

14

ABSTRACT

15 Eccentric contractions are thought to require a unique neural activation strategy. However,
16 due to greater intrinsic force generating capacity of muscle fibres during eccentric contraction,
17 the understanding of neural modulation of different contraction types during submaximal
18 contractions may be impeded by the force normalisation procedure employed. In the present
19 experiment, subjects performed maximal isometric dorsiflexion at shorter (80°), intermediate
20 (90°) and longer (100°) muscle lengths, and maximal concentric and eccentric contractions.
21 Thereafter, submaximal concentric and eccentric contractions were performed normalised to
22 either isometric maximum at 90° (ISO), contraction type specific maximum (CTS) or muscle
23 length specific maximum (MLS). When using ISO or MLS for normalisation, mean
24 submaximal eccentric torque levels were significantly lower when compared to CTS
25 normalisation (11 and 7% lower compared to CTS; $p = 0.003$ and $p = 0.018$ for ISO and
26 MLS, respectively). These experimentally observed differences closely matched those
27 expected from the predictive model. During submaximal concentric contraction, mean torque
28 levels were similar between ISO and CTS normalisation with similar discrepancies noted in
29 EMG activity. These findings suggest that normalising to ISO and MLS might not be accurate
30 for assessment and prescription of submaximal eccentric contractions.

31 **Words:** 191

32

INTRODUCTION

34 Recently, there has been a great deal of interest in the divergent neural modulation of different
35 contraction types, particularly of lengthening/eccentric contractions, which are thought to
36 require a unique activation strategy by the central nervous system (CNS; for a summary, see
37 Duchateau and Enoka, 2016). For example, muscle activity assessed by surface
38 electromyography (EMG) is usually smaller during eccentric compared to isometric and
39 concentric contractions at the same absolute load/force level (Aagaard et al., 2000; Kellis and
40 Baltzopoulos, 1998; Komi et al., 2000; Nardone and Schieppati, 1988). Furthermore,
41 corticospinal and spinal excitability as assessed by motor evoked potentials and either H-
42 reflexes or cervicomedullary evoked potentials, respectively, tend to be lower during maximal
43 and submaximal eccentric contractions (Abbruzzese et al., 1994; Duclay et al., 2014, 2011;
44 Gruber et al., 2009).

45 Whilst the force-producing capacity of human muscles during eccentric contraction appears to
46 be muscle-dependent (for review see Duchateau and Enoka, 2016), maximal eccentric
47 dorsiflexion force can be substantially greater compared to isometric and/or concentric
48 contractions (~30-50%; Pasquet *et al.*, 2000; Reeves & Narici, 2003; Klass *et al.*, 2007;
49 Duchateau & Enoka, 2016). Thus, due to this greater intrinsic force generating capacity of
50 muscle fibres during eccentric contractions (Edman, 1988; Morgan et al., 2000), submaximal
51 eccentric contractions may not be performed at an appropriate intensity relative to a maximal
52 eccentric contraction if not normalised appropriately, i.e. relative to the specific contraction
53 type. Whilst it seems clear that contraction type specificity should be accounted for when
54 normalising submaximal anisometric contractions, this is not reflected in the existing
55 literature. Indeed, there appear to be vast discrepancies regarding the procedures used for
56 normalising submaximal forces across isometric, eccentric and concentric contractions. For
57 example, anisometric contractions have been normalised relative to an isometric maximal

58 voluntary contraction (MVC; Gruber *et al.*, 2009; Kallio *et al.*, 2010), contraction-type
59 specific MVC (Rice *et al.*, 2015; Tallent *et al.*, 2012) or muscle-length specific MVC (Duclay
60 *et al.*, 2014; Pasquet *et al.*, 2006). Appropriate normalisation is of particular significance when
61 stimulations are performed to assess neuronal behaviour, such as corticospinal modulation of
62 different contraction types (e.g. Gruber *et al.*, 2009; Tallent *et al.*, 2013; Duclay *et al.*, 2014).
63 Specifically, inappropriate normalisation may result in different contraction types to be at
64 different levels of contraction intensity-stimulus response curve of various responses
65 (Capaday and Stein, 1987; Goodall *et al.*, 2009; Matthews, 1986; Oya *et al.*, 2008; Weavil *et*
66 *al.*, 2015), which could impede the understanding of the proposed divergent
67 neurophysiological response. Furthermore, appropriate normalisation is of vital importance
68 when assessing steadiness of force-matching tasks as the standard deviation and the
69 coefficient of variation of force/torque production (procedures commonly used to quantify
70 force steadiness) are dependent on relative intensity of force/torque production (Enoka *et al.*,
71 2003).

72 Given the discrepancy of normalising procedures described in the literature, the purpose of
73 this study was to directly assess and compare the influence of different normalising
74 procedures previously used under the same overall experimental conditions (i.e. the same
75 population, dynamometer setup, contraction velocity, posture and joint positioning) in torque-
76 matching tasks on mean torque and EMG activity during submaximal anisometric
77 contractions with the aim of informing practice and design of future studies. To visualise
78 discrepancies and inform a hypothesis, a predictive model based on experimentally acquired
79 different types of MVC was constructed. Based on that, it was hypothesised that the
80 experimental data will show that normalisation to an isometric MVC or muscle-length
81 specific MVC results in significantly lower submaximal torques and EMG activity compared
82 to when normalised to contraction-type specific MVC.

