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1 **Age-Related Neuromuscular Fatigue and Recovery after Cycling: Measurements in**

2 **Isometric and Dynamic Modes**

3 **Running title:** Age-Related Fatigue in Cycling

4

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25

26 **Abstract**

27 Studies have suggested that older individuals are more fatigable than young adults when
28 power loss, measured during single-joint contractions, is considered the fatigue index;
29 however, age-related differences in fatigue considering power measurements during multi-
30 joint movements (e.g., cycling) have not been fully elucidated yet. This study examined
31 age-related differences in dynamic and isometric measures of fatigue in response to three
32 cycling exercises. Ten young (27 ± 4 yrs.) and ten old (74 ± 4 yrs.) men performed
33 exercises on different days, 30-s Wingate, 10-min at severe-intensity, and 90-min at
34 moderate-intensity. Dynamic measures—maximal power, torque, and velocity—were
35 assessed after cycling and during recovery (1-8 min post-exercise) through 7-s cycling
36 sprints and isometric force and fatigue etiology (central and peripheral components)
37 through isometric contractions. There were no age-related differences in the relative
38 reduction of dynamic and isometric measures following the Wingate and moderate-
39 intensity tasks. Maximal power, isometric force, and indices of peripheral function (e.g.,
40 high-frequency doublet) decreased more in young compared with older individuals after the
41 severe-intensity exercise (all $p < 0.05$). The only observed age-related difference in the
42 recovery of NM fatigue was a slower recovery of power and torque from 1 to 8 min ($p <$
43 0.05) and at 4 min ($p = 0.015$), respectively, in younger males after the Wingate. Age-
44 related fatigue and recovery depend on the fatiguing exercise intensity and duration and on

45 the fatigue assessment mode. This study provides novel information on age-related
46 neuromuscular fatigue responses to multi-joint dynamic exercises performed at different
47 intensities and durations.

48

49 **Keywords:** Aging; Central fatigue; Contractile properties; Muscle; Peripheral fatigue;
50 Power output.

51

52 **1. Introduction**

53 Although reductions in both isometric force and power output are indicative of
54 neuromuscular (NM) fatigue, we have recently shown that these assessments are not
55 interchangeable (Krüger et al., 2019). In other words, isometric force and power output are
56 often decreased by different levels after a given exercise task. The distinction between
57 isometric force and power output responses is particularly important when examining age-
58 related NM fatigue (Krüger et al., 2018). For instance, while older individuals present a
59 greater decline in power output following fatiguing tasks (Dalton et al., 2010b; Dalton et
60 al., 2012; Power et al., 2012; Wallace et al., 2016; McNeil and Rice, 2007), isometric
61 maximal voluntary contraction (IMVC) is usually decreased by the same extent in both
62 groups after fatigue induced by slow-velocity contractions (Dalton et al., 2012; Power et
63 al., 2012), and more depressed in younger individuals following maximal fast-velocity
64 movements (Yoon et al., 2013; Dalton et al., 2010b). Despite the fact that these findings
65 have been contradicted by other studies (Senefeld et al., 2017; Lanza et al., 2004;
66 Thompson et al., 2015; Yoon et al., 2015), our meta-analysis study showed that older

67 individuals demonstrate a greater reduction in power after fatigue induced by either
68 dynamic or isometric tasks, but there is no difference in IMVC loss between young and old
69 people when fatigue is induced by dynamic exercises (Krüger et al., 2018).

70 The importance of measuring NM fatigue during dynamic contractions (e.g.,
71 walking, rising from a chair, climbing stairs) relies on the fact that these movements are
72 incorporated into activities of daily living. Any age-related decrease in the ability to
73 produce high levels of power during dynamic movements can affect the performance of
74 activities of daily living and, for example, increase the number of falls (Foulis et al., 2017).
75 Because power output measurements are more representative of human's ability to
76 overcome fatigue during dynamic exercises, several studies in the past have included this
77 measurement in combination with IMVC to explore the effects of aging on NM fatigue
78 (Dalton et al., 2010b; Dalton et al., 2015; Dalton et al., 2012; Power et al., 2012; Yoon et
79 al., 2015; Yoon et al., 2013; Callahan and Kent-Braun, 2011). The decrements in power
80 output after NM fatigue have been quantified during isotonic (Dalton et al., 2015; Dalton et
81 al., 2010b; Dalton et al., 2012; Power et al., 2012; Wallace et al., 2016; Yoon et al., 2015;
82 Yoon et al., 2013) or isokinetic (Callahan and Kent-Braun, 2011; Dalton et al., 2015)
83 contractions using the corresponding dynamometers.

84 Differently, the present study proposed to assess age-related differences in dynamic
85 measures of NM fatigue from cycling sprints. The advantage of using this novel approach
86 resides in three main factors: (i) it requires the activation of the knee extensors, which are
87 essential contributors to power output production during the cycling downstroke phase
88 (Driss and Vandewalle, 2013) and are an extremely important muscle group for daily

89 living; (ii) it does not require velocity or force to be held constrained during the sprints; and
90 (iii) it allows measurements of force production capacities over the entire range of
91 velocities, which facilitate the determination of maximal torque (T_{max}), velocity (V_{max}),
92 and power (P_{max}) (Driss and Vandewalle, 2013) through the associated torque-velocity (T-
93 V) and power-velocity (P-V) relationships obtained during a sprint protocol (Samozino et
94 al., 2007).

95 The first aim of the present study was to assess age-related differences in dynamic
96 measures of NM fatigue through the alterations of P_{max} , V_{max} , and T_{max} induced by
97 different intensities and durations of cycling exercises and during recovery (from 1 to 8 min
98 after). The cycling fatiguing exercises consisted of: a Wingate test (WING); a severe-
99 intensity, but long-duration task (SEV); and a moderate-intensity and longer duration task
100 (MOD). In accordance with the previous literature (Krüger et al., 2018; Wallace et al.,
101 2016; Callahan and Kent-Braun, 2011; Dalton et al., 2010b; Dalton et al., 2012; Power et
102 al., 2012), we hypothesized that P_{max} , V_{max} , and T_{max} would be reduced to a greater
103 extent in older individuals in comparison with their younger counterparts. Additionally, it
104 was expected that older participants would present a down and leftward shift on T-V
105 relationship curve at baseline (PRE) and after fatigue (POST) compared with young adults.
106 It remains to be explored if different intensities and durations of exercise will elicit distinct
107 age-related NM fatigue responses. It was hypothesized that P_{max} , V_{max} , and T_{max}
108 recovery kinetics would not be affected by aging as a few studies have shown no age-
109 related differences in these outcomes during the recovery of fatigue (Dalton et al., 2015;
110 Yoon et al., 2015; Yoon et al., 2013).

111 The second aim of this study was to examine age-related differences in isometric
112 measures of NM fatigue magnitude and etiology (central and peripheral fatigue) following
113 the same fatiguing tasks and during recovery. We hypothesized that WING exercise would
114 elicit greater decrease in IMVC and peripheral fatigue in young when compared with older
115 individuals while there would be no significant age-related difference in IMVC reductions
116 after the other exercise conditions. Although we have previously reported no age-related
117 difference in IMVC loss after dynamic fatiguing exercises (Krüger et al., 2018), some
118 studies showed greater IMVC decrements in young individuals following maximal
119 dynamic contractions (Yoon et al., 2013; Dalton et al., 2010b). It has been suggested that
120 older individuals (> 65 yrs. old) have a delayed isometric force recovery due to a slower
121 recovery of central mechanisms (e.g., delayed recovery of motor units firing rate) after
122 isometric fatiguing exercises (Dalton et al., 2010a; Hunter et al., 2008; Yoon et al., 2013;
123 Yoon et al., 2012). It remains to be explored if IMVC recovery is age-dependent after
124 multi-joint lower limb movement induced NM fatigue.

125

126 **2. Materials and Methods**

127 ***2.1 Participants***

128 Ten young (27 ± 4 yrs.) and ten old (74 ± 4 yrs.) men were recruited from local community
129 centers and from the University of Calgary active living facilities. Part of the data reported
130 from the young participants was previously published in a different study that aimed to
131 compare dynamic and isometric measures of fatigue (Krüger et al., 2019). In the present
132 study, the data from the young participants is used as a control group to identify age-related

133 NM fatigue responses to cycling. The participants were excluded from the study if: (i) their
134 resting electrocardiogram (ECG) showed any abnormality; (ii) their resting heart rate (HR)
135 > 90 bpm and/or a resting blood pressure >144/94 mmHg; (iii) they had any history of
136 severe disease that could increase the risk of developing cardiac arrhythmias and stroke;
137 and (iv) they had joint soreness that made biking difficult. Participants were cleared to
138 participate according to the “Physical Activity Readiness Questionnaire (PAR-Q)”.

139 Physical activity status was assessed through the leisure-score index (LSI) obtained from
140 the “Godin-Shephard Leisure-Time Physical Activity Questionnaire (GSLTPAQ)” (Godin,
141 1997). Leisure-score index (LSI) was calculated as shown: $(9 \times \text{Strenuous}) + (5 \times$
142 $\text{Moderate}) + (3 \times \text{Light})$ (Godin, 1997). All the participants were classified as physically
143 active according to the LSI (> 24) (Godin, 1997). Young and older participants were
144 individually matched by their physical activity level. Participants were instructed to refrain
145 from consuming caffeine and alcohol for at least 12 h prior to experimental sessions and
146 participating in any intense exercise for 24 h before testing. Written informed consent was
147 obtained from each participant before the beginning the study. This study was approved by
148 the Conjoint Health Research Ethics Board of the University of Calgary (REB #15-2430)
149 and it was conducted according to the guidelines of the Declaration of Helsinki, except for
150 registration in a database.

