1 Training induced changes in quadriceps activation during maximal eccentric 2 contractions. Dimitrios Voukelatos¹, Mathew Kirkland^{1,2}, and Matthew TG Pain¹ 3 4 ¹ School of Sport, Exercise and Health Sciences, Loughborough University, LE11 3TU, UK. ² St Peter's College, Johannesburg, South Africa 5 6 7 8 Submitted as Original Article Corresponding author: Matthew TG Pain 9 10 School of Sport, Exercise and Health Sciences 11 Loughborough University Loughborough LE11 3TU 12 UK 13 14 Email: m.t.g.pain@lboro.ac.uk 15 Tel. no: +44 (0)1509 226327 16 17 **Dimitrios Voukelatos** School of Sport, Exercise and Health Sciences 18 19 Loughborough University 20 Loughborough LE11 3TU 21 UK 22 Email: <u>D.Voukelatos@lboro.ac.uk</u> 23 Tel. no: +44 (0)1509 226322 24 25 Mathew Kirkland St Peter's College, Johannesburg, South Africa 26

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28 Abstract

29 Despite full voluntary effort, neuromuscular activation of the quadriceps group of muscles 30 appears inhibited during eccentric contractions. A nerve stimulation protocol during dynamic 31 contractions of the quadriceps was developed that employed triplets of supramaximal pulses 32 to assess suppressed eccentric activation. Subsequently the effects of a short training intervention, performed on a dynamometer, on eccentric strength output and neural inhibition 33 were examined. Torque-angular velocity $(T-\omega)$ and experimental voluntary neural drive-34 35 angular velocity (%VA- ω ; %VA, obtained via the interpolated twitch technique) datasets, 36 were obtained from pre- and post-training testing sessions. Non-linear regression fits of a seven parameter torque function and of a 3rd degree polynomial were performed on the pre-37 38 and post-training T- ω and %VA- ω datasets respectively. T-test showed a significant ($p < \infty$ 39 0.05) increase in the overall torque output post-training for the group, with three out of the six subjects demonstrating a significant (p < 0.05) increase in the torque output across the range 40 41 of angular velocities as shown by the extra-sum-of-squares F-test. A significant increase (p < p42 0.05) in the %VA post-training was also observed as well as a reduction in the plateauing of the torque output during fast eccentric contractions. 43

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45 **Keywords**: Neural inhibition, muscular contraction, stimulation, training.

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48 Introduction

49 The maximal force generating capacity of a muscle is a function of its velocity and length. During in vitro studies researchers have repeatedly shown isolated muscle fibres stretched 50 51 under maximal tetanic conditions produce a force that is 1.5 to 1.9 times higher than maximal 52 isometric force (Katz, 1939; Délèze, 1961; Edman et al., 1978; Edman, 1988). However, in 53 vivo measurements of the torque-velocity profile during maximum voluntary contractions 54 (MVC) show either little difference between isometric and eccentric torque across increasing angular velocities (Westing, 1988), or a tendency to decline with increasing velocity 55 56 (Westing et al., 1990; Dudley et al., 1990; Pain & Forrester, 2009; Forrester & Pain, 2010). EMG studies have shown a 10-30% decrease in the neural drive of the quadriceps under fast 57 58 eccentric MVC contractions (Westing et al., 1991; Enoka, 1997; Paillard et al., 2005). It has 59 been proposed that this apparent reduction in neural drive could be due to the existence of a 60 neural tension-limiting mechanism that only becomes active during maximal load 61 contractions of skeletal muscle (Westing et al., 1990; Westing et al., 1991). Pain and 62 Forrester (2009) used normalized wavelet transformed EMG to calculate EMG-corrected maximal voluntary torques (MVT) from a wide range of eccentric and concentric 63 64 contractions of the knee extensors. They arrived at a peak eccentric to isometric torque ratio (T_{ecc}/T_0) of 1.6. 65

Dudley et al. (1990) used sub-maximal transcutaneous electrical muscle stimulation (40-60% of MVT) to produce a torque-velocity profile for the knee extensors that was closer to the *in vitro* tetanic profile; T_{ecc}/T_0 of 1.4 and did not drop off at higher lengthening velocities. Westing et al. (1990) also used transcutaneous electrical muscle stimulation, in isolation and superposed on MVC, and although these authors attempted to obtain maximal activation levels using both methods the level of stimulation was subjectively limited between subjects based on their pain thresholds. They found that superposed stimulation increased eccentric

