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1 Effects of Muscle Action Type on Corticospinal Excitability and Triceps Surae  
2 Muscle-Tendon Mechanics.

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10 Running Head: Neuromechanical aspects of eccentric muscle action.

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31    **Abstract**

32    This study investigated if the specific motor control strategy reported for eccentric muscle actions  
33    is dependent on muscle mechanical behavior. Motor-evoked potentials , Hoffman reflex (H-  
34    reflex), fascicle length, pennation angle and fascicle velocity of soleus muscle were compared  
35    between isometric and two eccentric conditions. Ten volunteers performed maximal plantarflexion  
36    trials in isometric, slow eccentric (25°/s) and fast eccentric (100°/s) conditions, each on a different  
37    randomized testing session. H-reflex normalized by the preceding M-wave (H/M) was depressed  
38    in both eccentric conditions as compared to isometric ( $P < 0.001$ ), while no differences in fascicle  
39    length and pennation angle were found among conditions. Furthermore, although the fast eccentric  
40    condition had greater fascicle velocity than slow eccentric ( $P = 0.001$ ), there were no differences  
41    in H/M ratio. There were no differences in motor-evoked potentials size between conditions, and  
42    silent period was shorter for both eccentric conditions as compared to isometric ( $P = 0.009$ ). Taken  
43    together, the present results corroborates with the hypothesis that the central nervous system has  
44    an unique activation strategy during eccentric muscle actions and suggests that sensory feedback  
45    does not play an important role in modulating these muscle actions.

46    **Keywords**

47    Motor evoked potentials, corticospinal excitability, muscle-tendon dynamics.

48    **New & Noteworthy:** The present study provided new insight into the motor control of eccentric  
49    muscles actions. It was demonstrated that task-dependent corticospinal excitability modulation  
50    does not seem to depend on sensory information processing. These findings support the hypothesis  
51    that the central nervous system has a unique activation strategy during eccentric muscle actions.

52

53

54    **Introduction**

55 According to the in vitro force-velocity relationship described for maximally activated muscle,  
56 peak forces generated during muscle lengthening have reached 150 –240% of maximum isometric  
57 force (Edman et al. 1978; Katz 1939; Linari et al. 2004). However, human in vivo studies yielded  
58 controversial results: some reported no differences between maximal eccentric and isometric  
59 moments (Chino et al. 2006; Duclay et al. 2011; Gruber et al. 2009), while some reported a greater  
60 eccentric moment or force (Finni et al. 2003; Hahn et al. 2012; Komi et al. 1973). Furthermore,  
61 twitch interpolation technique and electromyography (EMG) have often shown voluntary inability  
62 to fully activate the involved muscles, as demonstrated by a higher electrically evoked torque and  
63 lower EMG during maximal eccentric as compared with maximal isometric actions, respectively  
64 (Amiridis et al. 1996; Babault et al. 2001; Pinniger et al. 2000). Nevertheless, these results are also  
65 controversial since some studies have also shown no differences or even increased EMG during  
66 maximal eccentric compared to isometric actions (Hahn et al. 2010; Tilp et al. 2009).

67

68 The reduction of neural drive during maximal eccentric muscle actions may be due to spinal and/or  
69 supraspinal modulation. Several research groups have reported decreased Hoffman reflex (H-  
70 reflex; Duclay et al. 2005, 2011, 2014; Grosprêtre et al. 2014), and decreased motor evoked  
71 potentials (MEPs) using transcranial magnetic stimulation (TMS; Duclay et al. 2011, 2014).  
72 Additionally, a lower plateau and maximum slope in the input-output curve utilizing TMS during  
73 eccentric as compared with concentric muscle actions have also been reported, indicating different  
74 neural control strategies for these actions (Sekiguchi et al. 2001, 2003). Furthermore, Gruber et al.  
75 (2009) compared MEPs elicited in biceps brachii and brachioradialis by TMS and  
76 cervicomedullary motor-evoked potentials (CMEPs) obtained by electrical stimulation of the  
77 corticospinal tract. They found reduced MEPs and CMEPs in maximal eccentric compared with

78 isometric actions, however the decrease was greater for CMEP in both muscles, reflecting greater  
79 inhibition at spinal level. Furthermore, the MEP/CMEP ratio, which is an index of cortical  
80 excitability, was increased during eccentric actions (Gruber et al. 2009).

81

82 Unlike the direct comparison between MEP and CMEP, another approach that has been used to  
83 probe corticospinal excitability is to compare the H-reflex with MEP. H-reflex is a measure of  
84 efficacy of the synaptic transmission in the Ia reflex arc (Capaday 1997), and it is modulated not  
85 only by the excitability of spinal motoneurons (MN), but also by a variety of interneurons (Nielsen  
86 et al. 1999; Romanò and Schieppati 1987) and supraspinal centers (Heckman et al. 2008, 2009;  
87 Rudomin and Schmidt 1999). Furthermore, MEPs and H-reflexes of similar size do not  
88 necessarily reflect activation of the same population of motoneurons (Morita et al. 1999).

89 Notwithstanding these limitations, Duclay et al. (2011) reported decreased MEPs and H-reflexes  
90 for soleus (SOL) muscle during maximal eccentric actions as compared with concentric and  
91 isometric actions, but no differences were found for medial gastrocnemius (MG). Duclay et al.  
92 (2011) reported a decreased silent period (SP) during the eccentric action for SOL suggesting  
93 decreased intracortical inhibition (Chen et al. 1999; Inghilleri et al. 1993; Roick et al. 1993). This  
94 finding corroborates with the increased cortical excitability proposed by Gruber et al. (2009).