151

152 ***2.2 Experimental design***

153 Participants were required to visit the laboratory in seven different occasions. Visit 1
154 consisted of screening measurements, a maximal incremental cycling test, and a

155 familiarization with the assessments. In each of the visits 2-7, the participants were
156 randomly assigned to perform one of the three fatiguing tasks in combination with either a
157 T-V relationship or a NM function protocol. The three exercises were a Wingate (WING)
158 test, a 10-min cycling at 5% above the second ventilatory threshold (VT2) (SEV), and a 90-
159 min cycling at 20% below the first ventilatory threshold (VT1) (MOD). The experimental
160 sessions were separated by at least 48 h to avoid residual effects of NM fatigue. Participants
161 were instructed to cycle at a constant cadence (60-80 rpm) during the fixed intensity
162 exercises (SEV and MOD). If they were not able to keep the cadence above 60 rpm during
163 the SEV exercise due to the task intensity, power output was slightly reduced (by 10 W) so
164 that they could finish the exercise (n = 3 young and 3 old). There was no statistical
165 difference between the mean power output developed during the WING performed in the
166 T-V relationship and the WING performed in the NM function protocols for young ($p =$
167 0.092) and older ($p = 0.231$) individuals.

168

169 *2.2.1 Visit 1: incremental exercise and familiarization*

170 All participants completed the questionnaires (PAR-Q and GSLTPAQ). The older
171 participants underwent a screening procedure composed by the assessment of resting HR,
172 blood pressure, and ECG. Then, vastus lateralis (VL) and rectus femoris (RF) cross-
173 sectional areas (CSA) were measured using real-time B-mode ultrasonography (Philips
174 M2540A, Bothell, United States). After that, the participants performed an incremental
175 exercise test to the limit of tolerance to determine VT1, VT2, and $\dot{V}O_{2peak}$. The
176 incremental exercise consisted of cycling on a recumbent cycling ergometer while having

177 oxygen uptake measured by an open circuit spirometry system (Quark CPET, COSMED,
178 Rome, Italy). The initial power output was 90 W for the young participants and 25 W for
179 the older participants. During the test, power output increased was by 15 W every minute.
180 HR and ECG were continuously monitored for participants older than 75 yrs. by a certified
181 exercise physiologist (CSEP-CEP). Finally, participants were familiarized with the
182 electrical stimulation and practiced isometric and dynamic contractions on the recumbent
183 cycling ergometer powered by Velotron Coaching Software (Racermate Inc) (Figure 1,
184 panel D) (Doyle-Baker et al., 2018).

185

186 *2.2.2 Visits 2-7: fatiguing exercises*

187 Upon arrival to the laboratory, electromyography (EMG) electrodes (10-mm diameter;
188 Meditrace 100, Covidien, Mansfield, United States) were placed on the VL and biceps
189 femoris (BF) and the reference electrode over the patella bone. Recording electrode
190 locations were based on SENIAM recommendations (Hermens et al., 2000). The cathode
191 stimulating electrode (10-mm diameter; Meditrace 100, Covidien) was placed on the
192 femoral nerve (inguinal triangle) and the anode electrode on the gluteal fold (Doyle-Baker
193 et al., 2018). After the electrodes placement, participants were adjusted on the recumbent
194 cycling ergometer seat with the knees and hips flexed at 90° to determine the femoral nerve
195 electrical stimulation intensity, as previously described (Doyle-Baker et al., 2018) and
196 secured by chest and hip straps. Then, a 5-min cycling warm-up was performed (30% of
197 $\dot{V}O_2$ peak for 3 min, 45% for 1 min, and 60% for 1 min). After 3 min of rest, T-V
198 relationship or NM function protocol was performed twice (see below). After that, one of

199 the three fatiguing exercises was performed. The testing protocol was repeated at ten
200 seconds (POST) as well as +1 min, +2 min, +4 min, and +8 min after the exercise
201 termination. There was no difference in the POST delay assessment between the T-V
202 relationship and NM function protocols (10.1 ± 1.4 vs. 10.4 ± 3.6 s, respectively, $p =$
203 0.752).

204

205 *2.2.3 Dynamic measures of NM fatigue*

206 The T-V and P-V relationships were determined from 7-s sprints on the same recumbent
207 cycling ergometer (Velotron). The aim of this testing protocol was to characterize lower
208 limb force production capacities over an entire functional movement (i.e., a lower limb
209 extension) at different velocities. This ergometer is equipped with an eddy current braking
210 system, which allows control of the flywheel resistance directly from the software. During
211 the 7-s sprints, the participants were vigorously encouraged to pedal as fast as possible
212 while remaining seated on the saddle and secured by chest and hip straps. Exactly 10 s after
213 the end of each sprint, a single twitch contraction (Pt, one stimulus) was delivered on the
214 femoral nerve when the pedals were locked (Figure 1, panel A). The Pt delivery delay was
215 matched between the T-V relationship and NM function protocols (26.8 ± 2.3 vs. 25.4 ± 4
216 s, respectively, $p = 0.151$). This ~26 s of interval comprises the 10-s delay from the exercise
217 cessation to beginning of the sprint, the sprint time, and about 10-s delay from the end of
218 the sprint to the Pt delivery.

219 Individual braking force during cycling sprints was determined in the first visit
220 based on the goodness of fit of the T-V and P-V relationships (Figure 1, panel B). The

221 goodness of fit criteria were a high coefficient of determination ($R^2 > 0.9$), a great range of
222 area covered by velocities obtained from pedal downstrokes, and an equal number of points
223 distributed to both sides of the P-V relationship curve (Dorel, 2018). Therefore, the ideal
224 individual resistance would allow the participants to achieve maximal power at about 50%
225 of the sprint duration at baseline (PRE). For that, young participants performed two 7-s
226 sprints against a resistance equivalent to 5 and 7% of body weight applied to the flywheel,
227 while older participants cycled against an equivalent resistance of 3 and 4% of body
228 weight. These resistances are lower than the optimal resistance usually used for T-V
229 relationship tests (7.5% of body weight) (Driss and Vandewalle, 2013) since the cycling
230 sprints in the present study were performed on a cycle ergometer presenting different
231 position (recumbent cycling ergometer) and flywheel (inertia and radius) characteristics
232 different than usual cycle ergometers. As indicated above, the applied resistance during the
233 T-V relationship test affects several properties of the T-V and P-V relationship (Dorel,
234 2018). As older participants were weaker and less powerful compared with young
235 participants (see Table 1), the resistance set to older participants was lower to assure T-V
236 relationship goodness of fit.

237

238 *2.2.4 Isometric measures of NM fatigue*

239 The NM function protocol consisted in performing 5-s IMVC coupled with a high
240 frequency doublet electrical stimulation (Db100, 10-ms inter-stimulus interval) evoked
241 during the IMVC force plateau. Three seconds after the IMVC, a Db100, a low frequency
242 doublet (Db10, 100-ms inter-stimulus interval), and a Pt were delivered on the relaxed

243 muscle. These three stimuli were interspaced by 3-s intervals. Before and after the fatiguing
244 exercises, the participants performed two 5-s knee flexion IMVCs to assess co-activation.

245

246 **2.3 Data analysis**

247 *2.3.1 Dynamic measures of NM fatigue*

248 The sprints were recorded with a video camera (Fujifilm FinePix XP80 Waterproof Digital
249 Camera with 2.7-Inch LCD, Tokyo, Japan) with a 240 Hz sampling frequency. Reflective
250 markers were placed on the crank and pedal to measure angular displacement during the
251 sprint. The camera was synchronized with the Labchart 8 software (ADInstruments, Bella
252 Vista, Australia) with a light signal. The instantaneous torque at the pedal crank was
253 obtained from the instrumented pedals (tangential force relative to the circular path) and
254 recorded at 240 Hz in the Imago Record (version 8.50; Radlabor GmbH, Freiburg,
255 Germany) software and the instantaneous angular velocity was calculated from camera and
256 Kinovea® software after tracking the crank angular displacement at each 4.17 ms (240 Hz).
257 Power was then calculated as the product of instantaneous torque and angular velocity.

258 Resultant torque, angular velocity, and power output were averaged from each pedal
259 downstroke of the acceleration phase (Samozino et al., 2007). Individual linear T-V
260 relationship was determined from pedal downstroke averaged values using an inverse linear
261 regression as previously described for multi-joint movements (Bobbert et al., 2016;
262 Samozino et al., 2010; Samozino et al., 2012). T-V relationship was extrapolated to obtain
263 T_{max} (theoretical maximal torque lower limbs could produce) and V_{max} (theoretical
264 maximal velocity until which lower limbs could still produce torque) as the intercepts of the

265 T-V relationship with the force and velocity axis, respectively. Pmax was determined as the
266 product of Tmax and Vmax divided by 4 (Vandewalle et al., 1987). When T-V relationship
267 fit is linear, the P-V relationship is fitted by a second order polynomial regression with
268 maximal value reached for $T = T_{max}/2$ and $V = V_{max}/2$ (Vandewalle et al., 1987;
269 Samozino et al., 2012). After the MOD condition, some individuals (1 young and 3 old)
270 could not achieve optimal velocity during the T-V relationship tests. The lower ability to
271 rapidly overcome the flywheel resistance after NM fatigue compromised the dynamic
272 properties assessment. Consequently, Vmax was highly extrapolated from the T-V
273 relationship curve, which increased the inaccuracy of Vmax and Pmax computations and
274 led to irrelevant values. Because of this, those participants were considered outliers and
275 were excluded from the analyses.