83

84

METHODS

85 *Participants*

86 Seven young, recreationally active (i.e. meeting the recommended activity guidelines of
87 World Health Organisation, 2010) men (age 25 ± 4 years; stature 179 ± 7 cm, mass 81 ± 10
88 kg) participated in the study. All participants were free from neurological illness or
89 musculoskeletal injury. Written informed consent was obtained prior to participation. The
90 study received institutional approval and conformed to the *Declaration of Helsinki*.

91

92 *Torque and EMG procedures*

93 Dorsiflexors were chosen as an experimental model due to their unique behaviour during
94 lengthening contractions. Specifically, whilst not all human muscles may exhibit greater force
95 capacity during eccentric contractions compared to other contractions types (for review see
96 Duchateau and Enoka, 2016), dorsiflexors have consistently demonstrated significantly
97 greater eccentric force (Pasquet *et al.*, 2000; Reeves & Narici, 2003; Klass *et al.*, 2007;
98 Duchateau & Enoka, 2016), making them a superior model compared to other muscles to
99 study discrepancies in force production across different contraction types. Dorsiflexion torque
100 from the right ankle was recorded on an isokinetic dynamometer (Cybex, Lumex Inc., USA)
101 with hip and knee angles set at 90° flexion. For anisometric contractions, range-of-motion
102 (ROM) moved from 10° dorsiflexion to 10° plantarflexion, with anatomical zero set with the
103 ankle joint at 90° . Contraction velocity was kept at $5^\circ \cdot s^{-1}$. Participants performed MVCs
104 under the following conditions: isometric contractions with the ankle at 80, 90 and 100°
105 (corresponding to shorter, intermediate and longer muscle lengths, respectively) and

106 anisometric contractions, i.e. isokinetic shortening and lengthening. For isometric
107 contractions, participants were instructed to increase torque to their maximal level and
108 maintain it for 4 s. During anisometric contractions, torque was produced during the 4-second
109 movement of the dynamometer. Surface EMG was recorded using bipolar self-adhesive
110 electrodes (8-mm diameter, 20-mm inter-electrode distance; Kendall 1041PTS, Tyco
111 Healthcare Group, USA) placed on tibialis anterior muscle belly according to SENIAM
112 recommendations at one-third of the length between the tip of the fibula and the tip of the
113 medial malleolus in the direction of this line (Hermens et al., 2000), with a ground electrode
114 placed on the patella. Prior to placement of electrodes, the recording site was shaved, abraded
115 with preparation gel and wiped clean with an alcohol swab to ensure appropriate electrode
116 resistance ($< 2\text{k}\Omega$). The EMG signal was amplified ($\times 1000$) and band pass filtered (3-1000
117 Hz; Neurolog System, Digitimer Ltd, UK). Torque and EMG signals were digitised (5 kHz;
118 CED 1401, CED, UK), acquired and analysed off line (Spike2, v8, CED, UK).

119

120 *Experimental protocol*

121 Participants attended the laboratory to complete a single measurement session. After initial
122 warm-up involving individually estimated 50% submaximal isometric contractions,
123 participants performed isometric MVCs at the pre-defined angles. Two MVCs per contraction
124 type were performed with a rest period of 60 s between each to avoid fatigue. The greatest
125 instantaneous value of the two attempts was recorded as the MVC. This was followed by the
126 first part of the experiment, which involved concentric and eccentric contractions in a
127 randomized order, set to a level equal to 50% isometric MVC at the intermediate muscle
128 length (isometric normalisation; ISO). The second part of the experiment involved obtaining
129 anisometric MVCs (randomised order, two trials per contraction type, 60 s rest) followed by

130 anisometric contractions at 50% of contraction-type specific MVC (contraction-type specific
131 normalisation; CTS). During ISO and CTS trials, participants were instructed to increase their
132 torque level to the target torque and attempt to follow the target line as closely as possible
133 throughout the 4-second contraction (visual feedback was provided through a monitor
134 displaying the target torque). Finally, the muscle length-specific (MLS) submaximal
135 anisometric contractions were performed. An example of a lengthening contraction during
136 MLS is depicted in Figure 1. Lengthening contractions were initiated by matching the torque
137 level with the line representing 50% of isometric MVC at shorter muscle length (Figure 1A).
138 As muscle length increased, participants resisted the motion of the dynamometer reaching the
139 line representing 50% of isometric MVC at an intermediate muscle length situated at the mid-
140 point in ROM (Figure 1B), and finished the contraction by matching the line signifying 50%
141 of isometric MVC at a longer muscle length (Figure 1C). For shortening contractions, the
142 order of torque matching was reversed. This protocol is similar to that previously described by
143 Pasquet *et al.* (2006). For each condition and torque level, participants were given at least 10
144 practice trials, as it has been reported that fluctuations in torque production plateau following
145 such practice (Hortobágyi et al., 2001). Subsequently, experimental trials were performed of
146 which four successful trials per condition, contraction type and contraction level were used
147 and averaged for all measures (ISO, CTS, and MLS). A trial was deemed successful if
148 participants produced a steady torque for 4 seconds (ISO, CTS) and produced a parabolic-like
149 shape of torque covering the three time points at appropriate times (MLS). Due to the practice
150 trials executed beforehand, no more than five experimental trials were needed for all
151 participants. A minimum of 30 s rest was given between each contraction to avoid fatigue.

