p=.013$, power=.694) were significantly lower in the boys
375 compared to the men. There was no significant difference between the first and second
376 potentiated twitch torque in the boys (18.3±7.3 and 17.1±7.4 Nm, respectively), nor in the men
377 (64.4±12.7 and 61.9±13.7 Nm, respectively).



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379 *Figure 4: Post activation potentiation (PAP) in peak twitch peak torque and*
 380 *development in boys and men.*

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383 ***Motor Unit Activation Patterns***

384 The average number of MUs, average MUF_R and MUA_{Pamp}, and minimum and
 385 maximum MUA_{Pamp} and MU recruitment threshold of each contraction, for the boys and men
 386 are shown in Table 4. Overall, more MUs were identified per participant in the men. In the low-
 387 intensity contraction, there was a reduction in average MUF_R with potentiation (state effect: $F(1,$
 388 $23)=5.11, p=.034, \text{power}=.582$), with a greater reduction in men compared with boys (group-by-
 389 state interaction: $F(1, 23)=11.02, p=.003, \text{power}=.889$). In the high-intensity contraction, average
 390 MUF_R was greater in the men than the boys (group effect: $F(1, 28)=11.61, p=.002, \text{power}=.908$)

391 with no effect of potentiation and no group-by-state interaction. For both contractions, the
392 average and maximum MUAPamps were significantly smaller in the boys compared to the men
393 (average group effect for low-intensity contraction: $F(1, 23)=5.52, p=.028, \text{power}=.615$; average
394 group effect for high-intensity contraction: $F(1, 28)=11.61, p=.002, \text{power}=.908$; maximum
395 group effect for low-intensity contraction: $F(1, 23)=5.50, p=.028, \text{power}=.613$; maximum group
396 effect for high-intensity contraction: $F(1, 28)=15.13, p<.001, \text{power}=.964$). The mean minimum
397 MUAPamps were significantly smaller in the boys in the low-intensity contraction only
398 (minimum MUAPamp group effect for low-intensity contraction: $F(1, 23)=4.41, p=.047,$
399 $\text{power}=.520$; minimum MUAPamp group effect for high-intensity contraction: $F(1, 28)=1.89,$
400 $p=.180, \text{power}=.265$). There were no state effects and no group-by-state interactions for average,
401 minimum, or maximum MUAPamps. Minimum recruitment threshold was significantly lower in
402 the potentiated state in the low- but not the high-intensity contraction (state effect for low-
403 intensity contraction: $F(1, 23)=14.04, p=.001, \text{power}=.948$; state effect for high-intensity
404 contraction: $F(1, 28)=1.84, p=.185, \text{power}=.259$). Conversely, maximum recruitment threshold
405 was significantly higher in the potentiated state in the high- but not the low-intensity contraction
406 (state effect for low-intensity contraction: $F(1, 23)=.55, p=.465, \text{power}=.110$; state effect for
407 high-intensity contraction: $F(1, 28)=10.09, p=.004, \text{power}=.865$). There were no group effects, or
408 group-by-state interactions for minimum or maximum recruitment thresholds at either
409 contraction intensities.

410 A summary of the mean MU firing patterns, along with the group effects (boys vs. men),
411 state effects (pre-CC vs. post-CC), and interactions (between groups and state) for the MUFR-
412 MUAPamp relationships are displayed in Table 5. At both contraction intensities, the rate of
413 decay of MUFR (B term) decreased (was more negative) in the potentiated state. In the low-

414 intensity contractions, the B term was not different between groups ($p=.056$) and there were no
415 group-by-state interactions in the decrease in B term ($p=.156$). In high-intensity contractions, the
416 rate of decay (B term) was greater (more negative) in the boys and decreased overall with
417 potentiation. This decrease was significant in the boys ($p<.001$), but not the men ($p=.379$). There
418 were no group differences in the A term in either contraction. In the high-intensity contraction,
419 there was an overall increase in the A term with potentiation, with no significant difference
420 between groups. For visual purposes, the mean regressions for the MUFR-MUAPamp
421 relationships (i.e., regressions made using the mean A and B terms), are also displayed in Figure
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	Boys		Men	
	Pre-CC	Post-CC	Pre-CC	Post-CC
Number of MUs				
20%MVIC	14.4±3.4	11.5±4.0	14.05±4.9	14.9±4.2
70%MVIC*	13.2±4.2	12.4±4.0	15.9±5.9	17.7±6.4
Average MUFR (pps)				
20%MVIC†¥	8.3±1.3	8.7±1.3	10.4±2.9	8.4±1.6
70%MVIC*	17.5±2.1	16.3±2.3	19.5±2.0	19.2±2.4
Average MUAPamp (mV)				
20%MVIC*	0.037±0.013	0.035±0.012	0.059±0.029	0.056±0.027
70%MVIC*	0.081±0.026	0.086±0.027	0.154±0.080	0.152±0.064
Minimum MUAPamp (mV)				
20%MVIC*	0.019±0.009	0.019±0.005	0.025±0.011	0.028±0.013
70%MVIC	0.034±0.013	0.039±0.014	0.046±0.032	0.044±0.019
Maximum MUAPamp (mV)				
20%MVIC*	0.060±0.023	0.053±0.021	0.101±0.060	0.094±0.051
70%MVIC**	0.155±0.058	0.167±0.074	0.339±0.190	0.335±0.128
Minimum recruitment threshold (%MVIC)				
20%MVIC†	2.4±2.2	0.5±1.2	2.4±1.5	1.6±1.5
70%MVIC	7.5±6.7	5.1±4.6	4.9±5.7	3.5±4.0
Maximum recruitment threshold (%MVIC)				
20%MVIC	13.9±3.6	14.4±4.2	15.5±3.7	16.3±3.3
70%MVIC†	45.8±8.0	52.8±13.4	48.5±8.8	56.1±10.4