95

96 It is generally assumed that when different muscle action types are tested in a specific joint angle,  
97 the muscle-tendon complex mechanical configuration (i.e. fascicle length and pennation angle)  
98 will be similar (Nordlund et al. 2002; Pinniger et al. 2001). Muscle-tendon mechanical  
99 configuration depends on the dynamics between the produced force and compliance of the series  
100 elastic component (SEC; Narici et al. 1996; Reeves and Narici 2003). SEC stiffness is dependent

101 on the applied force magnitude and velocity (Sugisaki et al. 2011; Theis et al. 2012, Tilp et al.  
102 2012). Since the muscle's force production capability varies with velocity (Edman 1988; Hill  
103 1938), and SEC behavior can also vary, the same joint angle may represent different mechanical  
104 configurations for different action types in different intensities and velocities. Furthermore, the  
105 angular velocity of limb movement differs from muscle velocity, as the movement velocity and  
106 the intensity of the muscle action will affect fascicle velocity (Chino et al. 2006; Finni et al. 2001;  
107 Narici 1996). Movement velocity during both passive joint movement and voluntary muscle  
108 actions have been reported to modulate H-reflex amplitude. Generally, higher velocity eccentric  
109 actions and passive muscle lengthening have lower H-reflexes than slower velocities for SOL,  
110 while diverging results have been shown for MG(Duclay et al. 2009; Grosprêtre et al. 2014;  
111 Nordlund et al. 2002; Romanò and Schieppati 1987). It remains unclear if the different velocities  
112 were capable of modifying muscle-tendon dynamics, and if the different afferent inputs would  
113 explain the larger inhibition at higher velocities. Although at higher velocities, increased Ia afferent  
114 discharge from muscle spindles is expected, increasing the excitability of the MN pool (Burke et  
115 al. 1978). Finally, changes in muscle architecture have been demonstrated to affect neural  
116 measurements utilizing EMG (Gerilovsky et al. 1989; Tucker et al. 2005).

117

118 The aim of the current study was to investigate if the specific motor control strategy reported for  
119 eccentric muscle actions is dependent of muscle mechanical behavior, and thus a reflection of  
120 differences in afferent information. We compared MEP and H-reflex modulation in SOL muscle  
121 between isometric and fast and slow eccentric conditions, while ultrasonography was utilized to  
122 access SOL and MG fascicle length (FL), pennation angle (PA) and fascicle velocity (FV). We  
123 hypothesized that all three conditions would have different fascicle velocities, although both

124 eccentric conditions would have equally lower corticospinal excitability compared to isometric.  
125 Furthermore, we also hypothesized that fascicle length and pennation angle would be similar  
126 among slow eccentric and isometric conditions, both having shorter FL and larger PA than fast  
127 eccentric. The first hypothesis was made under the assumption that there is a unique activation  
128 strategy for eccentric actions (Duchateau and Baudry 2014; Duchateau and Enoka 2008, 2016;  
129 Enoka 1996), while the second was based on an assumption of similar torque production among  
130 all conditions, but a higher joint passive resistance in the fast eccentric condition. While focusing  
131 on SOL muscle, we also report MG mechanical data because it is an important synergist muscle  
132 that has been shown to have a different control scheme from SOL (Duclay et al. 2009, 2011, 2014)  
133 and to have an influence on SOL mechanics (Bojsen-Moller et al. 2010; Finni et al. 2015). Neural  
134 measurements for MG were not performed as the number of maximal voluntary actions would  
135 have been too great for each testing session.

136

## 137 **Methods**

138

139 *Subjects.* Ten healthy male subjects (mean (SD) for age, height and weight were 23.8 yr (2.4), 1.81  
140 m (0.05), 81.1 Kg (5), respectively) with no history of neurological injuries or diseases participated  
141 in the study. All subjects gave their written informed consent after explanation of the experiment  
142 and the risks involved. The procedures were approved by the local university ethics committee and  
143 performed according to the *Declaration of Helsinki*.

144

145 *Study design.* The study consisted of four testing sessions, all separated by 48 – 72 hours. The first  
146 session was a familiarization session, in which the subjects performed several trials of the different

147 maximal muscle action types (isometric, fast and slow eccentric), experiencing TMS, H-reflex,  
148 ultrasonography and EMG procedures. The subsequent three sessions were randomized and  
149 consisted of one isometric and two eccentric test conditions. At the beginning of each session a  
150 standard warm up, consisting of 10 muscle actions (matching the action type of the particular  
151 experimental condition) with progressively higher intensities (60-100% of maximal voluntary  
152 contraction; MVC) were performed. This procedure was important not only to prepare the subjects  
153 for the upcoming series of MVCs, but to take into account tendon conditioning with consecutive  
154 muscle actions, in an attempt to reduce tendon elongation variability in the initial MVC trials  
155 (Maganaris 2003). After warm up, subjects performed a series of MVCs matching the session  
156 muscle action type (isometric, slow or fast eccentric) in which evoked potentials, torque,  
157 ultrasound and EMG data were collected. Before every test session, subjects were asked to palpate  
158 their triceps surae muscle and perform a standing unilateral plantarflexion, tests were only carried  
159 out if subjects reported no muscle soreness.

160

161 *Experimental setup.* Subjects were seated with the knee joint fully extended, hip joint at 120° of  
162 extension and the ankle joint at an initial position of 90° (i.e. the sole of the foot at right angles to  
163 the tibial axis) in an ankle dynamometer (Neuromuscular Research Center, University of  
164 Jyväskylä, Finland). All measurements were performed on the right leg while the left leg rested  
165 quietly on a support. The right foot was firmly attached to a footplate mounted on the rotation  
166 platform so that the rotation axes of the ankle joint and the motor driven platform coincided.  
167 Subjects were securely stabilized by an assembly of straps that fastened both shoulders and  
168 connected to a waist belt. An additional strap with a foam support prevented the right knee joint  
169 from flexing. The torque around the rotational axis of the motor was measured by a piezoelectric

170 crystal transducer (Kistler Holding AG, Winterthur, Switzerland) and the ankle joint angle was  
171 monitored by a linear potentiometer. Furthermore, a small stiff metal wire attached to a spring  
172 system, located under the calcaneus, continuously monitored heel displacement from the footplate  
173 throughout the experiments. Torque, joint angle and heel displacement signals were sampled at 1  
174 KHz utilizing a 16-bit AD converter (CED power 1401, Cambridge Electronics Design Limited,  
175 Cambridge, UK) and stored for later analysis.