152 [Insert Figure 1]

153

154 *Data analysis*

155 Maximal torques and corresponding root mean square EMG activity (RMS EMG) were
156 analysed first. For the purpose of better representation and visualisation of conceptual issues,
157 the mean MVC values of the sample were then used to construct a predictive model for
158 submaximal contractions using different normalising procedures. This was done as it allows
159 the assessment of what torque levels are expected to emerge from different normalisation
160 procedures which might be different to experimental values due to inaccurate torque
161 production, particularly during eccentric contractions (Hortobágyi et al., 2001). In the
162 predictive model, for CTS and ISO normalization, a single value of mean percentage torque
163 for concentric and eccentric contractions was calculated. For MLS normalization, the
164 percentage of torque at shorter, intermediate and longer muscle lengths and the percentage of
165 mean torque production were calculated. Whilst it is recognised that this type of normalisation
166 will result in a parabolic torque production as per torque-angle relationship (Billot et al.,
167 2011), for simplicity and the purposes of illustration, the percentage of mean torque
168 production during MLS was computed assuming separate linear relationships between the
169 shorter and intermediate lengths and between the intermediate and longer muscle lengths. For
170 all submaximal contractions in the experiment, data from 4 successful attempts for each
171 contraction type and intensity were analysed. Since the aim of the study was to compare the
172 so-called ‘torque-matching’ task (e.g. Rice et al., 2015) across different contraction types, to
173 allow for a valid comparison between them only the last 3.2 s of each trial was used to
174 calculate the mean torque and RMS. The first 0.8 s of each trial was excluded from analysis
175 since torque had yet to reach the target line in most attempts. This exclusion time removed
176 any issue that the acceleration phase at the start of the movement might be analysed as this
177 was typically restricted to the initial 0.05 s of movement. Also, the deceleration component at
178 the end of motion was not analysed as it was found to start just after the end point of the 3.2 s

179 analysis period. As such, the acceleration and deceleration phases of motion were ignored,
180 allowing for a ‘true’ torque-matching task comparison. Mean torque is presented both in
181 absolute and relative values, i.e. normalised to CTS MVC. The calculated RMS EMG activity
182 was normalized to RMS EMG obtained during CTS MVC.

183

184 *Statistical analysis*

185 Data are presented as mean \pm standard deviation, unless stated otherwise. All analyses were
186 performed using SPSS package (v20, SPSS Inc., USA). Statistical significance was set at an
187 alpha level of 0.05. Normality of the data was assessed using Shapiro-Wilks test. Sphericity
188 was assessed using Mauchly’s test, and if violated, a Greenhouse-Geisser correction was
189 employed. One-way repeated measures ANOVA was used to analyse the differences between
190 different types of MVC. A two-way (3×2) ANOVA with repeated measures design was
191 employed to analyse differences between different normalising procedures (ISO, CTS, MLS)
192 and contraction types (concentric, eccentric). If significant F-values were found, the post hoc
193 pairwise comparison was performed with the Fisher least significant difference test. Partial eta
194 squared (η_p^2) was calculated to estimate effect sizes associated with main effects of ANOVA.
195 To allow for a more nuanced interpretation of the data, Cohen’s d_z effect-sizes were
196 calculated for significant pairwise comparisons. Cohen’s d_z was calculated as the ratio of
197 mean difference and standard deviation of differences, which slightly differs from traditional
198 Cohen’s d calculation in that it is better suited for within-subject, rather than traditional
199 between-subject differences (Becker, 1988; Lakens, 2013; Smith and Beretvas, 2009). One
200 sample t-test was used to assess disparity of relative mean torque compared to the CTS MVC
201 and the predictive model.

202

203

RESULTS

204 *Maximal torque production and the associated RMS EMG*

205 Maximal torque showed contraction type dependency ($F_{2,0, 11.7} = 28.8, p < 0.001, \eta_p^2 = 0.8;$
206 Table 1). Post-hoc analysis showed, maximal eccentric torque was greater than any maximal
207 isometric torque value ($p < 0.005, d_z$ range = 1.2 – 2.2) or concentric maximal torque ($p =$
208 0.001, $d_z = 1.3$). Comparison between concentric and isometric MVC values showed a
209 difference to shorter muscle length only ($p = 0.005; d_z = 1.3$). Across isometric MVC values,
210 longer length was significantly greater compared to either intermediate ($p = 0.011, d_z = 0.7$) or
211 shorter muscle length ($p = 0.001, d_z = 1.6$) and intermediate length was greater than shorter
212 length ($p = 0.047, d_z = 0.9$). Contraction type had no effect on maximal RMS EMG values
213 ($F_{1,3, 7.7} = 1.3, p = 0.306, \eta_p^2 = 0.2$).