276

277 *2.3.2 Isometric measures of NM fatigue*

278 All the variables were analyzed in Labchart 8 software (ADInstruments). VA was assessed
279 by the interpolation twitch technique using the amplitude of superimposed and resting
280 Db100 (Merton, 1954). Since in some cases the Db100 was not applied during the IMVC
281 plateau, the magnitude of VA was calculated using a corrected formula for all the
282 individuals: $\%VA = 100 - D \times (Fb/IMVC) / Db100 \times 100$ (Strojnik and Komi, 1998),
283 where Fb is the force level just before the Db100 and D is the difference between Fb and
284 the maximum torque during the Db100. The highest amplitude of IMVC, VA, Db100, and
285 Pt was considered for the baseline analysis. Db10 amplitude was only considered for the

286 low-frequency fatigue (LFF) assessment, which was measured by the ratio between Db10
287 and Db100 (Db10:100) (Verges et al., 2009).

288 Pt properties assessment involved time to peak torque (TPT) (time between the
289 beginning of the contraction to the peak), half relaxation time (HRT) (the time period taken
290 for Pt to decline by 50%), maximal rate of force development (MRFD), and maximal rate
291 of force relaxation (MRFR), i.e., maximal and minimal values of the force-time derivative,
292 respectively, expressed in $N \cdot s^{-1}$.

293 The EMG data was recorded with the PowerLab data acquisition system (16/35,
294 ADInstruments). EMG activity was filtered with a Blackman -61 dB band-pass filter
295 between 10–500 Hz, amplified (bi-polar differential amplifier, input impedance = 2 M Ω ,
296 common mode rejection ratio > 110 dB min, gain \times 1000, noise > 5 μ V), and analog-to-
297 digitally converted (12 bit). Peak-to peak M-wave amplitude and M-wave area were
298 assessed using surface EMG of the VL muscle. The maximal root mean square EMG
299 (RMS) obtained during IMVC was normalized to M-wave amplitude (Mmax) to assess
300 maximal central motor drive (Place et al., 2007). BF EMG RMS recorded during knee
301 extension IMVCs was normalized to maximal BF EMG RMS obtained during 5-s knee
302 flexions IMVCs (the one with the highest RMS was considered) to assess co-activation.
303 This approach allows the calculation of the percent of BF activation during KE IMVC.

304

305 *2.3.3 Gas exchange and ventilatory variables*

306 $\dot{V}O_2$ peak was considered as the highest $\dot{V}O_2$ value computed over 30 s of the $\dot{V}O_2$ plateau
307 or at the end of the ramp-incremental test. VT1 was identified as the minimum workload at

308 which the ventilatory equivalent ratio for oxygen ($\dot{V}E/\dot{V}O_2$) increased without any
309 increment in the ventilatory equivalent ratio for carbon dioxide ($\dot{V}E/\dot{V}CO_2$) (Dekerle et al.,
310 2003; Wasserman and McIlroy, 1964). VT2 was determined as the lowest intensity where
311 both $\dot{V}E/\dot{V}O_2$ and $\dot{V}E/\dot{V}CO_2$ increased (Dekerle et al., 2003; Wasserman and McIlroy,
312 1964). VT1 and VT2 were analyzed by visual inspection of graphs by two independent
313 appraisers (R.L.K and L.M.J.). Disagreements were solved by a third reviewer (G.Y.M).

314

315 *Muscle cross-sectional area*

316 Participants rested in a supine position for 10 min before the data collection. Three VL and
317 RF muscles high-quality images were recorded at a depth of 5 cm from the transducer
318 surface that was positioned transversally to the muscle fibers at 50% of the distance
319 between the lateral condyle of femur and the greater trochanter (Baroni et al., 2015). The
320 images were recorded by applying consistent and minimal pressure in the muscle using the
321 panoramic scanning technique. VL and RF CSA were obtained through manual tracing of
322 the muscle borders using the Image-J software (National Institute of Health, USA) (Baroni
323 et al., 2015). The mean CSA from the three panoramic images was considered. All the
324 images were recorded and analyzed by the same independent researcher (R.L.K.). The
325 coefficients of variance across the three images were lower than 6% (RF CSA old: $6 \pm 3\%$;
326 VL CSA old: $3 \pm 1\%$; RF CSA young: $5 \pm 2\%$; and VL CSA young: $2 \pm 1\%$).

327

328 *2.4 Statistical analyses*

329 Data was described as mean and standard deviation (mean \pm SD), and 95% CI. The
330 Shapiro-Wilk test was used to assess the data normality for each variable. Levene's test was
331 used to test the homogeneity of variance and Mauchly's test to access sphericity
332 assumption. Greenhouse-Geisser correction factor was applied if the sphericity was not
333 assumed. Reliability of the dependent variables was assessed through coefficient of
334 variation (CV, intertrial SD divided by the mean of the two trials) and calculation of typical
335 error of measurement (TEM) (Hopkins, 2000) across values obtained for each age group at
336 baseline (PRE). It was completed by a one-way analysis of variance (ANOVA) to test the
337 differences in the dependent variables among the three sessions (WIN, MOD, and SEV).
338 Independent sample t-tests were performed to assess the difference in the mean of the
339 dependent variables at PRE between young and older participants.

340 Two different statistical approaches were used to test NM fatigue responses at
341 POST and during recovery. This is because we were interested in analyzing these two
342 parameters independently and the inclusion of all the time-points in the same ANOVA
343 would increase the number of independent t-tests and Bonferroni corrections, which would
344 enhance the possibility of type II error (i.e., failure to reject the false null hypothesis). To
345 assess the effect of aging on NM fatigue, independent t-tests on relative values (% of PRE)
346 were performed to compare the difference across the age groups at POST of each exercise
347 condition. Changes in T-V relationship curves with fatigue were assessed through a three-
348 way ANOVA (instantaneous torque and velocity \times age group \times time). If there was an
349 interaction, multiple independent sample t-tests (age difference) and paired t-tests (time
350 difference) followed by Holm-Bonferroni correction were conducted. To assess the effects

351 of age on NM fatigue recovery kinetics (difference from POST to +1, +2, +4, and +8 min),
352 a two-way mixed ANOVA (age group \times time) followed by Bonferroni post-hoc test on
353 relative values (% of PRE) was performed. If there was an interaction, multiple
354 independent sample t-tests followed by Holm-Bonferroni correction were performed to
355 assess the difference between young and older males at +1, +2, +4 and +8 min of recovery.
356 Additionally, we combined young and older individual's data to explore the association
357 between mean power output sustained during the exercise trials and the decrements in
358 dynamic measures of NM fatigue (% of PRE) using Pearson's correlation coefficient to
359 support some of the findings of this study. Effect sizes were reported as Cohen's D (Cohen,
360 1988). For hypothesis testing, 95% CI was predetermined as the minimum criterion to
361 denote a statistical difference ($p \leq 0.05$). The data was analyzed using the Statistical
362 Package for Social Sciences (SPSS) version 24 (SPSS Inc., Chicago, IL). The data that
363 support the findings of this study are available from the corresponding author upon request.

364

365 **3. Results**

366 ***3.1 Age-related differences at baseline (variables recorded at PRE)***

367 Reliability data is presented in SuppInfo 1 and 2. There was no difference in the baseline
368 responses of the dependent variables among the three exercise conditions (WING, SEV and
369 MOD) for young and older individuals (all $p > 0.05$). The differences between young and
370 old individuals for the outcomes measured at baseline are shown in Table 1. VL and RF
371 CSAs were significantly smaller in the older participants ($p < 0.001$, $d = 2.84$ and $p =$
372 0.004 , $d = 2.38$, respectively). Older participants had 20% lower IMVC force ($p = 0.013$, d

373 = 3.96) and were less powerful (Pmax) and weaker (Tmax) than their younger counterparts
374 ($p = 0.001$, $d = 1.83$ and $p = 0.021$, $d = 1.15$, respectively). The muscle force per muscle
375 cross-sectional area was also lower in older individuals ($p < 0.001$, $d = 3.16$). Older males
376 also presented ~40% lower Pt and Db100 in comparison with young adults (both $p < 0.001$,
377 $d \geq 4.22$). MRFD and MRFR were 60% and 74% lower, respectively (both $p < 0.001$, $d \geq$
378 3.27), while CT was 13% longer for the old vs young individuals ($p = 0.01$, $d = -1.00$).

379

380 **3.2 Exercise characteristics**

381 Older individuals presented lower $\dot{V}O_{2peak}$, peak power output, and power output at
382 ventilatory thresholds (VTs) in comparison with young participants (all $p < 0.001$, $d \geq 1.15$,
383 Table 2). The exercise intensity and total work were also lower for older individuals during
384 the WING, SEV and MOD conditions (all $p < 0.024$, $d \geq 1.11$, Table 2). Results from the
385 association between mean power output sustained during the exercise trials and the
386 decrements in dynamic measures of NM fatigue (Pmax, Vmax and Tmax expressed in % of
387 PRE) showed a negative correlation between mean power output and Pmax ($r = -0.843$, $p <$
388 0.001), mean power output and Vmax ($r = -0.833$, $p < 0.001$), and mean power output and
389 Tmax ($r = -0.508$, $p < 0.001$) when considering young and older individual's data.