Data shown as mean ± standard deviation. CC = conditioning contraction; MU = motor unit; MUFR = motor unit firing rate; MVIC = maximal volitional isometric contraction; RTD_{peak} = peak rate of torque development.

Group effect: $p < 0.05$ is indicated by: *

Group effect: $p < 0.001$ is indicated by: **

State effect: $p < 0.05$ is indicated by: †

Group-by-state interaction: $p < 0.05$ is indicated by: ¥, reflecting a decrease in men but not in boys

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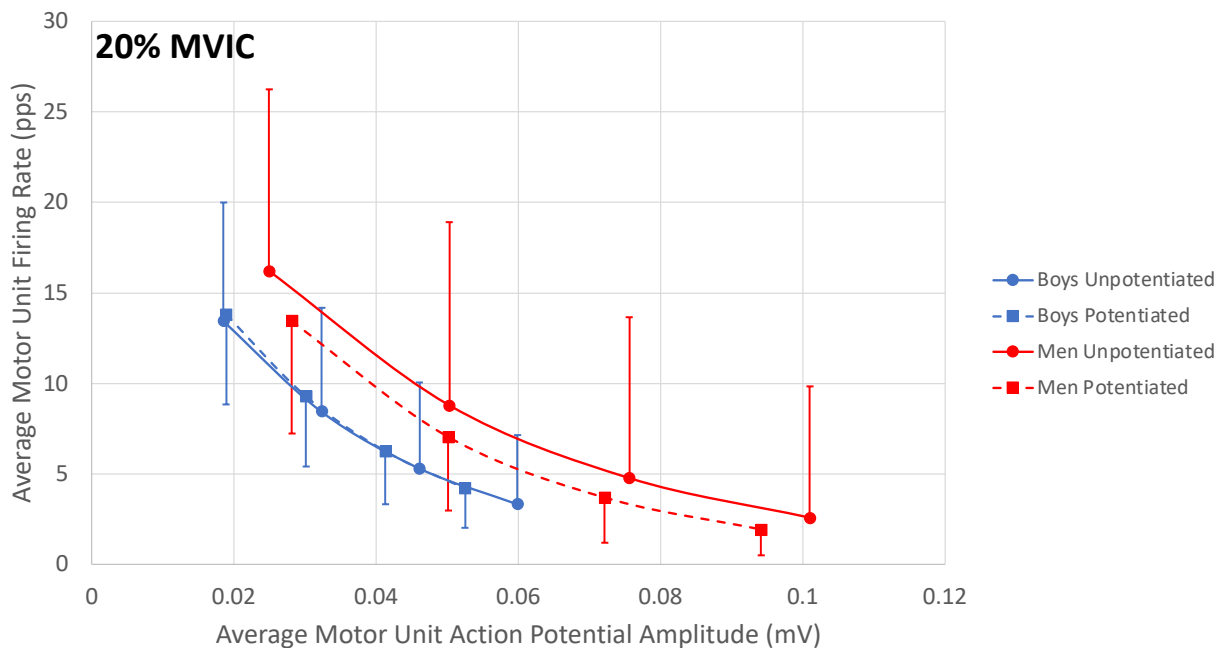
MUFR vs. MUAPamp	Boys		Men		Group effect	State effect	Interaction
	Pre-CC	Post-CC	Pre-CC	Post-CC			
20%MVIC: A term (pps)	25.12±6.64	26.92±6.80	29.59±6.57	30.69±8.27	$F(1, 23)=2.48$; $p=0.129$	$F(1, 23)=1.45$; $p=0.241$	$F(1, 23)=0.08$; $p=0.775$
20%MVIC: B term (pps/mV)	-33.69±8.74	-35.34±8.22	-24.13±11.25	-29.34±10.91	$F(1, 23)=4.07$; $p=0.056$	$F(1, 23)=8.03$; $p=0.009$	$F(1, 23)=2.15$; $p=0.156$
70%MVIC: A term (pps)	32.11±3.94	37.21±7.05	35.35±3.45	37.28±4.27	$F(1, 28)=1.57$; $p=0.220$	$F(1, 28)=9.35$; $p=0.005$	$F(1, 28)=1.91$; $p=0.178$
70%MVIC: B term (pps/mV)	-8.63±3.34	-11.29±4.62	-5.28±2.45	-5.78±3.06	$F(1, 28)=14.40$; $p<0.001$	$F(1, 28)=13.75$; $p<0.001$	$F(1, 28)=6.42$; $p=0.017$