176

177 *Experimental Procedures.* The ankle joint angle of observation in the isometric, slow eccentric  
178 and fast eccentric conditions was 80° (10° of dorsiflexion). Thus, nerve stimulation, TMS and  
179 ultrasound were always targeted and analyzed at this angle. In the isometric condition, the subject  
180 performed an isometric MVC lasting three seconds with the ankle joint at 80°. Stimulation timing  
181 for the isometric condition was 2 seconds after the initiation of the MVC, during a stable torque  
182 plateau. In the eccentric conditions the subjects were asked to perform a maximal isometric action  
183 lasting two seconds at 110° (20° of plantarflexion) ankle joint angle after which the foot plate  
184 moved to 75° at 25 °/s (slow eccentric) or 100 °/s (fast eccentric) while the subject maintained  
185 maximal effort throughout the movement. The stimulations were elicited 3.2 and 2.3 seconds after  
186 the initiation of the MVC for slow and fast eccentric actions, respectively. Maximal effort duration  
187 did not differ much between experimental conditions (3.00 s for isometric, 3.40 s for slow eccentric  
188 and 2.35 s for fast eccentric) minimizing variability in muscle-tendon mechanical behavior due to  
189 creep. Upon arrival at 75°, the subjects were instructed to relax and the footplate returned to the  
190 initial position at 20 °/s (Figure 1). Three maximal isometric, slow concentric (25°/s) and fast  
191 concentric (100°/s) dorsiflexions were performed at the end of the isometric, slow and fast  
192 eccentric conditions, respectively.

193

194 In each of the three experimental conditions the total number of trials varied from twenty to forty  
195 (mean = 32 trials). Ten trials were performed utilizing TMS, and a variable number of trials (never  
196 exceeding thirty) were used to gather H-reflex and maximal M-wave (Mmax) data. The order of  
197 TMS and nerve stimulation was randomized for every test session. Concomitantly, three trials  
198 were recorded utilizing ultrasound for each muscle (SOL and MG). All ultrasound images were  
199 immediately checked by one of the researchers, who was responsible for validating the trial (clear  
200 visualization of muscle fascicles, deep and superficial aponeurosis). Three minutes of rest were  
201 given between trials, and the test session had a mean duration of 130 minutes (range: 110-160).  
202 After a maximum of fifteen trials, the subject rested for 15 minutes to eliminate any possible  
203 fatiguing effects.

204

205 FIGURE 1– Representative recordings of EMG, joint angle, torque and evoked responses for  
206 isometric (left), slow eccentric (middle) and fast eccentric (right) conditions. From top to bottom:  
207 EMG activity for tibialis anterior and SOL muscles, joint angle displacement, torque during  
208 maximal plantarflexions, evoked responses for electrical stimulation and TMS.  
209

210 *Electromyography.* EMG activity was recorded from SOL and tibialis anterior (TA) of the right  
211 leg using bipolar self-adhesive electrodes (Blue Sensor N, Ag/AgCl, 0.28 cm<sup>2</sup>, Ambu, Ballerup,  
212 Denmark) and a ground electrode was placed on the head of the tibia. Additionally, a  
213 pseudomonopolar setting for SOL with a reference on the bony surface of tibia was employed. The  
214 pseudomonopolar electrode configuration was chosen to acquire SOL MEPs as it provides  
215 consistent waveforms, facilitating peak-to-peak and area analyses (Kumpulainen et al. 2012).  
216 Furthermore, although having the disadvantage of not having a common-mode rejection, the signal  
217 to noise ratio was still high, allowing easy MEP recognition and analysis.

218

219 Electrode placement and skin preparation were performed according to SENIAM (Hermens et al.  
220 2000). Reference lines were drawn on the skin and a picture was taken to provide accurate  
221 replacement of the electrodes in the following sessions. The electrodes were adjusted on the muscle  
222 belly in accordance with the underlying fiber direction (interelectrode distance = 2 cm;  
223 interelectrode resistance < 2 k $\Omega$ ). Alignment of the electrodes was checked according to the shape  
224 of the M-wave, which was ensured to be smooth during the maximal voluntary actions. EMG  
225 signals were amplified and high pass filtered (x1000, 10Hz) by a preamplifier (NL824, Digitimer  
226 Ltd., Hertfordshire, UK) then bandpass filtered (10 Hz to 1 KHz) by a differential amplifier  
227 (NL900D/NL820A Digitimer Ltd., Hertfordshire, UK). The signals were acquired on a personal  
228 computer at a rate of 5 KHz via a 16-bit AD converter (CED power 1401, Cambridge Electronics  
229 Design Limited, Cambridge, UK).

230

231 *Transcranial magnetic stimulation.* TMS was delivered using a single pulse, monophasic Magstim  
232 200<sup>2</sup> stimulator with a 9-cm double batwing coil (Magstim, Whitland, UK), oriented to deliver  
233 posterior–anterior directed current to the motor cortex. The coil was optimally positioned to elicit  
234 at rest SOL MEPs with the greatest amplitudes while eliciting minimal TA MEPs (less than 50%  
235 of SOL MEP amplitude). A custom-made coil holder with a neck support and two elastic bands  
236 passing around the subject’s chin were utilized to keep the coil’s position constant. Additionally,  
237 marks were drawn on the subject’s scalp to facilitate monitoring coil position throughout the  
238 testing session, and to enable accurate coil repositioning in the following sessions. Resting motor  
239 threshold (RMT) was defined as the lowest stimulus intensity to elicit a visible MEP with peak-  
240 to-peak amplitude of 70 $\mu$ V in three out of five consecutive trials (Opie and Semmler 2016). A

241 higher threshold than the standard bipolar practice ( $50\mu\text{V}$ ; Rossini et al. 2015) was set because the  
242 pseudomonopolar electrode setup has a higher noise level ( $42.6\mu\text{V}$  (SD 6.9). All experiments were  
243 performed with an intensity of 120% RMT (Temesi et al. 2014), corresponding to 67.1 % (SD 9.7)  
244 of maximal stimulator output.