390

391 **3.3 Wingate**

392 *Dynamic measures of NM fatigue*

393 No age-related differences were observed in the reduction of Pmax (young: $58 \pm 12\%$ and
394 old: $63 \pm 10\%$ of PRE, $p = 0.281$, Figure 2a), Vmax (young: $71 \pm 10\%$ and old: $77 \pm 5\%$ of

395 PRE, $p = 0.106$, Figure 2b), and Tmax (both: $82 \pm 9\%$ of PRE, $p = 0.980$, Figure 2c) after
396 the WING. There was an interaction between T-V relationship variables (i.e., instantaneous
397 torque and velocity) \times time \times age in the WING condition, which suggests an overall down
398 and leftward shift in the T-V relationship curve with aging and fatigue ($F(1,19) = 42.397$, p
399 < 0.001 , $d = 1.91$, Figure 3a). Instantaneous torque and velocity decreased after the WING
400 for both groups (all $p < 0.001$, $d \geq 3.01$). During the recovery, there was a time \times age
401 interaction for Pmax ($F(4,72) = 3.088$, $p = 0.021$, $d = 0.84$, Figure 2a) and Tmax ($F(4,72) =$
402 4.451 , $p = 0.003$, $d = 1.00$, Figure 2c). Young individuals had a slower recovery of Pmax
403 from +1 to +8 min of recovery (all $p < 0.026$, $d \leq -1.37$) and Tmax at +4 min ($p = 0.015$, d
404 $= -1.51$) compared with older participants. There was no difference in Vmax recovery
405 pattern between young and older males (all $p > 0.05$).

406

407 *Isometric measures of NM fatigue*

408 Young and older individuals presented similar levels of NM fatigue measured in isometric
409 mode after the Wingate (all $p > 0.05$). IMVC decreased to $81 \pm 8\%$ in young and $76 \pm 8\%$
410 of PRE in older individuals ($p = 0.177$, Figure 4a). There were no differences between the
411 age groups for VA (young: $100 \pm 3\%$ and old: $101 \pm 4\%$ of PRE, $p = 0.915$, Figure 5a),
412 Db100 (young: $79 \pm 15\%$ and old: $80 \pm 7\%$ of PRE, $p = 0.884$, Figure 5b), and Db10:100
413 (young: $73 \pm 12\%$ and old: $79 \pm 19\%$ of PRE, $p = 0.433$, Figure 5c) after the WING. M-
414 wave area did not change from baseline for both young and older individuals (young: $108 \pm$
415 9% and old: $100 \pm 14\%$ of PRE, $p = 0.145$, Figure 5d). Electromyography (EMG) and co-
416 contraction responses as POST were similar across the age groups after this condition (all p

417 > 0.05 , *data not shown*). During the recovery, there was no time \times age interaction for
418 IMVC, VA, Db100, Db10:100, and M-wave after the WING (all $p > 0.05$). These results
419 suggest the kinetics of recovery of these variables was similar between young and older
420 individuals in this condition.

421

422 *Pt properties*

423 All the Pt properties changed similarly after NM fatigue (i.e., at POST) in young and older
424 individuals (all $p > 0.05$). During the recovery, there was an interaction between time \times age
425 for HRT ($F(4,56) = 3.292$, $p = 0.017$, $d = 1.00$, *data not shown*), suggesting higher HRT
426 values for young than older individuals. Additionally, MRFR was lower in young
427 participants during the WING recovery (age effect: $F(1,16) = 4.737$, $p = 0.045$, $d = -1.09$,
428 *data not shown*). No age-related difference was observed for the other Pt properties during
429 the recovery of the WING (all $p > 0.05$).

430

431 **3.4 Severe-intensity exercise**

432 *Dynamic measures of NM fatigue*

433 In the SEV condition, Pmax losses were greater in young than in older individuals (young:
434 $74 \pm 8\%$ and old: $90 \pm 12\%$ of PRE, $t(18) = 3.399$, $p = 0.003$, $d = -1.57$, Figure 2d), but
435 there was an absence of age-related significant difference in the decrease of Vmax (young:
436 $87 \pm 11\%$ and old: $96 \pm 11\%$ of PRE, $p = 0.068$, Figure 2e) and Tmax (young: $87 \pm 15\%$
437 and old: $94 \pm 12\%$ of PRE, $p = 0.281$, Figure 2f). There was no interaction between the T-V
438 relationship variables \times time \times age in this condition ($p = 0.182$). However, there was a main

439 effect of time ($F(1,2) = 25.931, p < 0.001, d = 1.36$) and age ($F(1,20) = 7.560, p = 0.012, d$
440 $= 0.57$, Figure 3b), suggesting a down and leftward shift in the T-V relationship curve with
441 fatigue and aging. During the SEV exercise recovery, Pmax was significantly lower in
442 young compared with older males (age effect: $F(1,18) = 12.650, p = 0.002, d = -1.67$,
443 Figure 2d). Vmax and Tmax recovery patterns were similar in young and older males (all p
444 > 0.05).

445

446 *Isometric measures of NM fatigue*

447 IMVC decrements were greater in young than in older individuals after the SEV condition
448 ($62 \pm 12\%$ vs $81 \pm 10\%$ of PRE, respectively, $t(18) = 2.511, p = 0.022, d = -1.72$, Figure
449 4b). There was no difference between the age groups for VA (young: $92 \pm 11\%$ and old: 92
450 $\pm 7\%$ of PRE, $p = 0.932$, Figure 5b). Young individuals presented greater reductions of
451 Db100 (young: $67 \pm 12\%$ and old: $92 \pm 17\%$ of PRE, $t(18) = 3.812, p = 0.001, d = -1.70$,
452 Figure 5b) and Db10:100 (young: $69 \pm 15\%$ and old: $84 \pm 15\%$ of PRE, $t(18) = 2.315, p =$
453 $0.033, d = -1.00$, Figure 5c) after the SEV task. There was no difference in M-wave area
454 between young and older individuals (young: $113 \pm 7\%$ and old: $111 \pm 15\%$ of PRE, $p =$
455 0.720 , Figure 5d). Electromyography (EMG) and co-contraction responses were similar
456 across the age groups (all $p > 0.05$, *data not shown*). During the recovery, there was an age
457 effect for IMVC ($F(1,18) = 14.470, p = 0.001, d = 1.80$, Figure 4b) and Db100 ($F(1,18) =$
458 $18.120, p < 0.001, d = 2.00$, *data not shown*). VA, Db10:100, and M-wave responses were
459 not different between young and older males during the recovery of the SEV exercise (all p
460 > 0.05).

461

462 *Pt properties*

463 Young individuals demonstrated a greater decrease in Pt amplitude ($t(17) = 2.365$, $p = 0.03$,
464 $d = -1.09$) and TPT ($t(18) = -2.294$, $p = 0.034$, $d = -1.51$, Table 3) in the T-V relationship
465 test day after SEV task. In contrast, after the NM function test, TPT decrease more in older
466 individuals ($t(17) = 2.640$, $p = 0.045$, $d = 0.99$, Table 3). HRT, MRFD and MRFR
467 properties changed similarly after NM fatigue in young and older individuals (all $p > 0.05$).
468 During the recovery, there was only an age effect for Pt ($F(1,18) = 5.365$, $p = 0.033$, $d =$
469 1.09 , *data not shown*). No age-related differences were observed for Pt properties during
470 the recovery of the SEV task (all $p > 0.05$).

471

472 **3.5 Moderate-intensity exercise**

473 Following the MOD task, there were no age-related differences in Pmax (young: $94 \pm 10\%$
474 and old: $98 \pm 7\%$ of PRE, $p = 0.405$, Figure 2g), Vmax (both $103 \pm 9\%$ of PRE, $p = 0.974$,
475 Figure 2h), and Tmax (young: $91 \pm 7\%$ and old: $95 \pm 8\%$ of PRE, $p = 0.291$, Figure 2i).
476 There was a significant interaction between the T-V relationship variables \times time \times age
477 ($F(1,21) = 5.700$, $p = 0.026$, $d = 0.43$, Figure 3c). Instantaneous torque decreased after the
478 MOD task for both groups (all $p = 0.006$, $d = 0.81$). Pmax, Vmax, and Tmax recovery
479 patterns were similar in young and older males (all $p > 0.05$).

480

481 *Isometric measures of NM fatigue*

482 IMVC decreased similarly in young and older individuals after the MOD task (young: $79 \pm$
483 13% and old: $82 \pm 10\%$ of PRE, $p = 0.623$, Figure 4c). There was no difference between
484 the age groups for VA (young: $91 \pm 11\%$ and old: $92 \pm 9\%$ of PRE, $p = 0.819$, Figure 5a).
485 Db100 decreased more in young individuals (young: $84 \pm 10\%$ and old: $98 \pm 21\%$ of PRE,
486 $t(17) = 4.692$, $p < 0.001$, $d = -0.85$, Figure 5b), but Db10:100 levels were similar in young
487 and older males after the MOD exercise (young: $87 \pm 8\%$ and old: $91 \pm 10\%$ of PRE, $p =$
488 0.302 , Figure 5c). M-wave area was more depreciated after the MOD task in young when
489 compared with older males (young: $83 \pm 6\%$ and old: $96 \pm 10\%$ of PRE, $t(18) = 3.558$, $p =$
490 0.002 , $d = -1.58$, Figure 5d). During the recovery, there was an age effect for IMVC
491 ($F(1,18) = 7.284$, $p = 0.015$, $d = 1.28$, Figure 4c), M-wave area ($F(1,18) = 27.669$, $p <$
492 0.001 , $d = 2.50$, *data not shown*), and Db100 ($F(1,18) = 9.179$, $p = 0.007$, $d = 1.44$, *data not*
493 *shown*). These effects of age represent lower values—relative to PRE—in young
494 individuals during the recovery in comparison with older males. VA and Db10:100 levels
495 were similar in young and older individuals during the recovery period (all $p > 0.05$).

496

497 *Pt properties*

498 MRFD was lower in young individuals in the T-V relationship test ($t(17) = 2.182$, $p =$
499 0.043 , $d = -1.01$, Table 3). During the recovery, only MRFD was significantly lower in
500 young individuals throughout the recovery period ($F(1,17) = 5.409$, $p = 0.033$, $d = -1.15$,
501 *data not shown*). No age-related differences were found for other Pt properties after fatigue
502 and during the recovery period (all $p > 0.05$).