Data shown as mean ± standard deviation. CC = conditioning contraction; MUAPamp = motor unit action potential amplitude; MUFR = motor unit firing rate; MVIC = maximal volitional isometric contraction. Statistically significant ($p<.05$) findings are in bold.

436 Table 5. Motor unit activation patterns

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438 A.

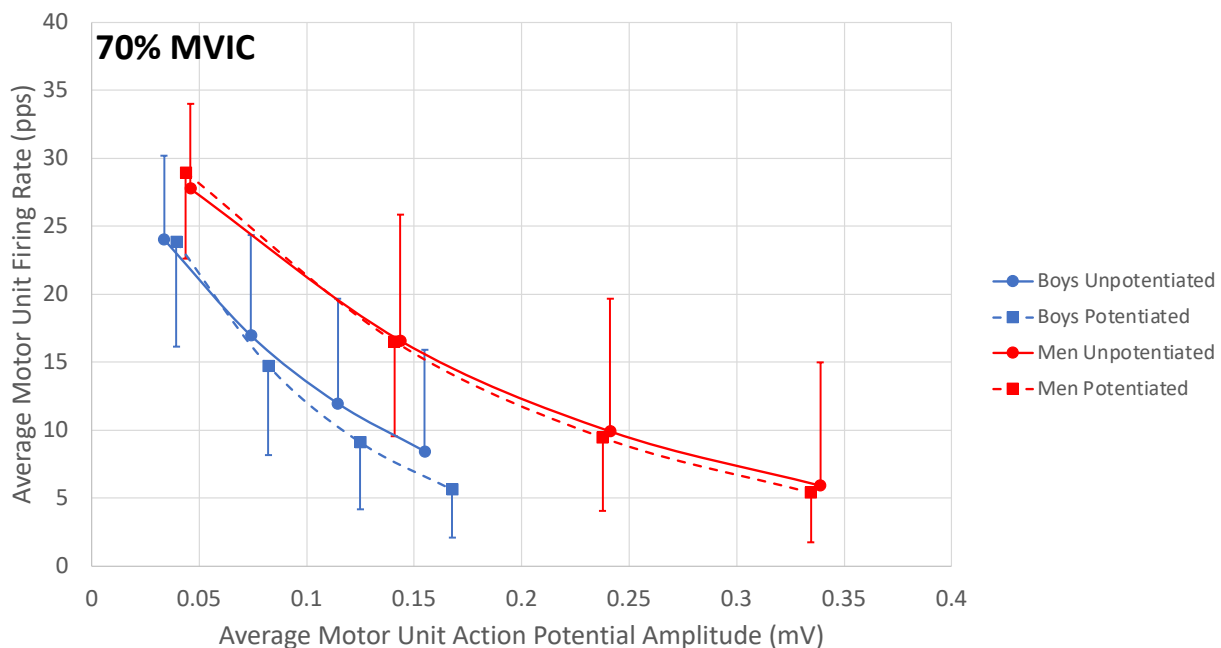


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443 **B.**

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445 *Figure 5: Mean prediction equations of the motor unit firing rate (MUFRR) vs. motor unit action*
 446 *potential amplitude (MUAPamp) relationships for boys and men during low- (a) and high-*
 447 *intensity (b) contractions. Error bars represent standard deviations. Note that the beginning and*
 448 *end of the regression lines were determined as the mean minimum and mean maximum*
 449 *MUAPamp values, respectively, for each group, in each state. In the high-intensity contractions,*
 450 *the reduction in MUFRRs was apparent in the boys ($p < .001$), but not the men ($p = .379$) (b; group-*
 451 *by-state interaction, $p = .017$).*

452

453 **Discussion**

454 Our results clearly indicate significantly lower PAP in the knee extensors, a mixed-fibre
 455 type muscle group, in boys compared with men. This lower PAP was demonstrated in peak

456 twitch torque, as well as in RTD_{peak}. To our knowledge, this is the first study to assess
457 potentiated MU firing patterns in children, demonstrating an overall reduction in MUFR decay
458 after CCs during both low- and high-intensity contractions, with a greater reduction in the boys
459 in the higher-intensity contraction. The sections below discuss PAP, as well as the MU patterns
460 in the low- and high-intensity contractions.