214 [Insert Table 1]

215

216 *Predictive model*

217 A predictive model was constructed so that ISO and MLS are presented relative to CTS
218 (Figure 2). For concentric contractions, mean torque level during ISO normalization is
219 expected to be very similar compared to CTS (3% difference, Figure 2A). With MLS
220 normalization, whilst the mean concentric torque level is expected to be very similar
221 compared to CTS (4% difference; Figure 2B), during the latter part of the contraction the
222 torque level is smaller than expected, being 12% less at the point of cessation. For eccentric
223 contractions, all predicted percentage torque levels for either ISO or MLS normalization are
224 lower than expected for CTS normalization (Figure 2C and 2D).

225 [Insert Figure 2]

226

227 *Absolute mean torque and RMS EMG during submaximal contractions*

228 There was a significant normalising procedure \times contraction type interaction for mean torque
229 during submaximal contractions ($F_{2, 12} = 8.3$, $p = 0.005$, $\eta_p^2 = 0.6$). Mean eccentric torque was
230 greater compared to concentric regardless of the normalising procedure employed ($p < 0.03$
231 for all, d_z range = 0.6 – 1.7; Figure 3 top row). Furthermore, CTS mean eccentric torque was
232 greater compared to ISO ($p = 0.003$, $d_z = 1.4$) or MLS ($p = 0.018$, $d_z = 1.0$). There was a
233 significant normalising procedure \times contraction type interaction for RMS EMG ($F_{2, 12} = 4.5$, p
234 = 0.035, $\eta_p^2 = 0.4$). RMS EMG was greater during concentric compared to eccentric
235 contraction regardless of the normalising procedure employed ($p \leq 0.001$ for all, d_z range =
236 1.9 – 3.8, Figure 3 bottom row). RMS EMG activity was greater during eccentric contraction
237 for CTS compared to ISO ($p = 0.021$, $d_z = 0.9$) or MLS ($p = 0.025$, $d_z = 1.0$).

238 [Insert Figure 3]

239

240 *Relative mean torque and the associated torque accuracy*

241 With CTS normalisation, individuals were able to match the expected/predicted 50% torque
242 level for eccentric contractions. However, relative mean concentric torque levels were
243 significantly lower compared to the 50% predicted value ($p = 0.002$; Figure 3-A2). Mean
244 percentage torque levels for concentric and eccentric contractions with ISO normalisation
245 were significantly smaller when compared to CTS normalization values ($p = 0.005$ and $p <$
246 0.001 , respectively; Figure 3-B2), but not different from the predictive values. Relative mean
247 eccentric torque level during MLS normalization was significantly smaller as compared to

248 CTS normalization ($p = 0.011$), but significantly greater when compared to the predictive
249 model ($p = 0.009$; Figure 3-C2).

250

251

DISCUSSION

252 The purpose of this study was to present and assess the disparities in mean torque production
253 and associated EMG activity during anisometric submaximal contractions arising from
254 different normalising procedures that have been previously used in the literature, with the aim
255 of informing future practice. The main finding of the present study is that normalising to ISO
256 and MLS is not an accurate approach when performing submaximal *eccentric* contractions
257 since these two types of normalisation were characterised by significant discrepancy relative
258 to CTS. However, the method of normalisation is less relevant during submaximal *concentric*
259 contractions due to the difference relative to CTS normalisation being small.

260 Maximal dorsiflexion eccentric torque was found to be ~27 and ~36% greater compared to
261 concentric and isometric at intermediate length, respectively, a finding comparable to
262 previous work (Klass et al., 2007; Reeves and Narici, 2003). As a result, with ISO
263 normalization, submaximal eccentric torque was predicted to be 13% lower compared to CTS
264 normalisation, which was supported by our experimental findings where the mean observed
265 difference was 11%. Thus, submaximal eccentric contractions with ISO normalisation cannot
266 be construed as an accurate submaximal representation of this specific contraction type when
267 comparing contraction types. From a perspective of mechanical output, normalising different
268 anisometric contractions to a constant value, as is the case with ISO normalisation, is similar
269 to lifting and lowering an arbitrary absolute load. For such a task, the associated conceptual
270 methodological issues have been highlighted previously (Duchateau and Enoka, 2016).
271 Specifically, due to aforementioned greater capacity to produce force during eccentric

272 contractions, less motor unit activity is needed to produce the same absolute force. This is
273 supported in the present experiment by lower EMG activity observed during submaximal
274 eccentric contractions with ISO normalization, compared to CTS. This finding could have a
275 significant confounding effect when neural behaviour of eccentric contractions is assessed via
276 stimulation techniques, such that with ISO and MLS normalisation, eccentric contractions at a
277 given percentage of maximum will be at a different level of the contraction type-stimulus
278 response curve relative to concentric and isometric contractions (Capaday and Stein, 1987;
279 Goodall et al., 2009; Matthews, 1986; Oya et al., 2008; Weavil et al., 2015). Furthermore,
280 submaximal eccentric contractions derived from ISO or MLS normalisation might exhibit
281 lower and higher standard deviation and coefficient variation of force, respectively (Enoka et
282 al., 2003), resulting in inaccurate assessment of steadiness.