503

504 **4. Discussion**

505 The findings of this study refute the hypothesis that Pmax, Vmax, and Tmax would be
506 reduced to a greater extent in older males. Different than expected, Pmax levels were more
507 reduced in young compared with older individuals after the SEV task. Our results support,
508 however, the hypothesis that older individuals present a down and leftward shift in the T-V
509 relationship curve at PRE and POST in comparison with their younger counterparts.

510 Additionally, this study refutes the hypothesis that WING exercise would induce greater
511 decrease in IMVC and peripheral fatigue in young when compared with older individuals.
512 These differences between age-groups were actually found for the SEV exercise. Young
513 males presented greater levels of NM fatigue in this condition when IMVC and evoked
514 forces (Db100 and Db10:100) were considered the fatigue index. No age-related difference
515 in Pmax, Vmax, and Tmax recovery kinetics was expected; however, our results showed
516 that young males present a slower recovery of Pmax and Tmax after the WING. These
517 results demonstrate that age-related differences in NM fatigue after dynamic cycling tasks
518 with large muscle mass are influenced by the exercise intensity and duration.

519

520 ***4.1 Age-related differences in NM fatigue***

521 The great amount of work and power output sustained during the SEV task by young
522 individuals may, at least partly, explain the higher decrease in IMVC and greater peripheral
523 fatigue (Db100 and Db10:100) observed in young, when compared with older males, in this
524 condition. While total work and mean power output were ~30% greater in young when
525 compared with older males during the WING, these differences were much higher during

526 the SEV and MOD tasks (total work and power output were ~67% and ~87%, respectively,
527 greater in young individuals). The lower differences between young and older individuals
528 in total work and mean power output developed during the WING may support the absence
529 of age-related difference in NM fatigue in this trial.

530 The lower ability of older individuals to produce and sustain high levels of power
531 output during cycling exercises can be explained by both neuromuscular and cardiovascular
532 age-related changes. In respect of the neuromuscular system, muscle maximal force and
533 mass decrements with aging (see IMVC and CSA age-related differences in Table 1) are
534 primarily related to the loss of motor units' number and atrophy of the survivor ones
535 (Andersen et al., 1999; Power et al., 2010). When motor units' axons deteriorate, single
536 muscle fibers can either lose their functionality or be sprouted by collateral axons (Hepple
537 and Rice, 2016). This last process leads to an increase in myosin heavy chain (MHC) co-
538 expression in the skeletal muscle fiber population (Hepple and Rice, 2016) and in the
539 number of fibers expressing MHC isoforms I (Andersen et al., 1999), which are slower and
540 weaker than MHC II isoforms (Bottinelli et al., 1994). Even when young and older
541 individuals are matched by physical activity status, older adults still present higher relative
542 abundance of MHC I and lower MHC II in the VL when compared with young adults
543 (Sundberg et al., 2018b). Another consequence of aging in the skeletal muscle system is the
544 decrease in muscle quality (i.e., IMVC:CSA, see Table 1). This aging process has been
545 associated with molecular alterations at the myosin structure level and with lower percent
546 of myosin strongly attached to actin in muscle fibers in rats (Canepari et al., 2010), and
547 reductions in muscle protein quantity in humans (Power et al., 2014). From a

548 cardiovascular perspective, there is a reduction in maximal aerobic capacity with aging
549 because of the natural age-related decrease in maximal heart rate and cardiac output
550 responses during exercise (Grey et al., 2015) (see Table 2). Impairments in cardiac output
551 with aging impact muscle O₂ delivery and, consequently, power output production during
552 exercise as cardiac output plays an important role in blood flow distribution and O₂
553 transport to active muscles (Betik and Hepple, 2008). In fact, it has been shown that the
554 age-related downward shift in the power-duration during exercise is associated with
555 reduced O₂ transport and utilization (Poole et al., 2016). This impacts our results because
556 the MOD and SEV exercises were prescribed based on the power output achieved at VT1
557 and VT2, respectively. As older individuals produced less power output during this test, the
558 absolute power output at VT1 and VT2 was lower in older individuals when compared with
559 their younger counterparts and, therefore, older males sustained lower power output levels
560 during the exercise conditions.

561 These natural age-related neuromuscular and cardiovascular changes during the
562 lifespan have a direct impact in motor performance (Hunter et al., 2016). The reduction in
563 the capacity to perform motor activities with aging is often marked by a lower ability to
564 produce and/or sustain high levels of force and power during dynamic exercises or even
565 during activities of daily living (Casas-Herrero et al., 2013). Briefly, the age-related
566 responses in NM fatigue during cycling exercises can be examined using two main
567 methods. The first approach consists of asking young and older individuals to cycle against
568 the same absolute intensity (e.g., 100 W). In this scenario, it is evident that older
569 individuals would present greater levels of NM fatigue because they would cycle at higher

570 relative intensities than young individuals (see Table 1 and Weavil et al., 2018 for more
571 details). In the second approach, both age groups cycle at the same relative intensity (e.g.,
572 10% above VT2). When using this last method to induce NM fatigue, young individuals
573 produce and sustain greater levels of force during the exercise task, which can lead to
574 greater levels of NM fatigue in this population (Weavil et al., 2018).

575 Interestingly, the only other study to date that examined age-related NM fatigue
576 after cycling also found a greater IMVC loss in young *vs* older individuals after both age
577 groups cycled at the same relative intensity (80% of peak power output) (Weavil et al.,
578 2018). Specific new insights from the present study are the use of a different method to
579 determine exercise intensity (based on the VTs). Furthermore, this study shows, for the first
580 time, that age-related NM fatigue after cycling depends on the exercise intensity and
581 duration. Young and older individuals presented similar overall levels of NM fatigue after
582 the WING and MOD tasks, but not after the SEV exercise. It is also important to note that
583 exercise intensities should ideally not be prescribed using a relative percent of peak power
584 output as peak power output determination depends on the exercise protocol (Keir et al.,
585 2018). This approach can be problematic as it assumes that exercises performed at a certain
586 percent of $\dot{V}O_2$ peak elicit similar metabolic demands between individuals (Keir et al.,
587 2018). For example, if the MOD exercise was performed at 70% of $\dot{V}O_2$ peak, young males
588 would be exercising at intensities slightly below VT1 whereas older males would be
589 exercising at intensities slightly above VT1 (see Table 2). Therefore, although our approach
590 has a few limitations too (Keir et al., 2018), it might be a more suitable method to
591 determine exercise intensity and age-related differences in NM fatigue.

592 The greater absolute intensity sustained during the SEV exercise by young males
593 implies greater force applied to the pedal. It has been established that higher absolute force
594 production during high-intensity cycling exercises leads to great accumulation of
595 metabolites with fatigue (Black et al., 2017). This could explain the great decrements in
596 force and power levels in young participants following the SEV exercise. To test this
597 hypothesis, we explored the association between mean power output sustained during the
598 exercise trials and the decrements in dynamic measures of NM fatigue (% of PRE). Our
599 findings outline that the greater the mean power output sustained during the task, the
600 greater the reduction in Pmax, Tmax, and Vmax levels after the task (i.e., greater levels of
601 fatigue).

602 Although muscle metabolites (e.g., inorganic phosphate) were not measured in this
603 study, we suspect the higher absolute PO sustained during the SEV task by young males led
604 to a greater metabolites' accumulation in young than in older individuals. This presumption
605 can be further supported by the greater levels of force reduction and LFF in young
606 compared with older males. The combination of acidosis and inorganic phosphate (Pi) is an
607 important mediator of muscle fatigue in humans because it causes a dissociation between
608 myosin and actin and, therefore, reverses force generation (Debold, 2012; Sundberg et al.,
609 2018a). When Pi concentrations are increased due to fatigue, Pi can bind to Ca²⁺ inside the
610 sarcoplasmic reticulum and decrease Ca²⁺ availability (Fryer et al., 1995). The reduction in
611 Ca²⁺ for muscle contraction leads to excitation-contraction coupling failure, which is
612 reflected by greater LFF (Jones, 1996).

613 Intramuscular metabolites are not expected to significantly accumulate during MOD
614 exercises (Black et al., 2017). Thus, the cellular mechanisms behind the lower levels of
615 Db100, M-wave, and MRFD observed in young individuals in MOD exercise remain to be
616 elucidated. It should be considered, however, that the lower sample size in this condition
617 might have reduced the power of these findings. Four participants (1 young and 3 old) were
618 excluded from the dynamic measures of fatigue analyses in the MOD condition.

619

620 *4.2 Age-related differences in NM fatigue recovery*

621 Despite the absence of age-related differences in NM fatigue at POST WING, young males
622 presented a slower recovery of Pmax, Tmax, and HRT in this condition. These results
623 suggest that Pmax and Tmax recovery may be at least partially limited by factors related to
624 prolongation of muscle relaxation time (Jones et al., 2006) caused by a slower cross-bridge
625 detachment rate in young individuals (Edwards et al., 1975). The recovery of Pmax after a
626 WING is commonly associated with muscle metabolites re-synthesis, such as PCr
627 (Bogdanis et al., 1995). Nevertheless, strong evidences suggest that oxidative capacity in
628 the knee extensors measured through PCr recovery kinetics is slower in older individuals
629 when compared with young adults (Fitzgerald et al., 2016). Therefore, although the slow
630 Pmax and Tmax recovery after the WING in young is a very interesting novel finding of
631 this study, the responsible mechanisms for the delayed recovery in young individuals
632 should be further explored.