461 *Post-Activation Potentiation*

462 After 5s CCs, the boys' twitch torque PAP was only ~69% that of the men. Further, the
463 boys' RTD_{peak} PAP was only ~76% that of the men. Although these results confirm our
464 hypothesis, they are inconsistent with previous work examining the same muscle group. Ratel
465 and colleagues (2015) found a similar, albeit non-significant difference (boys twitch potentiation
466 being ~67% that of men) in twitch torque PAP in boys and men after a 5s isometric MVIC. This
467 inconsistency may be due to their lower statistical power (0.153 vs. the present study's 0.898)
468 and overall lower PAP in both groups (21.3±32.0% and 31.7±16.9% in boys and men,
469 respectively, vs. the present study 68.8±18.3% and 98.3±37.1% in boys and men, respectively).
470 Methodological differences also exist between the studies, as Ratel et al. used magnetic
471 stimulation of the femoral nerve rather than electrical muscle stimulation, as well as
472 superimposed twitches during the CCs to assess volitional activation. In adults, no difference in
473 PAP was seen using electric and magnetic nerve stimulation (Neyroud et al. 2015). However,
474 electrical muscle stimulation was shown to evoke similar unpotentiated, but lower potentiated
475 twitch torque in the knee extensors compared with electrical nerve stimulation (Neyroud et al.
476 2015), suggesting that PAP may be underestimated using muscle stimulation. Nevertheless,
477 using electric muscle stimulation, we observed greater, rather than lower PAP compared with

478 Ratel et al. (2015), who used magnetic nerve stimulation. Thus, the explanation for the
479 discrepancies in PAP between the two studies is not clear.

480 In adults, PAP has been shown to be greater in muscles with more type-II muscle fibres
481 (Hamada et al. 2000b). Therefore, it is possible that the observed lower PAP among boys is a
482 reflection of their lower type-II muscle fibre composition (Lexell et al. 1992). Further, it is
483 possible that the boys' lower PAP reflects a lower volitional activation (Woods et al. 2022), and
484 a lower ability to activate their higher-threshold (presumably type-II) MUs during the preceding
485 conditioning contraction (Dotan et al. 2012; Woods et al. 2019, 2020). Nevertheless, this
486 interpretation should be treated with caution, as the proposed mechanism for fibre type
487 differences in potentiation (greater phosphorylation of the myosin regulatory light chain in type-
488 II fibres; (Hamada et al. 2000b) is primarily based on animal data (Vandenboom 2017), and has
489 not been shown in humans (Houston et al. 1987).

490 To our knowledge, child-adult differences in RTD_{peak} PAP have not been previously
491 assessed in the knee extensors. However, in the plantar flexors, boys did not experience a
492 decrease in evoked-twitch contraction time (which would be indicative of an increased RTD)
493 after a 5s isometric CC, while adolescent and adult males did (Pääsuke et al. 2000). Thus, our
494 findings of lower RTD_{peak} PAP in boys compared with men are in line with previous reports in
495 the plantar flexors. Lower RTD_{peak} PAP in boys may have especially important practical
496 implications. As described by Sale (2002), PAP can lead to a rightward shift in the force-velocity
497 curve that may allow for greater power outputs at submaximal loads. This phenomenon has been
498 referred to as post activation performance enhancement (PAPE) by some (Blazevich and Babault
499 2019), which is somewhat different from PAP, as expressed in this study. Lower RTD_{peak} PAP
500 in boys would therefore reduce any power enhancement following a CC. Indeed, after 3x3s

501 isometric squats, squat-jump performance was reported to improve in men, but not in boys
502 (Arabatzis et al. 2014). Thus, while children do display an enhancement in the rate of twitch
503 torque (or force) generation following a CC (Figure 3), it may be insufficient to significantly
504 enhance volitional muscle performance.

505 *Motor Unit Firing Patterns*

506 Independent of state, boys consistently showed lower MUFRRs than men, as reflected by
507 their average MUFRRs and consistently lower mean A and B terms in the MUFRR-MUAPamp
508 relationships (group effects at or approaching statistical significance, Tables 4 and 5). This is in
509 agreement with some (Chalchat et al. 2019; Parra et al. 2020), but not all (Miller et al. 2019b)
510 (Chalchat et al. 2019; Miller et al. 2019b) previous reports examining child-adult differences in
511 MU firing patterns. The discrepancy with the Miller et al. study (2019b), may be related to the
512 examination of a different muscle (small, upper-limb muscle), or greater coactivation in the
513 children, as suggested (but not measured) by the authors. In low-intensity contractions, there
514 was an overall reduction in MUFRRs post-CC, specifically, in the larger MUs recruited. This is
515 reflected in the significant reduction of the mean B terms for the MUFRR-MUAPamp
516 relationships. This reduction may have been greater in the men, as supported by their
517 significantly greater decrease in average MUFRR (Table 4), although the group-by-state
518 interaction for the B term in the MUFRR-MUAPamp relationship was not statistically significant
519 ($p=.156$). Thus, during low-intensity contractions, potentiation appears to be associated with a
520 decrease in MUFRR, and may not be different between boys and men.