MVT by 24% from MVC alone at 360°/s. They obtained a T_{ecc}/T_0 of 1.33 for stimulated 73 only, but 1.23 for superposed stimulation. For the latter the absolute torque values were 74 75 higher and this was seen as a good indicator of the tension limiting mechanism. Amiridis et al. (1996) also used this superposition method and found similar results to Westing et al. 76 (1990) for untrained subjects (torque with stimulation was 25% higher than MVT alone, and 77 T_{ecc}/T_0 was 1.23 for MVC plus stimulation), but little eccentric increase for trained athletes 78 79 when superposed electrical stimulation was used. For the athletes in the study of Amiridis et al. (1996) T_{ecc}/T_0 was 1.22 for superposed stimulation. More recently Pain et al. (2013) used 80 81 sub-maximal transcutaneous muscle stimulation, but with a wider range of velocities than previously used, to obtain a T_{ecc}/T_0 of 1.7 for both the quadriceps and hamstrings. In these 82 studies lower absolute eccentric torque is associated with higher T_{ecc}/T_0 ratios and is 83 84 supportive of the tension limiting hypothesis.

85 The aforementioned studies have all used muscle stimulation which can cause rapid fatigue and discomfort and also reduces concentric torque values compared to MVT values. 86 Transcutaneous stimulation of the femoral nerve is an alternative method for stimulating the 87 quadriceps muscles, and has been used repeatedly in studies utilising the interpolated 88 89 twitch technique (ITT) during isometric and slow dynamic contractions and in maximal rate 90 of force development studies using octets (Deutekom et al., 2000; de Ruiter et al., 2004; 91 Folland et al., 2014; Beltman et al., 2004). However, there does not appear to be any literature on repeated nerve stimulation during fast eccentric contractions and its 92 93 effect on neuromuscular activation.

The results of Amiridis et al. (1996) suggest that the MVC and stimulated torque-velocity profiles may depend upon the fitness level of subjects. Therefore, it can be hypothesised that specific strength training could induce a reduction in the inhibitive action and a number of studies tested that hypothesis using various training programmes. These, however, were

98 either performed using free weights (Aagaard et al., 2000), focused on the concentric phase of muscular contraction only (Caiozzo et al., 1981), or the aim was to establish 99 100 training-induced physiological changes of the contracting muscles (Coyle et al., 1981; 101 Aagaard et al., 2001). Spurway et al. (2000) performed a 6 week knee extension training 102 protocol with one leg concentric and one leg eccentric and surmised from their results that 103 eccentric strength was increased primarily from decreased inhibition. However, no measures 104 of neural activity were taken and morphological changes would also likely have started. 105 Furthermore, attempts to improve the force output during maximal voluntary eccentric 106 contractions by following a strictly isovelocity strength training protocol have given 107 contradictory results (Higbie et al., 1996; Seger & Thorstensson, 2005).

108 The aims of this study were: a) to develop a nerve stimulation protocol during dynamic 109 contractions without causing excessive discomfort or injury in order to examine suppressed 110 eccentric activation and b) to investigate whether performing a high velocity strength training 111 protocol using eccentric-concentric cycles on an isovelocity dynamometer would lead to a 112 decrease in the inhibitive action of the neural factors and an increase in torque output during 113 fast eccentric maximal voluntary contractions. The training protocol was specifically geared 114 to high velocity eccentric/concentric training on an isovelocity dynamometer over a period of 115 3 weeks to limit adaptations to predominately neural changes (Corriander & Tesch, 1990). It was hypothesized that at the end of the training cycle subjects would exhibit significantly 116 117 higher torque outputs and a reduction in neural inhibition.

118 Method

Two similar groups of male volunteers, (n = 9 and n = 6), who had not previously engaged in any systematic form of strength training or high level sports practice, were recruited for the study (mean \pm standard deviation: age 26.3 \pm 2.7 years, body mass 72.9 \pm 11.7 kg, height, 172.2 \pm 8.4 cm;). They all gave written, informed consent and the study was conducted in accordance with the approval given by the Loughborough University Ethical Advisory Committee. The study was divided into two phases to address aims (a) and (b) above.