633 Different from what has been found after isometric tasks (Dalton et al., 2010a;
634 Yoon et al., 2013; Yoon et al., 2012), our results suggest that NM fatigue recovery kinetics

635 assessed in isometric mode is overall not affected by age after fatigue induced by dynamic
636 movements. Some studies have suggested that the delayed recovery of force in older
637 individuals is 25-35% explained by a slower recovery of central neural drive (i.e., VA
638 recovery) (Hunter et al., 2008; Dalton et al., 2010a; Yoon et al., 2013; Yoon et al., 2012).
639 However, we did not find any age-related significant difference in IMVC and VA during
640 the recovery period across the exercise conditions.

641

642 ***4.3 Limitations***

643 Because the exercises were not performed to volitional exhaustion, participants did not
644 achieve maximal rate of perceived exertion at the end of the trials (e.g., mean of rate of
645 perceived exertion was 18 out of 20 after the SEV task). There was, however, a clear
646 evidence of large NM fatigue in both age groups, which is notable by the decrease in IMVC
647 following all the exercise trials. In addition, young and older participants cycled at the same
648 relative intensity during the three exercises (i.e., maximal intensity for WING and same
649 percentage of VTs for the other two submaximal exercises). Another limitation is the
650 absence of exercise-related metabolites measurements, which could have supported the
651 presumption of greater accumulation of by-products in the SEV exercise in young vs older
652 participants. It should also be addressed that the redistribution of joint torques with aging
653 can impact T-V relationship assessments. Furthermore, the T-V relationships plotted during
654 7-s cycling sprints represent the force production capacities of all the lower limbs' extensor
655 muscles (Elmer et al., 2011). Differently, during IMVC the quadriceps muscles are mainly
656 recruited during the contraction (Bampouras et al., 2017).

657

658 5. Conclusion

659 In conclusion, by using a novel methodological approach to assess Pmax (i.e., during multi-
660 joint lower limb movements), our results add new information to the current literature as
661 we showed that age-related NM fatigue depends on the exercise intensity and duration and
662 that young males are as fatigable—for the WING and MOD exercise—or more fatigable—
663 for SEV exercise—than older participants. These results partially confirm previous findings
664 as we showed greater IMVC loss in young adults when young and older individuals cycled
665 at the same relative intensity in the SEV condition. Additionally, we inferred that the
666 mechanism responsible for the greater fatigability response in young individuals in the SEV
667 condition was a greater metabolites accumulation. Interestingly, the only age-related
668 difference in the recovery of NM fatigue was a slower recovery of Pmax, Tmax, and HRT
669 in young males after the WING. These findings suggest that NM recovery in young males
670 may be at least partially limited by factors related to prolongation of muscle relaxation time
671 in this condition.

672

673 CONFLICTS OF INTEREST

674 The authors have no conflict of interest in relation to the present scientific paper.

675

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680

681 **AUTHOR CONTRIBUTIONS**

682 Design of the study: R.L.K., S.J.A., M.A.V., P.S. and G.Y.M. Data collection, analysis and
683 interpretation: R.L.K., S.J.A. and L.M.J. Draft the paper and critical review: R.L.K., S.J.A.,
684 L.M.J., M.A.V., P.S. and G.Y.M. All persons designated as authors qualify for authorship
685 and all authors have approved the final version of the manuscript.

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Table 1. Age-related differences at baseline.

	Young (n = 10)	95% CI	Old (n = 10)	95% CI	<i>p-value</i>
Age (years old)	27 ± 4	24-30	74 ± 4*	71-77	<0.001
Height (cm)	181 ± 6	176-185	174 ± 9	169-180	0.073
Weight (kg)	79 ± 9	73-86	77 ± 8	71-83	0.577
BMI (kg/m ²)	24 ± 2	23-26	25 ± 3	23-28	0.326
LSI	48 ± 27	28-67	42 ± 29	22-63	0.633
VL CSA (cm ²)	30 ± 4#	22-35	17 ± 3*	15-20	<0.001
RF CSA (cm ²)	8 ± 1#	6-9	5 ± 1*	5-6	0.004
IMVC (N)	359 ± 17	321-397	299 ± 13*	269-330	0.013
IMVC:CSA (N·cm ⁻²)	4.5 ± 1.0#	3.5 – 5.4	2.0 ± 0.5*	1.6-2.0	< 0.001
Pmax (W)	981 ± 197	829-1099	707 ± 79*	643-759	0.001
Vmax (rad·s ⁻¹)	25 ± 4	23-26	22 ± 2	21-23	0.054
Tmax (N·m)	158 ± 34	133-182	127 ± 17*	114-140	0.021
Db100 (N)	186 ± 14	171-200	129 ± 13*	118-141	<0.001

Db10:100	1.02 ± 0.05	0.97-1.06	1.03 ± 0.06	0.99-1.10	0.532
Pt (N)	128 ± 7	116-141	92 ± 8*	79-105	<0.001
VA (%)	95 ± 2	93-97	97 ± 2	95-98	0.116
TPT (s)	0.07 ± 0.01	0.06-0.07	0.08 ± 0.01*	0.08-0.09	0.010
HRT (s)	0.08 ± 0.01	0.07-0.09	0.08 ± 0.02	0.07-0.09	0.866
MRFD (N·s ⁻¹)	3552 ± 353	3172-3932	2220 ± 450*	1897-2542	<0.001
MRFR (N·s ⁻¹)	1638 ± 259	1391-1885	937 ± 222*	778-1096	<0.001
EMG (RMS·Mmax ⁻¹)	0.04 ± 0.01	0.03-0.05	0.06 ± 0.01	0.04-0.07	0.094
Co-contraction (%)	12 ± 4	9-15	9 ± 2*	7-10	0.048

949 * Significant difference between young and old ($p < 0.05$). # $n = 7$. CI: confidence interval; BMI: body mass index; LSI: Leisure-
950 score index; VL: vastus lateralis; RF: rectus femoris; CSA: cross-sectional area; IMVC: isometric maximal voluntary
951 contraction; Db100: high-frequency doublet; Db10:100: ratio between Db10 and Db100; Pt: peak twitch; VA: voluntary
952 activation; TPT: time to peak torque; HRT: twitch half-relaxation time; MRFD: twitch maximal rate of force development;
953 MRFR: twitch maximal rate of force relaxation; EMG: electromyography during IMVC. Co-contraction: BF EMG RMS
954 recorded during knee extension IMVCs normalized to maximal BF EMG RMS obtained during 5-s knee flexions IMVCs. Peak
955 Twitch properties (CT, HRT, MRFD and MRFR) from the neuromuscular function protocol were analyzed at baseline.

Table 2. Exercises characteristics.

	Young (n = 10)	95% CI	Old (n = 10)	95% CI	<i>p-value</i>
Incremental exercise					
$\dot{V}O_{2peak}$ (mL·kg ⁻¹ ·min ⁻¹)	49 ± 7	44-54	31 ± 8*	25-37	<0.001
Peak power output (W)	304 ± 53	266-342	199 ± 42*	168-229	<0.001
Peak heart rate (bpm)	182 ± 9	177-188	144 ± 18*	136-155	<0.001
<i>Ventilatory threshold 1</i>					
Intensity relative to $\dot{V}O_{2peak}$ (%)	65 ± 5	62-68	72 ± 7*	67-76	0.018
Power output (W)	155 ± 10	148-162	82 ± 12*	74-91	<0.001
<i>Ventilatory threshold 2</i>					
Intensity relative to $\dot{V}O_{2peak}$ (%)	85 ± 4	82-88	87 ± 4	84-90	0.362
Power output (W)	226 ± 30	205-248	135 ± 22*	120-151	<0.001
Fatiguing tasks					
WING mean power output (W)	652 ± 169	531-772	507 ± 74*	451-563	0.024
WING mean cadence (rpm)	130 ± 14	120-140	103 ± 7*	98-108	<0.001

Table 3. Age-related differences in peak twitch properties responses to NM fatigue.

WING total work (kJ)	20 ± 5	16-23	15 ± 2*	14-17	0.021
SEV mean power output (W)	238 ± 32	215-261	142 ± 22*	126-159	<0.001
SEV mean cadence (rpm)	76 ± 5	72-80	76 ± 4	72-79	0.894
SEV total work (kJ)	143 ± 18	129-156	85 ± 14*	75-95	<0.001
MOD mean power output (W)	124 ± 8	118-130	66 ± 9*	59-73	<0.001
MOD mean cadence (rpm)	76 ± 6	72-81	76 ± 5	72-80	0.857
MOD total work (kJ)	669 ± 39	639-698	355 ± 51*	319-391	<0.001

956 * Significant difference between young and old ($p < 0.05$). CI: confidence interval; $\dot{V}O_{2peak}$: peak oxygen uptake; $\dot{V}O_2$: oxygen

957 uptake; WING: Wingate; SEV: 10-min at severe-intensity; MOD: 90-min at moderate-intensity exercise.

	WING		SEV		MOD	
	Young	Old	Young	Old	Young	Old
<i>T-V relationship test</i>						
PT	46 ± 12	57 ± 13	58 ± 17	74 ± 12*	81 ± 18	97 ± 22
TPT	127 ± 28	128 ± 43	73 ± 9	89 ± 12*	93 ± 12	91 ± 29
HRT	139 ± 51	131 ± 45	103 ± 42	121 ± 31	98 ± 14	98 ± 13
MRFD	44 ± 13	49 ± 15	62 ± 22	84 ± 32	86 ± 19	115 ± 37*
MRFR	36 ± 16	53 ± 16	60 ± 24	67 ± 31	88 ± 25	97 ± 29
<i>NM function test</i>						
PT	50 ± 19	60 ± 18	56 ± 18	74 ± 29	86 ± 7	88 ± 21
TPT	117 ± 20	124 ± 30	102 ± 12	85 ± 21*	97 ± 10	88 ± 22
HRT	120 ± 27	128 ± 31	108 ± 37	114 ± 23	94 ± 20	108 ± 35
MRFD	43 ± 13	57 ± 31	52 ± 12	77 ± 52	93 ± 43	108 ± 25
MRFR	53 ± 17	53 ± 17	55 ± 19	81 ± 41	88 ± 10	102 ± 24

958 All data are expressed in % of PRE.

959 * Significant difference between young and old ($p < 0.05$). WING: Wingate; SEV: 10-min at severe-intensity; MOD: 90-min at
960 moderate-intensity exercise; PT: peak twitch; TPT: time to peak torque; HRT: twitch half-relaxation time; MRFD: twitch
961 maximal rate of force development; MRFR: twitch maximal rate of force relaxation.