283 Due to similarity in peak torque obtained during concentric and intermediate length isometric,
284 the difference between CTS and ISO normalisation procedures is less profound. Indeed, based
285 on the predictive model this difference is 3% and experimental data supports this, with a ~1%
286 difference. Therefore, if investigations are only concerned with submaximal concentric
287 contractions, normalisation can be performed to CTS MVC or isometric MVC at either
288 intermediate or longer muscle lengths. The latter is valid as peak torque during anisometric
289 contractions usually occurs at longer muscle lengths as per torque-angle relationship (Billot et
290 al., 2011).

291 In an attempt to assess a similar change in torque during anisometric contractions, some
292 researchers have normalised submaximal contractions to MLS maximal isometric contraction
293 (Duclay et al., 2014; Pasquet et al., 2006). Theoretically, this should allow torque production
294 to match the torque-angle curve of the muscle. However, this procedure does not appear to
295 give a valid submaximal representative of a given anisometric contraction type for several
296 reasons. Firstly, the capacity of a muscle to produce torque throughout ROM is unlikely to be

297 linear. This is highlighted in the torque trace presented in our theoretical model, using a 3-
298 point target normalisation rather than a 2-point one used previously (Duclay et al., 2014;
299 Pasquet et al., 2006). Secondly, even though the first half of the contraction, and the mean
300 torque production during concentric MLS appear to be close to CTS, the latter part of the
301 contraction will eventually result in 12% smaller torque level, as per the predictive model
302 (Figure 2). However, if submaximal torque production is assessed in the first portion of the
303 contraction or stimulations are performed at anatomical zero (e.g. Duclay et al., 2014), then
304 MLS normalisation could still be considered accurate during *concentric* contractions only.
305 Thirdly, during eccentric contractions, the starting and finishing point of a contraction were
306 predicted to be 20 and 9% smaller, respectively, compared to CTS, resulting in 14% smaller
307 mean torque production throughout ROM. Our experimental findings showed that maximal
308 torque during longer and shorter muscle length fell significantly short of maximal torque
309 produced during eccentric and concentric contractions in the present study. This was then
310 reflected in submaximal mean torque production and the associated EMG activity insofar as
311 mean eccentric torque was significantly smaller compared to CTS, but still greater than
312 predicted with our theoretical model, possibly due to overshooting the target torque (see
313 below). Furthermore, RMS EMG activity during MLS was significantly smaller, compared to
314 submaximal eccentric contraction using CTS. Theoretically, basing MLS normalisation on
315 each instant of ROM should allow a complete match of the torque-angle curve, thereby
316 making it more representative of a specific contraction type throughout the whole ROM.
317 However, such a task might require a great degree of learning to follow a significant
318 curvilinear torque profile rather than a steady torque level, potentially rendering it less
319 practical. Since the aim of this study was to compare existing normalisation procedures used
320 in the literature directly, a procedure whereby normalisation is performed at each instant of
321 ROM was not investigated, but future studies should assess its effect and practicality.

322 In theory, when ISO and MLS normalisation are performed, mean torque during concentric
323 and eccentric contractions should be similar, which is not accurate relative to their respective
324 maximums due to greater force capacity during eccentric contractions. However, we show
325 that mean torque production is greater during eccentric contraction during these two
326 procedures, which likely stems from impaired torque accuracy. Indeed, eccentric contractions
327 during MLS were characterised by significant overshooting of the target torque (7% greater
328 mean torque production than predicted), which is reportedly a feature of eccentric
329 contractions (Hortobágyi et al., 2001). During MLS, impaired torque accuracy is likely to be
330 even more apparent due to the target not being a constant line.

331 Whilst CTS normalisation appears to be the most ecologically valid normalising procedure, it
332 is not without its limitations. Because the capacity of muscle torque is dependent on muscle
333 length, maximal concentric and eccentric contractions are characterised by descending and
334 ascending torque profiles, respectively. When submaximal contractions are performed, and a
335 constant target torque is set, it is based on the peak value achieved during maximal
336 contractions. This results in increasing and decreasing effort required to produce a given
337 torque level throughout ROM during submaximal concentric and eccentric contractions,
338 respectively. Differences in effort could potentially influence the associated EMG activity as
339 when the muscle is at a shorter length greater neural drive is required to maintain the same
340 absolute torque output. Regardless, this could be considered a representative of a real-world
341 scenario. For example, when dorsiflexors are used to control foot drop during heel strike
342 (Byrne et al., 2007), muscle length varies but the force produced needs to be relatively
343 constant to prevent tripping.