125 *Phase 1*.

126 The minimum required sample size was determined by performing a power analysis on the 127 MVC and superimposed eccentric torque values reported by Westing et al., (1990). The 128 analysis showed that a minimum sample size of four was required to achieve a power value 129 of 0.8 and p < 0.05. To account for drop out a total of nine subjects took part in this phase of 130 the study and data collection finished when six had completed the protocol. As this protocol 131 was painful for some subjects, and pain was associated with an increased risk of injury, the subject numbers were kept minimal for ethical considerations, and two more than the 132 minimum completed testing in case of later issues with data. Testing took place on an 133 134 isovelocity dynamometer with built-in gravitational torque correction (Con-Trex, CMV AG, Switzerland) over three sessions. In each session subjects were seated on the dynamometer 135 136 with their dominant leg strapped tightly to the unpadded crank arm directly above the ankle 137 joint using a protective moulded plastic shin guard. The anterior hip angle was set at 100° (seat was set at 80° incline). To minimise differences between the crank and joint 138 139 kinematics, the rotational axis of the crank arm was aligned with the centre of the knee joint 140 during near-maximal efforts.

141 Dynamometer and stimulator data were recorded simultaneously at 512 Hz with Spike2 software (Spike 2, CED, Cambridge, UK). The dynamometer data were filtered at 8 Hz 142 143 using a low-pass fourth order Butterworth filter. Knee joint angles were measured with a 144 mechanical goniometer during four isometric trials and the instantaneous crank arm angle 145 was converted to joint angle using a linear regression equation (Pain & Forrester, 2009). For 146 each dynamic trial the maximum eccentric and concentric isovelocity phases were identified 147 and the isovelocity plateau was defined as the region where the angular velocity was within 5% of the peak value. 148

149 Each session was initiated with a standardized warm up protocol. Session 1 was a familiarisation session where subjects performed one maximal MVC at crank angles of 15° 150 through to 75° in 15° steps (with 0° corresponding to full extension) and a number of MVC 151 and electrically stimulated dynamic (eccentric-concentric) contractions at 50, 200 and 350°/s. 152 The optimum angle of peak torque was determined by fitting a quadratic to the torque-angle 153 dataset obtained from the isometric MVCs. During the second session maximum, eccentric-154 concentric contractions were performed at: 50, 200 and 350°/s, according to the protocol of 155 Yeadon et al. (2006) with two-minute rest intervals between trials. Once MVCs were 156 completed subjects performed one stimulated trial at each isovelocity to further familiarise 157 themselves with the sensation. Subsequently, optimum peak torque angles per isovelocity 158 were determined for each subject as well as the time lapse between onset and effect of 159 160 stimulation in order for the latter to coincide with the optimum angle. The onset of stimulation varied with angular velocity and acceleration (Figure 1). However, the 161 162 changing width of stimulation twitch response with angular velocity (Gandevia et al., 163 1998) was not accounted for. In the third session subjects performed one MVC and one supramaximal stimulation trial at each isovelocity and each contraction mode and the 164 165 respective peak torque values were recorded and used in the subsequent analysis.

166 Electrical stimulation. Transcutaneous electrical stimulation of the quadriceps was achieved 167 using a stimulator (DS7AH, Digitimer Ltd., UK) controlled by Spike 2 software. Two electrodes, a ball probe cathode of 10 mm in diameter, and a rectangular anode (90x50 mm) 168 169 both coated with a thin layer of conductive gel were placed at the femoral nerve and the gluteal fold respectively (Tillin et al., 2011). The individual stimulation intensity was 170 171 determined by sending single rectangular pulses (0.2 ms) of increasing strength starting from a current intensity of 30 mA, in 30 mA steps, until the twitch response plateaued. 172 173 A supramaximal stimulation level was set at 20% above this intensity. In the first 174 session a singlet supramaximal pulse was sent through the femoral nerve in order to gradually familiarise the subjects to electrical stimulation, however, this became a triplet in 175 176 subsequent sessions. The pulses were timed to coincide with optimum knee angle.