962 **FIGURE LEGENDS**

963 **Figure 1. Experimental design.**

964 Panel A: Torque-velocity (T-V) relationship protocol; Panel B: T-V and power-velocity (P-
965 V) relationships plotted from 7-s cycling sprints (reprinted with permission from Krüger et
966 al., 2019); Panel C: Neuromuscular (NM) function test; and Panel D: The innovative
967 recumbent cycling ergometer (reprinted with permission from Doyle-Baker et al., 2018).
968 Db100: high-frequency doubled; Db10: low-frequency doublet; Tw: twitch; Pmax:
969 maximal power output; Vmax: maximal velocity; and Tmax: maximal torque.

970

971 **Figure 2. Age-related differences in dynamic measures of NM fatigue 10-s after the**
972 **exercise conditions (POST) and during recovery (+1-8 min).**

973 WING: Wingate; SEV: 10-min at severe-intensity; MOD: 90-min at moderate-intensity
974 exercise; Pmax: maximal power output; Vmax: maximal velocity; Tmax: maximal torque.

975 * Significant difference between young and old at POST (Independent t-test, $p < 0.05$).

976 # Age effect (Two-way ANOVA followed by Bonferroni post-hoc test, $p < 0.05$).

977

978 **Figure 3. Torque-velocity (T-V) relationship before (PRE) and 10-s after the exercise**
979 **conditions (POST).**

980 WING: Wingate; SEV: 10-min at severe-intensity; MOD: 90-min at moderate-intensity
981 exercise; Pmax: maximal power output; Vmax: maximal velocity; Tmax: maximal torque.

982

983 **Figure 4. Age-related differences in isometric measures of NM fatigue 10-s after the**
984 **exercise conditions (POST) and during recovery (+1-8 min).**

985 WING: Wingate; SEV: 10-min at severe-intensity; MOD: 90-min at moderate-intensity
986 exercise; IMVC: isometric maximal voluntary contraction.

987 * Significant difference between young and old at POST (Independent t-test, $p < 0.05$).

988 # Age effect (Two-way ANOVA followed by Bonferroni post-hoc test, $p < 0.05$).

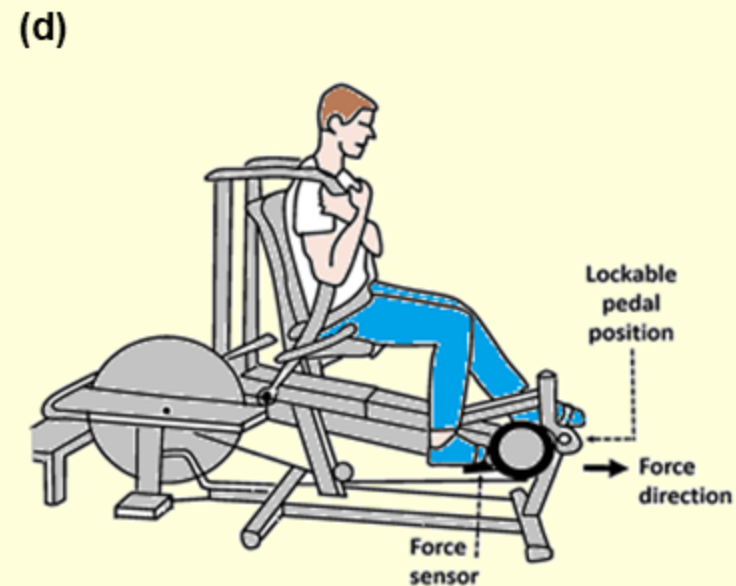
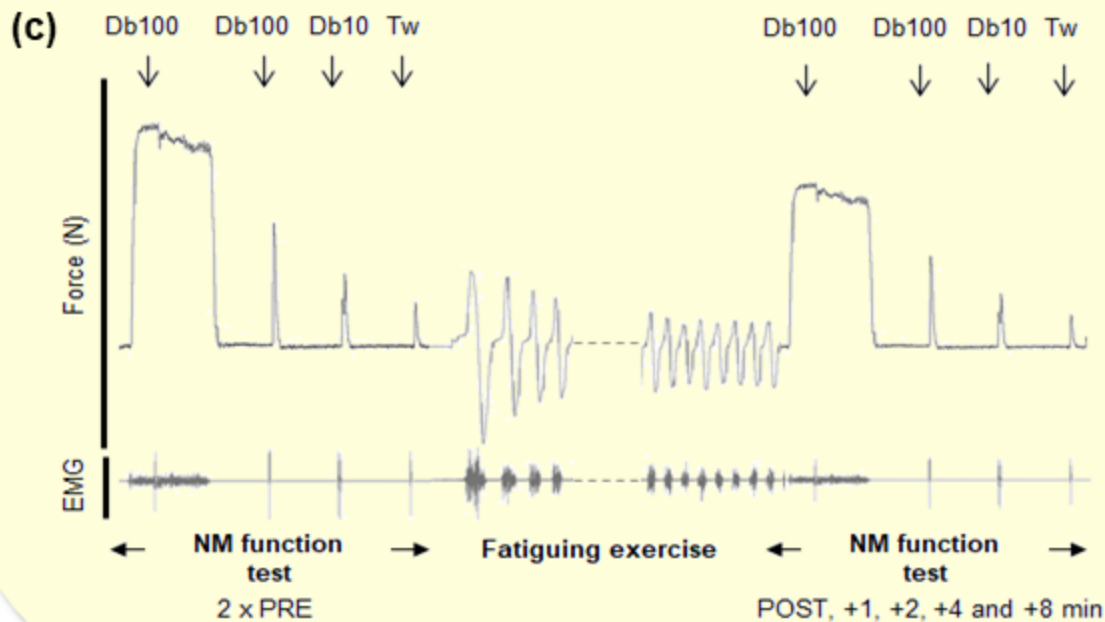
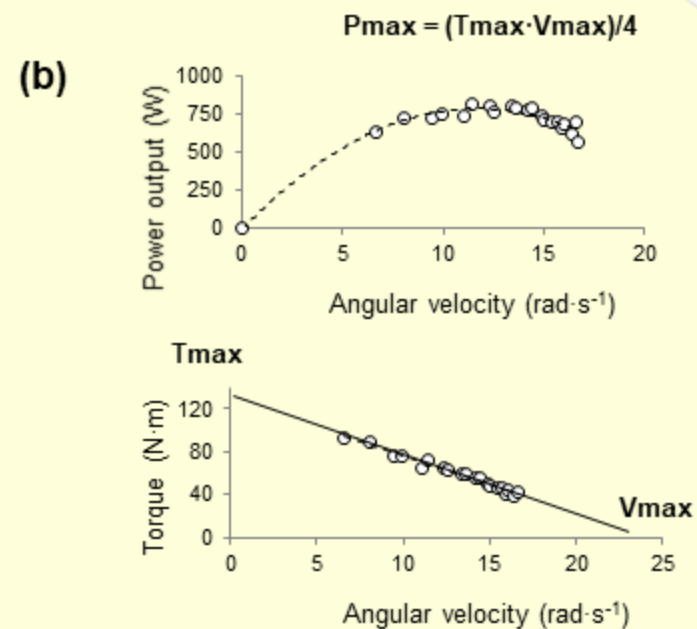
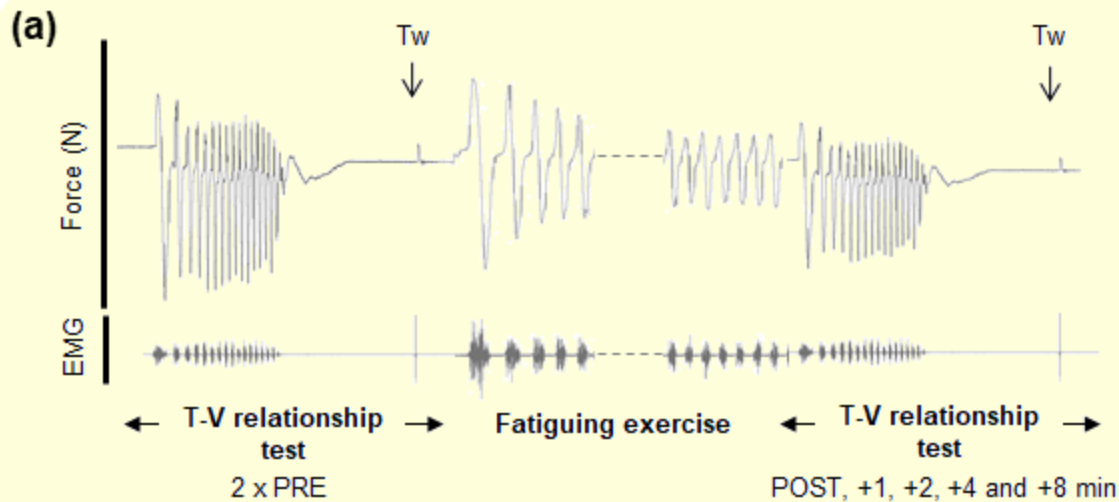
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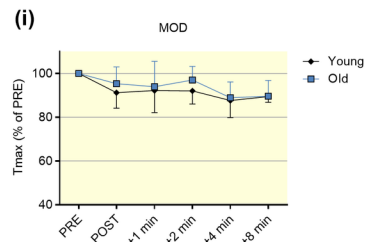
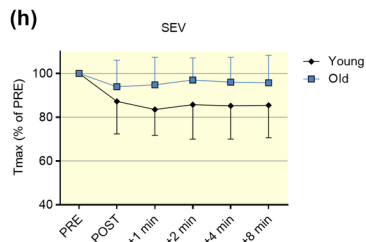
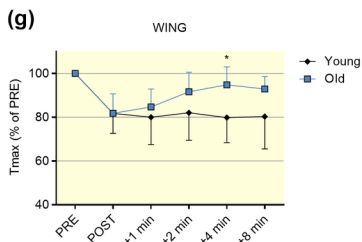
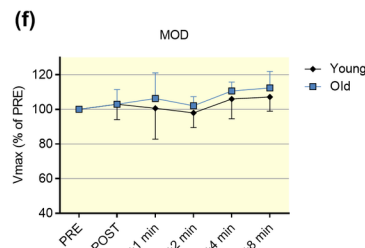
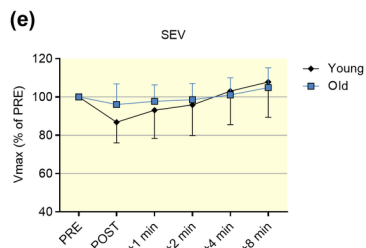
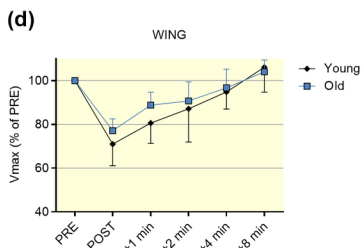
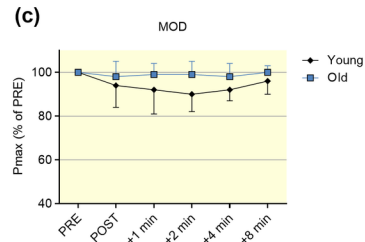
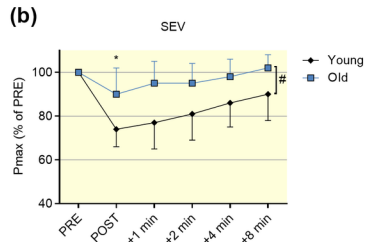
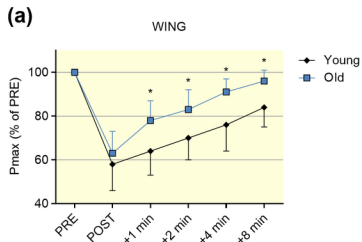
990 **Figure 5. Age-related differences in central and peripheral mechanisms of fatigue 10-s**
991 **after the exercise conditions (POST).**