245

246 *Electrical stimulation.* H-reflexes and M-waves were evoked in SOL by percutaneous electrical  
247 stimulation of the tibial nerve. A single rectangular pulse (1ms) was delivered from a constant  
248 current stimulator (DS7AH, Digitimer Ltd., Hertfordshire, UK). A circular cathode with a pickup  
249 area of  $0.77\text{ cm}^2$  (Unilect 4535M, Ag/AgCl, Unomedical Ltd., Redditch, UK) was placed over the  
250 tibial nerve on the popliteal fossa, and an oval shaped,  $5.08 \times 10.16\text{ cm}$  anode (V-trodes, Mettler  
251 Electronics corp., Anaheim, USA) was placed above the patella. The stimulation site providing the  
252 greatest amplitude of evoked responses in SOL while evoking minimal evoked responses in TA  
253 was first located by a hand-held cathode electrode which was later replaced by a self-adhesive  
254 electrode. Three to five trials utilizing supramaximal stimulation (1.5 times the maximum M-wave  
255 stimulus intensity) were performed and the mean value was considered Mmax for each  
256 experimental condition. Stimulation intensity was then decreased to elicit H-reflexes with a  
257 preceding M-wave of  $20 \pm 2\%$  of Mmax, only values within this range were analyzed.

258

259 *Ultrasound.* A real-time ultrasound apparatus (SSD- $\alpha$ 10, Aloka, Tokyo, Japan) was used to record  
260 continuously longitudinal images of SOL and MG during each test session. A B-mode linear array  
261 probe (scanning frequency = 7.5 MHz; field of view = 6 cm) was firmly fixed on the right leg  
262 using a foam pad and elastic tapes. The probe was coated with a water-soluble transmission gel  
263 and securely fixated to the dermal surface to ensure constant pressure. For SOL, the probe was

264 positioned at 50% of the distance between the popliteal crease and the lateral malleolus.  
265 Exceptionally, for one subject, the probe was positioned proximally at 30% of the same reference  
266 line, as only at this position the fascicle visualization was sufficiently clear for measurement. For  
267 MG, the probe was positioned proximally at 30% of the distance between the popliteal crease and  
268 the medial malleolus. Probe position was carefully selected so that the plane of the ultrasonogram  
269 was parallel to the muscle fascicles, avoiding fascicle length underestimation (Hodgson et al.  
270 2006). The images were sampled at 100 Hz.

271

## 272 **Data analysis**

273

274 Digital data analysis was performed offline utilizing the Spike2 software (v4. CED, Cambridge,  
275 UK). The same software was programed to synchronize and control automatically the stimulation,  
276 dynamometer movement, ultrasound and EMG.

277

278 *Torque, tendon force, heel displacement and EMG.* For all experimental conditions, peak torque  
279 and mean heel displacement were calculated in a 50 ms window prior to stimulation (80°). Ten  
280 consecutive trials were selected pseudorandomly (i.e. chosen by chance using a standardized  
281 procedure) from which torque, heel displacement and EMG were averaged. SOL and TA EMG  
282 activity were quantified using root mean square (RMS) values of the EMG signal over a 50 ms  
283 window prior to the stimulation. SOL EMG was normalized by the Mmax measured in the same  
284 muscle action type. TA coactivation was normalized by TA RMS obtained in a 50 ms window  
285 during maximal dorsiflexion at the same ankle joint angle with the same velocity. Heel  
286 displacement was similar among the three experimental conditions, thus ankle rotation influenced

287 tissue displacement in a similar manner in all conditions. Additionally, torque and EMG were  
288 calculated in a 50 ms window before the onset of the eccentric movement (i.e. isometric pre-  
289 activation) for both eccentric conditions.

290

291 *H-reflex.* Peak-to-peak amplitudes for Mmax, M-wave and H-reflex were calculated between the  
292 initial deflection of the EMG from the baseline (i.e. response latency) to the second crossing of the  
293 horizontal axis (i.e. response duration). H-reflex amplitude values were normalized by the  
294 preceding M-wave of the same trial, and were expressed as H/M. Three trials were averaged.

295

296 *MEP and SP.* Peak-to-peak amplitudes and areas of MEPs were calculated between the initial  
297 deflection of the EMG from the baseline (i.e. MEP onset) to the second crossing of the horizontal  
298 axis (i.e. MEP offset). Peak-to-peak amplitude and area were normalized to the mean Mmax value  
299 measured in the same action type. Results for peak-to-peak amplitudes and areas were similar, and  
300 thus only peak-to-peak amplitudes are reported. The duration of the absolute silent period was  
301 assessed by visual inspection from the MEP offset to the return of EMG activity. Variables from  
302 ten TMS trials were averaged for each individual.

303

304 *Fascicle Behavior.* FL was defined as the distance between the insertions of the fascicle into the  
305 superficial and deep aponeurosis. PA was defined as the angle between the fascicle and deep  
306 aponeurosis. Measurement of PA was performed manually utilizing Image J (Bethesda, Maryland,  
307 USA). Moreover, FL and FV were tracked utilizing an automated fascicle tracking method based  
308 on the Lucas-Kanade optical flow algorithm with an affine optic flow extension (Cronin et al.  
309 2011; Gillett et al. 2013) in a custom written Matlab graphical user interface (Matlab, The

310 MathWorks Inc. Massachusetts, USA). FV was obtained by differentiating the corresponding  
311 length change value with time (100 ms window). The mean of three measurements for each trial  
312 was utilized.