521 In the high-intensity contractions, men and boys experienced a significant reduction in
522 MUFRRs post-CC specifically in larger MUs recruited, as reflected by the significant reduction of
523 the mean B terms in the MUFRR-MUAPamp relationships (potentiation effects; figure 5b). The

524 reduction in MUFRRs, especially in the larger MUs (larger MUAPamp) is in line with previous
525 studies that have shown decreases in MUFRRs after a CC in men (Klein et al. 2001; Inglis et al.
526 2011; Miller et al. 2017; Zero et al. 2022). Further, the fact that MUFRRs appear to decrease to a
527 greater extent in larger (presumably more type-II) MUs is in line with past animal studies that
528 have demonstrated greater skeletal myosin light chain kinase activity, regulatory light chain
529 phosphorylation, and PAP in fast-twitch compared with slow-twitch muscle fibres (Moore and
530 Stull 1984; Vandenoorn 2017). The results are also in line with findings in humans, where PAP
531 in the knee extensors was greater among those with a greater percentage of type-II muscle fibres
532 (Hamada et al., 2000b).

533 Surprisingly, the post-CC reduction in the rate of decay of the MUFRR-MUAPamp
534 relationship (B term) in the high-intensity contraction was greater in the boys than in the men
535 (significant group-by-state interaction, Figure 5, Table 5), suggesting that boys had a greater
536 potentiation effect on MUFRR reduction in their larger-sized MUs compared to men. This is
537 contrary to our hypothesis and may be related to greater fatigue resistance in boys compared to
538 men (Falk and Dotan 2006; Ratel and Blazevich 2017). It is possible that the longer ramp
539 duration in the higher intensity contraction (7s ramp for the high-intensity contractions vs. 2s
540 ramp for the low-intensity contractions) induced some fatigue in the high-intensity contractions.
541 It is speculated that, since children are more fatigue-resistant than adults during high-intensity
542 contractions (Hatzikotoulas et al. 2014; Ratel et al. 2015; Bontemps et al. 2019; Pignonier et al.
543 2019), despite lower twitch PAP the boys experienced a greater reduction in MUFRRs. In support
544 of this speculation, it is noted that, although there was no decline in potentiated twitch torque in
545 either the boys nor the men, MVIC torque decreased during the experimental session in the men
546 but not the boys. It is also possible that the lower potentiation effect on MUFRRs in the high-

547 intensity contractions in men is related to the known lower impact of muscle potentiation during
548 high frequency (intensity) contractions (Vandenboom et al. 1993; Sale 2002). Thus, a lesser
549 effect of potentiation on MU firing patterns during high-intensity contractions may be seen in
550 adults but not in children.

551 *Limitations*

552 While this is the first study to examine discrete MU firing patterns following potentiation
553 in boys and men, it does have several limitations. First, we acknowledge multiple limitations
554 related to the sample examined. This study cannot be generalized to both sexes, as only males
555 were included. This is especially important since PAP has been shown to be greater in
556 prepubescent boys compared with girls (Pääsuke et al. 2003). Furthermore, the boys in the
557 present study were more physically active than the men. While this age-related difference in
558 physical activity level is to be expected, it may have impacted potentiation effects. Most of the
559 men participated in resistance training, while the boys participated more in team sports. Some of
560 the group differences may therefore be a result of differences in training/habitual activity rather
561 than maturation (Hamada et al. 2000a).

562 We also acknowledge limitations to the methodology used. Only one of the knee
563 extensors (vastus lateralis) was investigated with sEMG decomposition, and the muscle volume
564 captured was relatively small (i.e., using the relatively small Delsys Trigno Galileo sensor),
565 compared to that of high-density surface EMG decomposition methods. Explanations for any
566 group differences and changes in MU firing patterns assume that MU patterns in the whole
567 muscle and in all the knee extensors were similarly affected by potentiation. Further, the
568 interpretation of our data is dependent on the accepted positive relationship between MUAPamp
569 and MU size (Hakansson 1956; Henneman and Camille 1965; Milner-brown et al. 1973). It is

570 acknowledged that this relationship may be influenced by numerous factors, including
571 subcutaneous adipose tissue thickness and the MU's distance from the recording electrodes
572 (Gabriel 2022). MUFrs were compared based on MUAPamps rather than recruitment thresholds
573 because one of the goals of this study was to uncover potentiation-related changes in MUFrs,
574 independent of shifts in recruitment which may occur in analyses of MUFr vs. recruitment
575 threshold relationships. Additionally, although the high-intensity contraction protocol (i.e.,
576 70%MVIC for 7s, followed by 40%MVIC for an additional 15s) was successful in improving the
577 MU yield, it may have led to a bias towards the detection of relatively smaller MUs. The
578 contraction as a whole was perceived as "high intensity/difficult" by the participants, so we are
579 confident that this contraction was, overall, performed at a high intensity. It was also not possible
580 to track the same MU in unpotentiated and potentiated contractions. Therefore, changes in MU
581 firing patterns with potentiation were limited to analyzing the A and B terms of regressions for
582 all MUs within each contraction. Finally, when evoking the twitch response, we used a
583 supramaximal stimulation intensity of 110% the intensity which elicited the highest twitch
584 amplitude at the beginning of the experimental session. It was verified that there was no further
585 increase in unpotentiated twitch torque. However, it is acknowledged that hyperpolarization
586 effects may occur during repeated contractions and stimulations and that a stimulation intensity
587 of 120% (or higher) could have overcome such potential hyperpolarization