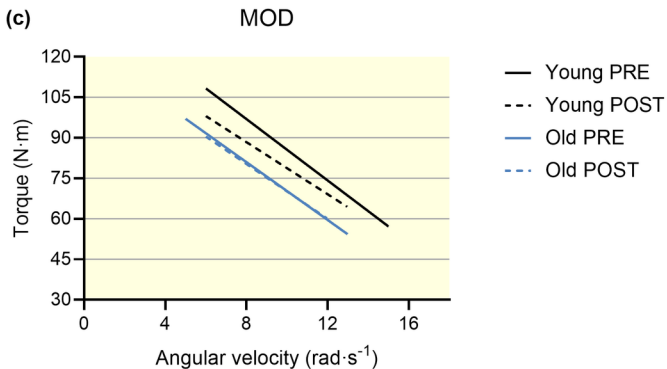
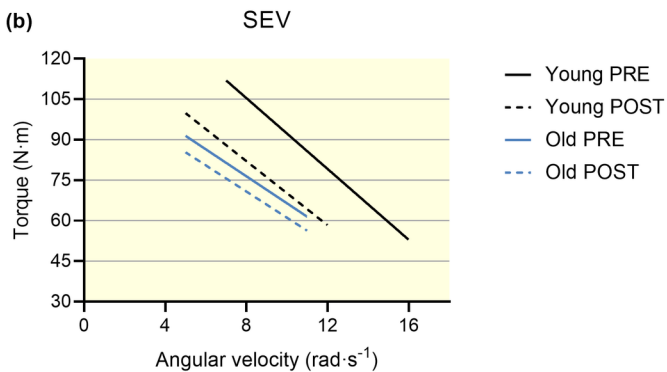
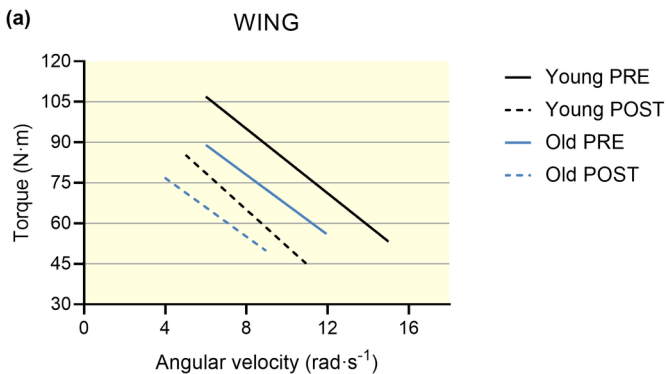
992 Voluntary activation (VA, panel A); high-frequency doublet (DB100, panel B); low-
993 frequency fatigue (Db10:100, panel C); and M-wave area (panel D).

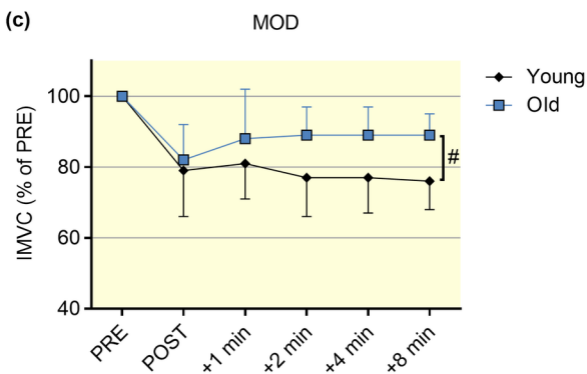
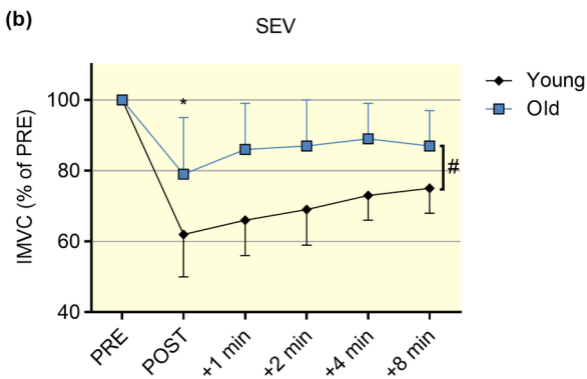
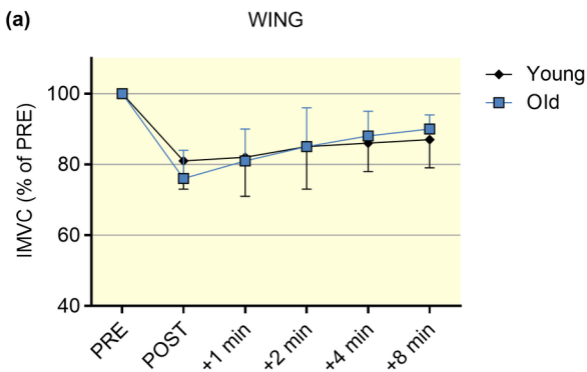
994 * Significant difference between young and old (Independent t-test, $p < 0.05$).

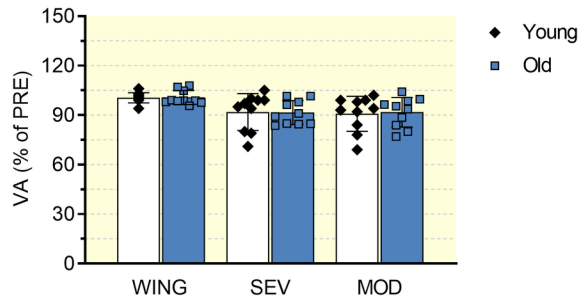
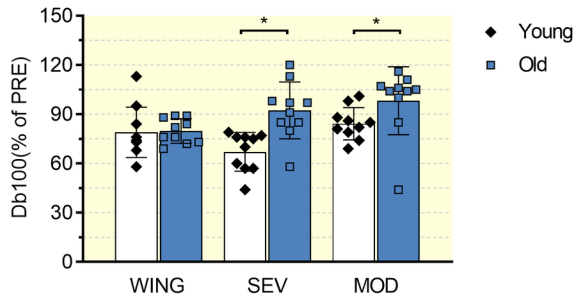
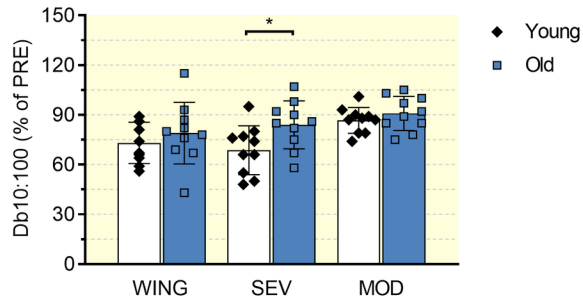
995









(a)**(b)****(c)****(d)**