313

314 *Repeatability and reliability of measurements.* Since data were collected during 3 experimental  
315 sessions, it was important to verify repeatability for all variables. A pilot study ( $n = 4$ ) consisting  
316 of 2 pairs of testing sessions with identical conditions for isometric and slow eccentric was  
317 performed. Intraclass correlation coefficient (ICC) was calculated using a 2-way fixed-effect  
318 model addressing random error (ICC 3.1, Weir 2005). Additionally, the coefficient of variation  
319 (CV) was calculated for each variable. CV and ICC are reported in table 1. These variables were  
320 not calculated for the automatic fascicle tracking method, as it has already been shown reliable  
321 and repeatable (Cronin et al. 2011; Gillett et al. 2013). Another important concern was to compare  
322 unfatigued maximal voluntary actions. Trials were only accepted when torque values were within  
323 a specific range from the mean of the first 6 trials. The acceptance range was determined utilizing  
324 2 criteria simultaneously: (1) 2 standard deviations; (2) minimal difference (MI) constructed for a  
325 99% confidence interval (CI).

326

327 MI 99% CI = standard error of the mean  $\times 2.575 \times \sqrt{2}$ ,

328

329 The total number of trials for the 3 experimental conditions was 964, in which 42 (4.36%) were  
330 excluded due to low torque levels. A non-significant Pearson correlation coefficient between trial  
331 number and number of exclusions reflects their random distribution throughout the experiments  
332 and the fact that excluded trials were not associated with fatigue.

TABLE 1. Coefficient of variation (CV) for Isometric (Iso), slow eccentric (Slow Ecc) and fast eccentric (Fast Ecc) conditions and intraclass correlation coefficient (ICC) for Iso and Slow Ecc conditions (pilot study).

Variables	CV (%)			ICC	
	Iso	Slow Ecc	Fast Ecc	Iso	Slow Ecc
Torque	3.4	4.9	4.4	0.99	0.94
SOL EMG	13.6	12.5	15.1	0.89	0.85
TA EMG	12.4	13.9	13.5	0.91	0.92
HD	26.4	34.5	31.7	0.69	0.94
MEP	19.7	20.8	20.3	0.85	0.99
SP	6.9	11.2	10.9	0.95	0.99
Mmax	4.3	6.1	4.7	0.85	0.77
M-wave	8.1	6.9	6.4	0.82	0.69
H/M	9.3	23.2	25.4	0.77	0.82
PA	8.9	6.2	8.0	0.84	0.88

SOL and TA EMG = soleus and tibialis anterior electromyography; HD = heel displacement; MEP = motor evoked potential; SP = silent period; H/M = normalized H-reflex; PA = pennation angle.

334 *Statistical analysis.* All data are presented as mean (SD). Data normality was tested using the  
 335 Shapiro-Wilks test. All variables except heel displacement and SOL EMG had a normal  
 336 distribution. One-way repeated-measures ANOVA with a Holm-Sidak post hoc test was used to  
 337 test differences between isometric, fast and slow eccentric conditions for all variables. The non-  
 338 parametric analog Friedman repeated-measures ANOVA on Ranks test was used when  
 339 appropriate. Two-way repeated-measures ANOVA with a Holm-Sidak post hoc was used to test  
 340 differences between muscle action type and muscles for FL, FV and PA. Paired t-test was used to  
 341 test differences in torque and EMG between the eccentric conditions in the pre-activation phase.  
 342 Pearson correlation coefficient was calculated between neural (i.e. MEP, SP, H/M) and mechanical

343 (i.e. FL, FV) variables. All statistical analyses were performed using SigmaPlot v.10 (Systat  
344 Software Inc., San Jose, USA). Significance level was set at  $P < 0.05$ .

345 **Results**

346

347 *Torque and EMG.* Peak torque differed between experimental conditions ( $F_{(2,10)} = 4.0$ ,  $P = 0.037$ ).  
348 Post hoc tests identified that slow eccentric had higher torque than fast eccentric ( $P = 0.015$ ).  
349 Regarding EMG, there were no differences in SOL activity ( $P = 0.192$ ) or TA coactivation ( $P =$   
350 0.160) between experimental conditions. Table 2 presents torque, EMG and heel displacement  
351 measures for all experimental conditions. Pre-activation torque before the eccentric muscle actions  
352 was similar between fast and slow eccentric condition ( $P = 0.487$ ). There were no differences in  
353 SOL EMG ( $P = 0.934$ ) and TA EMG ( $P = 0.846$ ) during the pre-activation phase.

354

TABLE 2. Effect of muscle action type on mechanical and neural variables.

Variables	Isometric	Slow Eccentric	Fast Eccentric
Torque (Nm)	224.4 (36.1)	228.9 (38.3)*	198.2 (34.7)
HD (mm)	4.4 (4.4)	3.1 (1.9)	3.6 (2.4)
SOL EMG (rms/Mmax)	0.029 (0.013)	0.023 (0.005)	0.024 (0.005)
TA (coactivation %)	10.3 (3.42)	11.9 (4.83)	14.1 (4.42)

355 Data are mean (SD). HD = heel displacement; SOL = soleus; TA = tibialis anterior; RMS = root mean  
356 square; Mmax = maximal M-wave. \*Significant at  $P < 0.05$ : Slow Eccentric vs. Fast Eccentric.

357

358 *Evoked potentials.* Analysis of repeated measures for normalized MEP amplitude revealed no  
359 differences between experimental conditions ( $P = 0.750$ ). Silent period was different among  
360 experimental conditions ( $F_{(2,9)} = 6.3$ ,  $P = 0.009$ ); isometric had higher values than both eccentric  
361 conditions ( $P < 0.01$ ; Figure 2a). Mmax ( $P = 0.950$ ) and M-wave ( $P = 0.981$ ) had similar amplitude  
362 values among the three experimental conditions. H/M was different among experimental

363 conditions ( $F_{(2, 10)} = 12.6$ ,  $P < 0.001$ ); isometric had higher values than both eccentric conditions  
364 ( $P < 0.001$ ; Figure 2b).