588 ***Conclusions***

589 In conclusion, the current study demonstrates that PAP of the knee extensors is lower in
590 boys than men. However, this blunted twitch PAP did not necessarily coincide with smaller
591 changes in potentiated MU firing patterns, as boys had greater reductions in MUFrs for a given

592 MU size (MUAPamp) with potentiation compared with men, specifically in high-intensity
593 contractions.

594

595

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599 collection.

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603 **References**

- 604 Arabatzi F, Patikas D, Zafeiridis A, et al (2014) The post-activation potentiation effect on squat
605 jump performance: Age and sex effect. *Pediatr Exerc Sci* 26:187–194.
606 <https://doi.org/10.1123/pes.2013-0052>
- 607 Armstrong N, Welsman JR, Chia MYH (2001) Short term power output in relation to growth and
608 maturation. *Br J Sports Med* 35:118–124. <https://doi.org/10.1136/bjism.35.2.118>
- 609 Baudry S, Duchateau J (2004) Postactivation potentiation in human muscle is not related to the
610 type of maximal conditioning contraction. *Muscle Nerve* 30:328–336.
611 <https://doi.org/10.1002/mus.20101>
- 612 Belanger AY, McComas AJ (1989) Contractile properties of human skeletal muscle in childhood
613 and adolescence. *Eur J Appl Physiol Occup Physiol* 58:563–567.
614 <https://doi.org/10.1007/BF00418500>
- 615 Blazeovich AJ, Babault N (2019) Post-activation Potentiation Versus Post-activation Performance
616 Enhancement in Humans: Historical Perspective, Underlying Mechanisms, and Current
617 Issues. *Front Physiol* 10:. <https://doi.org/10.3389/fphys.2019.01359>
- 618 Bontemps B, Piponnier E, Chalchat E, et al (2019) Children exhibit a more comparable
619 neuromuscular fatigue profile to endurance athletes than untrained adults. *Front Physiol*
620 10:1–11. <https://doi.org/10.3389/fphys.2019.00119>
- 621 Bottinelli R, Reggiani C (2000) Human skeletal muscle fibres: Molecular and functional
622 diversity. *Prog Biophys Mol Biol* 73:195–262. [https://doi.org/10.1016/S0079-
623 6107\(00\)00006-7](https://doi.org/10.1016/S0079-6107(00)00006-7)
- 624 Chalchat E, Piponnier E, Bontemps B, et al (2019) Characteristics of motor unit recruitment in
625 boys and men at maximal and submaximal force levels. *Exp Brain Res* 237:1289–1302.
626 <https://doi.org/10.1007/s00221-019-05508-z>
- 627 Dalton BH, Power GA, Paturel JR, Rice CL (2015) Older men are more fatigable than young
628 when matched for maximal power and knee extension angular velocity is unconstrained.
629 *Age (Omaha)* 37:1–16. <https://doi.org/10.1007/s11357-015-9790-0>
- 630 Dalton BH, Power GA, Vandervoort AA, Rice CL (2010) Power loss is greater in old men than
631 young men during fast plantar flexion contractions. *J Appl Physiol* 109:1441–1447.
632 <https://doi.org/10.1152/jappphysiol.00335.2010>
- 633 De Luca CJ, Adam A, Wotiz R, et al (2006) Decomposition of surface EMG signals. *J*
634 *Neurophysiol* 96:1646–1657. <https://doi.org/10.1152/jn.00009.2006>
- 635 Dotan R, Mitchell C, Cohen R, et al (2012) Child-adult differences in muscle activation - A
636 review. *Pediatr Exerc Sci* 24:2–21. <https://doi.org/10.1123/pes.24.1.2>