344 In conclusion, the findings of the present study suggest that normalising to ISO and MLS is
345 not an accurate approach for assessment and prescription of submaximal *eccentric*
346 contractions based on the predictive model and the experimental data showing both ISO and

347 MLS normalisation resulted in significantly lower mean torque during submaximal eccentric
348 contractions. As such, future research, particularly in the area of assessment of neural
349 behaviour of submaximal eccentric contraction should carefully consider the appropriate
350 normalising procedure, with CTS likely being the most accurate approach. For assessment
351 and prescription of submaximal *concentric* contractions, normalization to CTS MVC or
352 isometric MVC at either intermediate or longer muscle length may be accurate and used
353 interchangeably.

354

REFERENCES

- 355
- 356 Aagaard, P., Simonsen, E.B., Andersen, J.L., Magnusson, S.P., Halkjær-Kristensen, J., Dyhre-
- 357 Poulsen, P., 2000. Neural inhibition during maximal eccentric and concentric quadriceps
- 358 contraction: effects of resistance training. *J. Appl. Physiol.* 89, 2249–2257.
- 359 Abbruzzese, G., Morena, M., Spadavecchia, L., Schieppati, M., 1994. Response of arm flexor
- 360 muscles to magnetic and electrical brain stimulation during shortening and lengthening
- 361 tasks in man. *J. Physiol.* 481 (Pt 2), 499–507.
- 362 Becker, B.J., 1988. Synthesizing standardized mean-change measures. *Br. J. Math. Stat.*
- 363 *Psychol.* 41, 257–278. <https://doi.org/10.1111/j.2044-8317.1988.tb00901.x>
- 364 Billot, M., Simoneau, E.M., Ballay, Y., Van Hoecke, J., Martin, A., 2011. How the ankle joint
- 365 angle alters the antagonist and agonist torques during maximal efforts in dorsi- and
- 366 plantar flexion. *Scand. J. Med. Sci. Sports* 21, 273–281.
- 367 Byrne, C.A., O’Keeffe, D.T., Donnelly, A.E., Lyons, G.M., 2007. Effect of walking speed
- 368 changes on tibialis anterior EMG during healthy gait for FES envelope design in drop
- 369 foot correction. *J. Electromyogr. Kinesiol.* 17, 605–616.
- 370 Capaday, C., Stein, R.B., 1987. A method for simulating the reflex output of a motoneuron
- 371 pool. *J. Neurosci. Methods* 21, 91–104.
- 372 Duchateau, J., Enoka, R.M., 2016. Neural control of lengthening contractions. *J. Exp. Biol.*
- 373 219, 197–204.
- 374 Duclay, J., Pasquet, B., Martin, A., Duchateau, J., 2014. Specific modulation of spinal and
- 375 cortical excitabilities during lengthening and shortening submaximal and maximal
- 376 contractions in plantar flexor muscles. *J. Appl. Physiol.* 117, 1440–1450.
- 377 <https://doi.org/10.1152/jappphysiol.00489.2014>

378 Duclay, J., Pasquet, B., Martin, A., Duchateau, J., 2011. Specific modulation of corticospinal
379 and spinal excitabilities during maximal voluntary isometric, shortening and lengthening
380 contractions in synergist muscles. *J. Physiol.* 589, 2901–16.
381 <https://doi.org/10.1113/jphysiol.2011.207472>

382 Edman, K.A., 1988. Double-hyperbolic force-velocity relation in frog muscle fibres. *J.*
383 *Physiol.* 404, 301–21.

384 Enoka, R.M., Christou, E.A., Hunter, S.K., Kornatz, K.W., Semmler, J.G., Taylor, A.M.,
385 Tracy, B.L., 2003. Mechanisms that contribute to differences in motor performance
386 between young and old adults. *J. Electromyogr. Kinesiol.* 13, 1–12.

387 Goodall, S., Romer, L.M., Ross, E.Z., 2009. Voluntary activation of human knee extensors
388 measured using transcranial magnetic stimulation. *Exp. Physiol.* 94, 995–1004.
389 <https://doi.org/10.1113/expphysiol.2009.047902>

390 Gruber, M., Linnamo, V., Strojnik, V., Rantalainen, T., Avela, J., 2009. Excitability at the
391 motoneuron pool and motor cortex is specifically modulated in lengthening compared to
392 isometric contractions. *J. Neurophysiol.* 101, 2030–2040.

393 Hermens, H.J., Freriks, B., Disselhorst-Klug, C., Rau, G., 2000. Development of
394 recommendations for SEMG sensors and sensor placement procedures. *J. Electromyogr.*
395 *Kinesiol.* 10, 361–374.

396 Hortobágyi, T., Tunnel, D., Moody, J., Beam, S., DeVita, P., 2001. Low- or high-intensity
397 strength training partially restores impaired quadriceps force accuracy and steadiness in
398 aged adults. *J. Gerontol. A. Biol. Sci. Med. Sci.* 56, B38-47.