365  
366  
367 FIGURE 2 – Effect of action type on evoked potentials. Figure 2a – Normalized MEP amplitude and silent  
368 period. MEP = motor evoked potential; SP = silent period. \* Significant at  $P < 0.01$ : Isometric vs. Fast and  
369 Slow Eccentric. Figure 2b – Absolute M-wave and Mmax amplitude, and normalized H-reflex amplitude.  
370 # Significant at  $P < 0.001$ : Isometric vs. Fast and Slow Eccentric. Data presented as mean  $\pm$  95% CI.

371  
372 *Muscle fascicle behavior.* There were no differences in SOL FL between conditions ( $P = 0.722$ ),  
373 while MG FL differed ( $F_{(2, 10)} = 4.4$ ,  $P = 0.030$ ), being longer in fast eccentric as compared to  
374 isometric ( $P = 0.01$ ). There was no significant interaction between conditions and muscles ( $P =$   
375 0.426). FV in SOL was different among the experimental conditions ( $F_{(2, 10)} = 40.0$ ,  $P < 0.001$ );  
376 fast eccentric had higher values as compared with the other two conditions ( $P < 0.001$ ). In MG,  
377 all experimental conditions had different FV values ( $F_{(2, 10)} = 51.6$ ,  $P < 0.001$ ); fast eccentric having  
378 the highest values and isometric the lowest ( $P < 0.05$ ). There was an interaction between  
379 experimental conditions and muscles for FV ( $F_{(2, 7)} = 6.1$ ,  $P = 0.015$ ). FV values were similar in  
380 both muscles for the isometric condition, while MG had higher FV in both eccentric conditions as  
381 compared to SOL ( $P < 0.05$ ). There were no differences in PA between the experimental conditions  
382 for SOL and MG ( $P = 0.293$ ). In all conditions MG had smaller PA than SOL ( $F_{(1, 9)} = 22.3$ ,  $P <$   
383 0.001). There was no interaction between condition and muscle ( $P = 0.768$ ). Results for FL, FV  
384 and PA are presented in table 3. Figure 3 depicts FL behavior in a 900 ms window before  
385 stimulation for the three experimental conditions.

386  
387

388 FIGURE 3 – Fascicle length values for SOL (left) and MG (right) acquired 900 ms before electrical or  
389 magnetic stimulation which occurred at time 0 s (arrow). Data points are presented as mean  $\pm$  95% CI of  
390 100 ms window.

391

TABLE 3. Effect of action type on FL, FV and PA for SOL and MG, measured at 80° ankle joint angle.

	Isometric SOL/MG	Slow Eccentric SOL/MG	Fast Eccentric SOL/MG
FL (mm)	42 (8)/45 (8)*	43 (9)/52 (6)	44 (9)/54 (6)
FV (mm/s)	-0.1 (1)/0.1 (0.3)†	8.3 (3.1)/14.7 (4.9)†#	39(16)‡/56(17.1)†#
PA (°)	31.2 (5.3)/23.9 (6.9)#	32.0 (4.9)/24.4 (4.6)#	32.7 (4.2)/26.6 (6.2)#

392 Data are mean (SD). FL = fascicle length; FV = fascicle velocity; PA = pennation angle; SOL = soleus  
393 muscle; MG = medial gastrocnemius muscle. Negative values for FV = fascicle shortening. \* Significant  
394 at  $P < 0.05$ : Isometric vs. Fast Eccentric. ‡ Significant at  $P < 0.05$ : Fast Eccentric vs. Isometric and Slow  
395 Eccentric. † Significant at  $P < 0.05$ : All conditions were statistically different. # Significant at  $P < 0.05$ :  
396 MG vs. SOL.

397

398 *Correlations.* FL had no significant correlation with H/M ( $P > 0.6$ ), MEP ( $P > 0.6$ ), and SP ( $P > 0.416$ )  
399 in all conditions . The only exception was a significant correlation between FL and SP for the isometric  
400 condition ( $P = 0.045$ ,  $r = 0.717$ ). Pooled data from all three experimental conditions yielded significant  
401 correlations between FV and H/M ( $P = 0.004$ ,  $r = -0.56$ ) and FV and SP ( $P = 0.028$ ,  $r = -0.43$ ). Changes in  
402 FL between isometric and both eccentric conditions (i.e. delta FL) were not correlated to changes in H/M  
403 between isometric and both eccentric conditions (i.e. delta H/M) ( $P = 0.126$ ,  $r = -0.43$ ; Figure 4).

404

405

406 FIGURE 4 – Correlation between changes in fascicle length and H/M. FL delta was computed as isometric  
407 FL – eccentric FL, positive values = muscle shorter in the eccentric condition. Delta H/M was computed as  
408 isometric H/M – eccentric H/M, positive values = lower H/M in the eccentric condition. Eccentric data  
409 from both slow and fast conditions were pooled together (2 data points for each subject,  $n = 7$ ).

## 410 Discussion

411

412 The present study provided new data regarding the motor control of SOL eccentric muscle actions.

413 We probed corticospinal excitability during maximal isometric and eccentric muscle actions while

414 monitoring muscle-tendon dynamics. The main finding was that SOL H/M was depressed during  
415 both fast and slow eccentric conditions as compared to isometric, while no differences in fascicle  
416 length and pennation angle were found among experimental conditions. Furthermore, although the  
417 fast eccentric condition had greater fascicle velocity than slow eccentric, there were no differences  
418 in H/M ratio. There were no differences in MEP size among experimental conditions, but SP was  
419 shorter for both slow and fast eccentric as compared to isometric condition. There was no  
420 significant correlation between the changes in FL and H/M between isometric and eccentric  
421 conditions.