A 2x4 repeated measures ANOVA was performed in order to determine the effects of
stimulus (MVC vs STIM) and velocity on the torque values. Effect sizes were calculated and
subsequently used in a second power analysis to determine the minimum sample size for the
training part of the study.

181 *Phase 2*

182 Having established that triplets would not drive eccentric values high enough to reach 183 theoretical T_{ecc}/T_0 values the use of doublet stimulation was chosen for the ITT, since it has 184 been shown that the method is not sensitive to the number of pulses used, allowing the 185 measurement of reduced voluntary activation but with less discomfort (Behm et al., 1996; 186 Folland & Williams, 2007). This would help mitigate the risk of losing subjects in the latter 187 stages of the testing protocol when replacements would not be possible. Power analysis 188 based on Phase 1 showed that a minimum sample size of n = 5 was required to achieve a 189 power value of 0.8 and p < 0.05. Six new subjects were recruited in this phase of the study.

Phase 2 consisted of eleven sessions, a familiarisation session that followed the 190 191 familiarisation protocol of Phase 1, eight training sessions and two testing sessions that took 192 place pre- and post-training respectively. Training took place over a 3-week period. Sessions 193 lasted no more than 30 minutes, where subjects performed up to 10 sets of dynamic eccentric-194 concentric knee extension cycles at velocities ranging between 50 and 350°/s. The number of cycles and velocities increased as subjects adapted. Since the intensity of the training could 195 196 not be quantified by counting the number of repetitions and loads, sets were time-matched. 197 Specifically, one eccentric-concentric cycle was performed at 50°/s and 100°/s, two at 150°/s, 198 three at 250°/s and four at 350°/s. All training sessions were supervised by the investigators.

199 The testing protocol consisted of maximal voluntary and supramaximally 200 electrically stimulated isometric and dynamic contractions. The range of isometric 201 contractions was the same as in previous sessions but this time the dynamic contractions 202 were measured at 5 angular velocities: 50, 100, 150, 250 and 350°/s. During isometric contractions subjects performed one MVC and one stimulation contraction per joint angle. 203 204 The same order was maintained during dynamic contractions. Electrical stimulation was 205 achieved following the procedure described in Phase 1 with doublet pulses.

206 The percentage of voluntary activation (%VA) of the quadriceps muscle was expressed by207 the following formula:

208 [Equation 1]

where the superimposed twitch is the torque increment noted during a maximal contraction at the time of stimulation and the control twitch is that evoked in the relaxed muscle (Shield & Zhou, 2004; Folland & Williams, 2007). The torque increment was defined as follows. If torque was increasing in value prior to stimulation then the value of the torque in the absence of stimulation was calculated by extrapolating the last 25 data points prior to stimulation onset, taking the corresponding extrapolated value and subtracting it from the peak twitch
torque, similar to Gandevia et al. (1998). If torque value was decreasing prior to stimulation,
and in order to avoid overestimating the torque increment, the last value prior to onset of
stimulation was subtracted from the peak twitch torque value, similar to Beltman et al. (2004)
(Figure 1).

219 In order to assess possible group changes in performance the torque vs. angular velocity (T-220 ω) curves were plotted for every subject pre and post-training. These were numerically 221 integrated and the eccentric and concentric areas compared at group level using a one-tailed 222 paired t-test. A 2x2x6 repeated measures ANOVA (time x velocity x contraction mode) was also used to determine the effects of velocity and training on the neural inhibition during 223 224 eccentric contractions. Due to difficulties in eliciting stimulated contractions at the 225 predetermined angles during efforts at high isovelocities it was not possible to repeat the t-226 test comparison for the ITT dataset due to the small number of data points obtained.