399 Kallio, J., Avela, J., Moritani, T., Kanervo, M., Selänne, H., Komi, P., Linnamo, V., 2010.
400 Effects of ageing on motor unit activation patterns and reflex sensitivity in dynamic

401 movements. *J. Electromyogr. Kinesiol.* 20, 590–598.
402 <https://doi.org/10.1016/j.jelekin.2009.12.005>

403 Kellis, E., Baltzopoulos, V., 1998. Muscle activation differences between eccentric and
404 concentric isokinetic exercise. *Med. Sci. Sports Exerc.* 30, 1616–23.

405 Klass, M., Baudry, S., Duchateau, J., 2007. Voluntary activation during maximal contraction
406 with advancing age: a brief review. *Eur. J. Appl. Physiol.* 100, 543–51.
407 <https://doi.org/10.1007/s00421-006-0205-x>

408 Komi, P., Linnamo, V., Silventoinen, P., Sillanpää, M., 2000. Force and EMG power
409 spectrum during eccentric and concentric actions. *Med. Sci. Sports Exerc.* 32, 1757–
410 1762.

411 Lakens, D., 2013. Calculating and reporting effect sizes to facilitate cumulative science: a
412 practical primer for t-tests and ANOVAs. *Front. Psychol.* 4, 863.
413 <https://doi.org/10.3389/fpsyg.2013.00863>

414 Matthews, P.B., 1986. Observations on the automatic compensation of reflex gain on varying
415 the pre-existing level of motor discharge in man. *J. Physiol.* 374, 73–90.

416 Morgan, D.L., Whitehead, N.P., Wise, A.K., Gregory, J.E., Proske, U., 2000. Tension
417 changes in the cat soleus muscle following slow stretch or shortening of the contracting
418 muscle. *J. Physiol.* 522 Pt 3, 503–13.

419 Nardone, A., Schieppati, M., 1988. Shift of activity from slow to fast muscle during voluntary
420 lengthening contractions of the triceps surae muscles in humans. *J. Physiol.* 395, 363–81.

421 Oya, T., Hoffman, B., Cresswell, A., 2008. Corticospinal-evoked responses in lower limb
422 muscles during voluntary contractions at varying strengths. *J. Appl. Physiol.* 115, 1527–

423 1532. <https://doi.org/10.1152/jappphysiol.90586.2008>

424 Pasquet, B., Carpentier, A., Duchateau, J., 2006. Specific modulation of motor unit discharge
425 for a similar change in fascicle length during shortening and lengthening contractions in
426 humans. *J. Physiol.* 577, 753–65. <https://doi.org/10.1113/jphysiol.2006.117986>

427 Pasquet, B., Carpentier, A., Duchateau, J., Hainaut, K., 2000. Muscle fatigue during
428 concentric and eccentric contractions. *Muscle Nerve* 23, 1727–35.

429 Reeves, N.D., Narici, M. V., 2003. Behavior of human muscle fascicles during shortening and
430 lengthening contractions in vivo. *J. Appl. Physiol.* 95, 1090–1096.
431 <https://doi.org/10.1152/jappphysiol.01046.2002>

432 Rice, D.A., McNair, P.J., Lewis, G.N., Mannion, J., 2015. Experimental knee pain impairs
433 submaximal force steadiness in isometric, eccentric, and concentric muscle actions.
434 *Arthritis Res. Ther.* 17, 259. <https://doi.org/10.1186/s13075-015-0768-1>

435 Smith, L., Beretvas, S., 2009. Estimation of the Standardized Mean Difference for Repeated
436 Measures Designs. *J. Mod. Appl. Stat. Methods.*

437 Tallent, J., Goodall, S., Hortobágyi, T., St Clair Gibson, A., French, D.N., Howatson, G.,
438 2012. Repeatability of corticospinal and spinal measures during lengthening and
439 shortening contractions in the human tibialis anterior muscle. *PLoS One* 7, e35930.
440 <https://doi.org/10.1371/journal.pone.0035930>

441 Tallent, J., Goodall, S., Hortobágyi, T., St Clair Gibson, A., Howatson, G., 2013.
442 Corticospinal responses of resistance-trained and un-trained males during dynamic
443 muscle contractions. *J. Electromyogr. Kinesiol.* 23, 1075–81.
444 <https://doi.org/10.1016/j.jelekin.2013.04.014>

445 Weavil, J., Sidhu, S., Mangum, T., Richardson, R., Amann, M., 2015. Intensity-dependent
446 alterations in the excitability of cortical and spinal projections to the knee extensors
447 during isometric and locomotor exercise. *Am. J. Physiol. Regul. Integr. Comp. Physiol.*
448 308, R998-1007.

449 World Health Organisation, 2010. *Global recommendations on physical activity for health.*
450 WHO Press, Geneva, Switzerland.

451

452 **Table 1.** Torque and RMS EMG activity during different maximal contractions.