422

423 *Torque and EMG.* In a classical in situ experiment on cat SOL muscle the eccentric muscle force  
424 has been shown to be virtually independent of velocity above a certain initial velocity (Joyce et al.  
425 1969). Also, previous human studies have reported triceps surae muscle maximal torques to be  
426 independent of eccentric velocity (Chino et al. 2006; Pinniger et al. 2000). Surprisingly, our study  
427 reports lower torque in fast compared to slow eccentric, which cannot be explained by pre-  
428 activation torque, TA coactivation and SOL EMG during or preceding (i.e. isometric pre-  
429 activation) the eccentric phases as these variables were similar in both conditions. By performing  
430 the pre-activation away from the force-length plateau (~83% of the maximal isometric torque at  
431 80°), the time available to increase torque in the fast eccentric action was short (300 ms)  
432 compared to slow eccentric (1200 ms), possibly explaining the differences between conditions.  
433 It is important to ascertain that the subjects were able to perform maximal voluntary muscle actions  
434 in all three conditions, we propose that this was the case based on the following: 1) the  
435 familiarization session lasted 2 hours, and the subjects performed a mean of 15 MVCs for each  
436 condition; 2) the test-retest ICC for torque in the pilot measures was 0.94-0.99 (table 1); 3) during

437 each testing protocol, the subjects performed a mean of 36 MVCs, with stable torque values  
438 throughout, yielding very small CV (4.4%, Table 1). SOL EMG analysis had a low power (0.2)  
439 due to the large inter-subject variability (CV = 20 - 40%). Although not statistically different, SOL  
440 EMG during slow and fast eccentric conditions was 21 and 17% lower than isometric (ES =  
441 0.61/0.51) respectively, suggesting neural inhibition and possibly explaining the lack of force  
442 potentiation during the eccentric conditions as compared to isometric. Force potentiation during  
443 eccentric actions has been reported in other studies (Grosprêtre et al. 2014; Hahn et al. 2012).

444

445 *Corticospinal excitability and fascicle behavior.* In the present study, both eccentric conditions  
446 had reduced H/M as compared with isometric, and although there was a tendency for lower values  
447 of H/M in fast eccentric (ES = 0, 43), it was not significantly different than slow eccentric. Reduced  
448 H-reflex during eccentric compared with isometric and concentric muscle actions have been  
449 consistently reported (Abbruzzese et al. 1994; Duclay et al. 2005, 2009, 2011; Grosprêtre et al.  
450 2014; Romanò and Schieppati 1987). Duclay et al. (2009, 2011) reported the only exception for  
451 MG muscle, in which no differences in H-reflex were found between concentric, eccentric and  
452 isometric muscle actions. Regarding muscle action velocity, higher eccentric velocities (studied  
453 velocity range: 12°/s - 60°/s) have been reported to have lower H-reflex than slower velocities  
454 (Duclay et al. 2009; Romanò and Schieppati 1987).

455

456 The novel finding in this study is that SOL H/M was depressed during eccentric as compared with  
457 isometric muscle action, although muscle-tendon configuration (i.e. FL and PA) was the same.  
458 Additionally, the higher FV in fast eccentric condition which should have increased motoneuron  
459 excitability by increased Ia afferent discharge from muscle spindles did not occur, oppositely, fast

460 eccentric had a trend towards lower H/M. Although FV and H/M were significantly correlated ( $R^2$   
461 = 31%), the lack of significant correlation between the changes in FL and H/M (figure 4) suggests  
462 that afferent information coming from muscle spindles cannot be responsible for modulating the  
463 corticospinal excitability during eccentric muscle actions. Interestingly, the only participant  
464 engaged in regular track and field athletic training had a shorter FL at the test angle during the  
465 eccentric conditions (29,4% and 31,4% for slow and fast eccentric; Figure 4 upper-right corner),  
466 even though FV was positive indicating fiber lengthening in the last 100 milliseconds before the  
467 test angle. A high inter-subject variability in FL ( $CV = 19\text{-}21\%$ ) rendered the comparison between  
468 conditions a low power ( $\beta = 0.05$ ); nevertheless, isometric FL was only 2.4% ( $ES = 0.11$ ) and 4.8%  
469 ( $ES = 0.23$ ) shorter than slow and fast eccentric conditions respectively. Thus, it seems reasonable  
470 to consider FL to be similar between experimental conditions. Furthermore, it is noteworthy that  
471 no differences in FV were found between slow eccentric and isometric protocols due to the large  
472 inter-subject variability ( $\beta = 0.7$ ). Corroborating with Chino et al. (2006), our study showed that  
473 the effect of muscle action type and joint velocity on muscle fascicle dynamics was more  
474 pronounced in MG as compared to SOL, demonstrated by much greater differences in FL and FV.  
475 Duclay et al. (2011, 2014) reported no differences in MEP or H-reflex for MG during maximal  
476 eccentric muscle actions, contrasting with a consistent reduction of both parameters for SOL. Since  
477 the testing position in their study was the same as ours, it is plausible to suggest that the mechanical  
478 changes in MG did not affect corticospinal excitability, as afferent inputs were overwritten by  
479 centrally mediated inputs.

480 In the present study, no differences in SOL MEP size were found between isometric and eccentric  
481 muscle actions, corroborating with previous studies (Duclay et al. 2011; Hahn et al. 2012). Duclay  
482 et al. (2011), only found significant differences at the highest stimulation intensities, which

483 induced MEPs on or close to the plateau of the input-output curve. Direct comparisons between  
484 the effective stimulation intensity in these two experiments are not possible since different coil  
485 shapes were utilized (i.e. circular vs. batwing), generating different magnetic fields (Cohen et al.  
486 1990). Lower MEPs during maximal and submaximal eccentric muscle actions have also often  
487 been reported for biceps brachii and brachioradialis (Abbruzzese et al. 1994; Gruber et al. 2009).  
488 Although obtaining the whole input-output curve for each muscle action type surely provides much  
489 more information about the task-dependent modulation of the corticospinal excitability (Devanne  
490 et al. 1997, Duclay et al. 2011; Sekiguchi et al. 2001, 2003, 2007), the number of trials in the  
491 current experiment would have been excessive, leading subjects into fatigue and affecting the  
492 results.