- 637 Esbjörnsson ME, Dahlström MS, Gierup JW, Jansson EC (2021) Muscle fiber size in healthy
638 children and adults in relation to sex and fiber types. *Muscle Nerve* 63:586–592.
639 <https://doi.org/10.1002/mus.27151>
- 640 Falk B, Dotan R (2006) Child-adult differences in the recovery from high-intensity exercise.
641 *Exerc Sport Sci Rev* 34:107–112. <https://doi.org/10.1249/00003677-200607000-00004>
- 642 Falk B, Usselman C, Dotan R, et al (2009) Child–adult differences in muscle strength and
643 activation pattern during isometric elbow flexion and extension. *Applied Physiology,*
644 *Nutrition, and Metabolism* 34:609–615. <https://doi.org/10.1139/H09-020>
- 645 Gabriel DA (2022) Teaching Essential EMG Theory to Kinesiologists and Physical Therapists
646 Using Analogies Visual Descriptions , and Qualitative Analysis of Biophysical Concepts.
647 *Sensors* 22:
- 648 Godin G, Shephard RJ (1985) A simple method to assess exercise behavior in the community.
649 *Canadian journal of applied sport sciences* 10:141–146
- 650 Hakansson CH (1956) Conduction Velocity and Amplitude of the Action Potential as Related to
651 Circumference in the Isolated Fibre of Frog Muscle. *Acta Physiol Scand* 37:14–34.
652 <https://doi.org/10.1111/j.1748-1716.1956.tb01338.x>
- 653 Hamada T, Sale DG, Macdougall JD (2000a) Postactivation potentiation in endurance-trained
654 male athletes. *Med Sci Sports Exerc* 32:403–411. <https://doi.org/10.1097/00005768-200002000-00022>
- 656 Hamada T, Sale DG, MacDougall JD, Tarnopolsky MA (2000b) Postactivation potentiation,
657 fiber type, and twitch contraction time in human knee extensor muscles. *J Appl Physiol*
658 88:2131–2137. <https://doi.org/10.1152/jappl.2000.88.6.2131>
- 659 Hatzikotoulas K, Patikas D, Ratel S, et al (2014) Central and peripheral fatigability in boys and
660 men during maximal contraction. *Med Sci Sports Exerc* 46:1326–1333.
661 <https://doi.org/10.1249/MSS.0000000000000239>
- 662 Hebestreit H, Mimura KI, Bar-Or O (1993) Recovery of muscle power after high-intensity short-
663 term exercise: Comparing boys and men. *J Appl Physiol* 74:2875–2880.
664 <https://doi.org/10.1152/jappl.1993.74.6.2875>
- 665 Henneman E, Camille BO (1965) Relations Between Structure and Function in the Design of
666 Skeletal Muscles. *Journal of Neurophysiology* 28:581–598.
667 <https://doi.org/10.1152/jn.1965.28.3.581>
- 668 Hermens HJ, Freriks B, Merletti R, et al (1999) European Recommendations for Surface
669 ElectroMyoGraphy. Roessingh Research and Development
- 670 Houston ME, Lingley MD, Stuart DS, Grange RW (1987) Myosin light chain phosphorylation in
671 intact human muscle. *FEBS Lett* 219:469–471. [https://doi.org/10.1016/0014-5793\(87\)80274-0](https://doi.org/10.1016/0014-5793(87)80274-0)
- 672

- 673 Inglis JG, Howard J, Mcintosh K, et al (2011) Decreased motor unit discharge rate in the
674 potentiated human tibialis anterior muscle. *Acta Physiologica* 201:483–492.
675 <https://doi.org/10.1111/j.1748-1716.2010.02233.x>
- 676 Kanehisa H, Yata H, Ikegawa S, Fukunaga T (1995) A cross-sectional study of the size and
677 strength of the lower leg muscles during growth. *Eur J Appl Physiol Occup Physiol* 72:150–
678 156. <https://doi.org/10.1007/BF00964130>
- 679 Klein CS, Ivanova TD, Rice CL, Garland SJ (2001) Motor unit discharge rate following twitch
680 potentiation in human triceps brachii muscle. *Neurosci Lett* 316:153–156.
681 [https://doi.org/10.1016/S0304-3940\(01\)02389-8](https://doi.org/10.1016/S0304-3940(01)02389-8)
- 682 Lexell J, Sjöström M, Nordlund A -S, Taylor CC (1992) Growth and development of human
683 muscle: A quantitative morphological study of whole vastus lateralis from childhood to
684 adult age. *Muscle Nerve* 15:404–409. <https://doi.org/10.1002/mus.880150323>
- 685 Long D, Dotan R, Pitt B, et al (2017) The electromyographic threshold in girls and women.
686 *Pediatr Exerc Sci* 29:84–93. <https://doi.org/10.1123/pes.2016-0056>
- 687 Miller JD, Herda TJ, Trevino MA, et al (2017) Time-related changes in firing rates are
688 influenced by recruitment threshold and twitch force potentiation in the first dorsal
689 interosseous. *Exp Physiol* 102:950–961. <https://doi.org/10.1113/EP086262>
- 690 Miller JD, Lund CJ, Gingrich MD, et al (2019a) The effect of rate of torque development on
691 motor unit recruitment and firing rates during isometric voluntary trapezoidal contractions.
692 *Exp Brain Res* 237:2653–2664. <https://doi.org/10.1007/s00221-019-05612-0>
- 693 Miller JD, Sterczala AJ, Trevino MA, et al (2019b) Motor unit action potential amplitudes and
694 firing rates during repetitive muscle actions of the first dorsal interosseous in children and
695 adults. *Eur J Appl Physiol* 119:1007–1018. <https://doi.org/10.1007/s00421-019-04090-0>
- 696 Milner-brown HS, Stein RB, Yemm R (1973) The Contractile Properties of Human Motor Units
697 During Voluntary Isometric Contractions. *Journal of Physiology* 228:285–306
- 698 Mirwald RL, G Baxter-jones AD, Bailey DA, et al (2002) An assessment of maturity from
699 anthropometric measurements. *Med Sci Sports Exerc* 34:689–694
- 700 Moore RL, Stull JT (1984) Myosin light chain phosphorylation in fast and slow skeletal muscles
701 in situ. *Am J Physiol Cell Physiol* 16:462–471.
702 <https://doi.org/10.1152/ajpcell.1984.247.5.c462>
- 703 Neyroud D, Temesi J, Millet GY, et al (2015) Comparison of electrical nerve stimulation,
704 electrical muscle stimulation and magnetic nerve stimulation to assess the neuromuscular
705 function of the plantar flexor muscles. *Eur J Appl Physiol* 115:1429–1439.
706 <https://doi.org/10.1007/s00421-015-3124-x>
- 707 Pääsuke M, Ereline J, Gapeyeva H (2000) Twitch contraction properties of plantar flexor
708 muscles in pre- and post-pubertal boys and men. *Eur J Appl Physiol* 82:459–464.
709 <https://doi.org/10.1007/s004210000236>