	<i>Isometric</i>			<i>Anisometric</i>	
	Shorter	Intermediate	Longer	Concentric	Eccentric
MVC (N·m)	37.7 ± 7.7 [#]	46.4 ± 6.3	51.9 ± 4.3 [§]	49.7 ± 5.7	63.1 ± 8.3 [*]
RMS (mV)	0.49 ± 0.12	0.53 ± 0.13	0.46 ± 0.10	0.49 ± 0.09	0.49 ± 0.10

453 *MVC = maximal voluntary contraction torque; RMS = root mean square EMG activity. *p <*
 454 *0.005 compared to all others; §p < 0.015 compared to eccentric, intermediate length*
 455 *isometric and shorter length isometric; #p < 0.05 compared to all others.*

456

Figure legends.

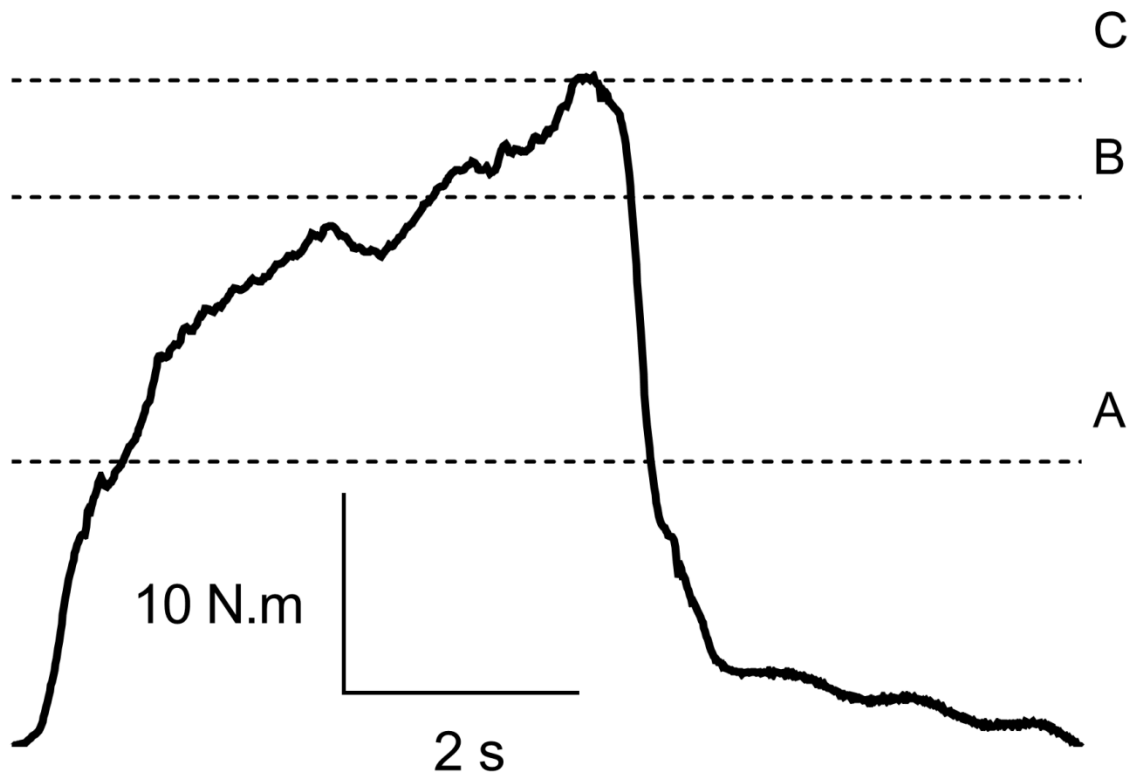
457 **Figure 1.** An example of submaximal eccentric muscle length-specific contraction. The motor
458 of the device moved once participant reached the line representing 50% of the shorter muscle
459 length isometric MVC (A). Thereafter, participants were instructed to resist the motion of the
460 device reaching the line representing 50% of the intermediate muscle length isometric MVC
461 about half-way throughout the range-of-motion (B), and finishing the contraction at the line
462 representing 50% of the longer muscle length isometric MVC (C).

463 **Figure 2.** Predictive model of submaximal concentric (A, B) and eccentric (C, D)
464 contractions based on experimental mean MVC values. Dotted lines represent submaximal
465 contraction for CTS normalisation, whereas solid lines represent submaximal contractions for
466 ISO (A, C) or MLS normalisation (B, D). Percentages of torque production, relative to CTS,
467 are depicted in all panels. For A and C, values are shown in the middle as torque production is
468 constant. For MLS (B, D), values are presented at the onset, the midpoint and the cessation of
469 the contraction, with mean percentage torque presented in the brackets.

470 **Figure 3.** Torque and EMG activity during submaximal concentric and eccentric contractions.
471 CTS, ISO and MLS normalisation relate to columns A, B & C respectively. Row 1 – Mean
472 torque. Row 2 – Mean torque relative to CTS MVC. Row 3 – Mean RMS EMG relative to
473 CTS RMS EMG. * $p < 0.030$ compared to concentric; # $p \leq 0.025$ compared to when
474 normalised to isometric MVC and muscle length specific isometric MVC; † $p < 0.015$
475 compared to 50% contraction-type specific maximum; § $p < 0.010$ compared to the predictive
476 model.

477

478 Figure 1



479