493

494 Since in the present study no differences were found in SOL MEP amplitude, which combined  
495 with stimulation intensity can modulate SP (Inghilleri et al. 1993; Säisänen et al. 2008), the  
496 decrease in SP during eccentric muscle actions suggests decreased cortical and/or spinal inhibition.  
497 The silent period has been used as an index of intracortical inhibition, as it is generally thought  
498 that it results from an early spinal inhibitory mechanism (< 50 ms) followed by later intracortical  
499 inhibition (Chen et al. 1999; Inghilleri et al. 1993; Roick et al. 1993). However, recent results have  
500 shown that the spinal inhibitory contribution can be much longer (i.e. up to 150 ms; Yacyshyn et  
501 al. 2016), casting doubt into the correct interpretation of SP data. Duclay et al. (2011) also found  
502 decreased SP during eccentric plantarflexion as compared to isometric, while other researches have  
503 shown evidence that supraspinal excitability seems to be higher during eccentric muscle actions  
504 (Fang et al. 2001, 2004; Gruber et al. 2009). Fang et al. (2001, 2004) reported greater movement-  
505 related cortical potential and a larger brain area involved during eccentric elbow flexion (maximal

506 and submaximal) as compared to concentric. The demonstrated differences suggest that the brain  
507 is more involved in the preparation, planning and execution of the movement and with the  
508 processing of sensory input during eccentric actions. Interestingly, in the present study eccentric  
509 velocity did not affect SP, suggesting that differences in afferent information (i.e. muscle spindle  
510 discharge) does not modulate these inhibitory mechanisms. Despite decreased cortical and/or  
511 spinal inhibition demonstrated by a shorter silent period in the present study and a higher  
512 MEP/CMEP ratio (i.e. higher cortical excitability demonstrated for elbow flexors; Grubber et al.  
513 2009), the responsiveness of the SOL motoneuron pool is lower during eccentric muscle actions  
514 (i.e. lower H/M), indicating that changes in neural control during eccentric muscle actions possibly  
515 occurs both at spinal and cortical sites. However, contrary to the previously exposed results, Hahn  
516 et al. (2012) reported no differences in MEP and CMEP between isometric and eccentric muscle  
517 actions for SOL muscle, evidencing the need for further research in this area.

518

519 *Proposed control mechanisms during eccentric muscle actions.* Although it is currently not  
520 possible to pinpoint the exact neural pathways responsible for the eccentric motor control, several  
521 considerations are warranted: (1) Previous experiments have shown similar depression in muscle  
522 activation for submaximal and maximal eccentric muscle actions, suggesting that Ib afferents are  
523 not likely to contribute to the spinal inhibition observed (Abbruzzese et al. 1994; Duclay et al.  
524 2014, Gruber et al. 2009; Sekiguchi et al. 2001); (2) since TA coactivation was similar among  
525 experimental conditions, reciprocal inhibition should not be responsible for the lower spinal  
526 excitability of SOL during the eccentric muscle actions; (3) recurrent inhibition mediated by  
527 Renshaw Cells can limit motor unit discharge rate (Windhorst 2007), and function as a variable  
528 gain regulator for motor output (Hultborn et al. 1979). Animal experiments have shown that

529 descending pathways can modulate recurrent inhibition (Baldissera et al. 1981), however indirect  
530 recurrent inhibition assessment in humans has shown it to decrease as the contraction intensity  
531 increased (Hultborn and Pierrot-Deseilligny 1979). Clearly, more information is needed in order  
532 to ascertain if recurrent inhibition is a possible candidate for the modulation seen in our study; (4)  
533 Presynaptic inhibition (PSI; Hultborn et al. 1987, Rudomin and Schmidt 1999) could reduce the  
534 responsiveness of the motoneuron pool during eccentric muscle actions, by reducing the stretch  
535 reflex gain (Bawa and Sinjær 1999; Nagazawa et al. 1997, 1998). Grosprêtre et al. (2014)  
536 conditioned the H-reflex with a subthreshold stimulation of the motor cortex and demonstrated  
537 that descending pathways appear to control spinal inhibition during eccentric muscle actions. The  
538 later study suggests that supraspinal modulation of PSI by primary afferent depolarization is a  
539 possible candidate for lowering spinal excitability during eccentric muscle actions; (5) intracortical  
540 inhibition (i.e. GABAergic inhibition) differences during eccentric and isometric muscle actions  
541 have been recently shown by Opie and Semmler (2016). Utilizing a paired pulse TMS over M1,  
542 they showed that short-interval intracortical inhibition was decreased whereas long-interval  
543 intracortical inhibition was increased in eccentric muscle actions as compared to isometric.

## 544 Conclusion

545 The present study showed a decreased responsiveness of the SOL motoneuron pool to Ia excitatory  
546 inputs (i.e reduced H/M) during eccentric muscle actions, while muscle mechanics (i.e. fascicle  
547 length and pennation angle) remained the same as compared with isometric muscle action.  
548 Although fascicle velocity was greater in the fast eccentric condition as compared with slow  
549 eccentric, no differences in corticospinal excitability were found between conditions, suggesting  
550 that Ia excitatory afferent input was not successful in increasing MN excitability. Additionally, the  
551 decrease in SP during eccentric muscle actions, while MEP values remained similar among the

552 different test conditions, suggests increased supraspinal and/or spinal excitability, even though the  
553 responsiveness to Ia excitatory inputs was lower.

554

555 Taken together, the present results corroborate with the hypothesis that the central nervous system  
556 has an unique activation strategy during eccentric muscle actions (Duchateau and Enoka 2008,  
557 2016; Duchateau and Baudry 2014; Enoka 1996). Furthermore, our results do not support the  
558 hypothesis that sensory information plays an important role in modulating spinal excitability  
559 during SOL eccentric muscle actions. A centrally mediated feedforward control scheme seems  
560 adequate to induce the observed excitability modulation, future studies are necessary to verify the  
561 exact mechanisms.

562

563

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565

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