- 710 Pääsuke M, Ereline J, Gapeyeva H, et al (2003) Comparison of twitch contractile properties of
711 plantar flexor muscles in 9-10-year-old girls and boys. *Pediatr Exerc Sci* 15:324–332.
712 <https://doi.org/10.1123/pes.15.3.324>
- 713 Parra ME, Miller JD, Sterczala AJ, et al (2020) Differences in the firing rate versus recruitment
714 threshold relationships of the vastus lateralis in children ages 7–10 years and adults. *Hum*
715 *Mov Sci* 72:102650. <https://doi.org/10.1016/j.humov.2020.102650>
- 716 Piponnier E, Martin V, Bourdier P, et al (2019) Maturation-related changes in the development
717 and etiology of neuromuscular fatigue. *Eur J Appl Physiol* 119:2545–2555.
718 <https://doi.org/10.1007/s00421-019-04233-3>
- 719 Pitt B, Dotan R, Millar J, et al (2015) The electromyographic threshold in boys and men. *Eur J*
720 *Appl Physiol* 115:1273–1281. <https://doi.org/10.1007/s00421-015-3100-5>
- 721 Ratel S, Blazeovich AJ (2017) Are Prepubertal Children Metabolically Comparable to Well-
722 Trained Adult Endurance Athletes? *Sports Medicine* 47:1477–1485.
723 <https://doi.org/10.1007/s40279-016-0671-1>
- 724 Ratel S, Kluka V, Vicencio SG, et al (2015) Insights into the mechanisms of neuromuscular
725 fatigue in boys and men. *Med Sci Sports Exerc* 47:2319–2328.
726 <https://doi.org/10.1249/MSS.0000000000000697>
- 727 Sale D (2002) Postactivation potentiation: Role in performance. *Br J Sports Med* 38:386–387.
728 <https://doi.org/10.1136/bjism.2002.003392>
- 729 Tanner JM (1962) Growth at adolescence
- 730 Vandenoorn R (2017) Modulation of Skeletal Muscle Contraction by Myosin Phosphorylation.
731 *Compr Physiol* 7:212
- 732 Vandenoorn R, Grange RW, Houston ME (1993) Threshold for force potentiation associated
733 with skeletal myosin phosphorylation. *Am J Physiol Cell Physiol* 265:.
734 <https://doi.org/10.1152/ajpcell.1993.265.6.c1456>
- 735 Woods S, Dotan R, Jenicek N, et al (2019) Isometric-based test improves EMG-threshold
736 determination in boys vs. men. *Eur J Appl Physiol* 119:1971–1979.
737 <https://doi.org/10.1007/s00421-019-04185-8>
- 738 Woods S, Dotan R, Jenicek N, Falk B (2020) Isometric-based EMG threshold in girls and
739 women. *Eur J Appl Physiol* 120:907–914. <https://doi.org/10.1007/s00421-020-04331-7>
- 740 Woods S, O'Mahoney C, Maynard J, et al (2022) Increase in Volitional Muscle Activation from
741 Childhood to Adulthood. *Med Sci Sports Exerc Publish Ah*:789–799.
742 <https://doi.org/10.1249/mss.0000000000002853>
- 743 Zero AM, Kirk EA, Rice CL (2022) Firing rate trajectories of human motor units during activity-
744 dependent muscle potentiation. *J Appl Physiol* 132:402–412.
745 <https://doi.org/10.1152/jappphysiol.00672.2021>