227 T- ω and %VA- ω data sets per subject were obtained in both testing sessions. The individual pre- and post-training T- ω data sets for each subject were statistically compared by 228 229 performing a nonlinear regression fit of the 7-parameter MVT function defined in Forrester et 230 al. (2011), first separately and subsequently to the combined pre and post-training data sets 231 (Figure 2). The fits for each profile were statistically compared using the extra-sum-of-232 squares F-test (Motulsky & Christopoulos, 2004; Voukelatos & Pain, 2015). The same statistical process was repeated for the %VA- ω data set by fitting a 3rd degree polynomial to 233 establish the training effect on voluntary activation (Figure 3). 234

Normal distribution was checked using a Shapiro-Wilk test of normality. Analysis of the
Con-Trex data was performed using Matlab (version 8.1, The MathWorks Inc., Natick, MA,
USA) and statistical analysis was performed using SPSS (version 21, SPSS Inc., Chicago,

- 238 Illinois, USA). The power analyses were performed using GPower (Erdfelder et al., 2009).
- A statistical level of significance, p < 0.05, was used throughout. Cohen's, d, was used as an
- effect size for the t-tests considering 0.2, 0.5, 0.8 as small, medium and large effects. Effect
- size for the factorial ANOVAs used the partial eta squared statistic, η_p^2 , (Cohen, 1992). Data
- 242 are reported as mean \pm SD unless otherwise stated.

243	Results
240	Results

Phase1

The 2x4 factorial ANOVA showed that there was a significant main effect for stimulus ($F = 67, \eta_p^2 = 0.94$). Contrasts between the baseline torque value recorded at 350°/s showed significant increase in torque outputs during stimulation contractions with respect to torque outputs from 200°/s and 50°/s (Table 1).

[Table 1]

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Phase 2

The comparison of the numerically integrated T- ω plots using a paired t-test showed significant increase (t = 3.2, d = 1.3) between pre and post-training data. There were significant increases in area under the T- ω curve post-training for both the eccentric section, t= 2.0, d = 0.82 and the concentric section, t = 2.3, d = 0.93.

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The 2x2x6 factorial ANOVA revealed a significant main effect for time ($F = 6.6, \eta_p^2 = 0.57$)

with overall post-training torque output being significantly higher than pre-training values $(239 \pm 12 \text{ vs } 261 \pm 15 \text{ Nm}$ for pre and post-training respectively). There was no significant time x velocity interaction. Contrasts were also performed comparing peak torque output from 0-250°/s to the baseline value of 350° /s. Those revealed a significant increase in eccentric peak torque from 0-250°/s to the baseline value of 350° /s, relative to peak torque values at 150° /s (Table 2).

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263 [Table 2]

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265 The individual MVT fit to each subject's T- ω datasets (Figure 2) showed that 3 out of the 6 266 subjects had significantly higher torque output post-training (Table 3). When the MVT

267	function was fitted to the pooled pre and post $T-\omega$ datasets of all subjects a significant				
268	increase in torque output post-training was found at group level ($F = 2.06, d = 0.63$).				
269	Applying the extra-sum-of-squares F-Test (Figure 3) to the %VA- ω datasets of each subject				
270	individually revealed one subject with a significant difference in %VA post-training (Table				
271	3). However, the combined curve fit to the pooled pre and post-training %VA- ω datasets				
272	showed a significant increase in the %VA ($F = 3.3$, $d = 0.39$).				
273					
274	[Table 3]				
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276	[Figure 1]				
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278	[Figure 2]				
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280	[Figure 3]				
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282	[Figure 4]				
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284	Discussion				
285	The aim of the first phase was to develop a nerve stimulation protocol during dynamic				
286	contractions in order to examine suppressed eccentric activation and was for the most part				
287	successful. Subjects achieved significantly higher torque outputs during electrically				

289 (Table 1). Moreover the repeated measures ANOVA contrasts showed that triplet stimulation

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stimulated eccentric contractions of the quadriceps compared to the respective MVC values

290 successfully reduced the torque suppression in the eccentric region of the T- ω curve. At

291 350°/s the peak torque with stimulation superposed was 31% higher than that of MVC alone 292 and this is greater than that seen in Westing et al. (1990) and Amiridis et al. (1996). In this 293 study T_{ecc}/T_0 was 1.24 during superposed nerve stimulation, which is the same as the 1.23 294 times found in both Westing et al. (1990) and Amiridis et al. (1996). The differences in the ratios of increased eccentric torque and T_{ecc}/T_0 between this study and the previous ones 295 296 are likely due to the low eccentric MVT values of the subjects in this study. A limitation of our method can be found in the accuracy of timing of the triplet stimulation, particularly at 297 298 high velocity. Consequently, the peak STIM torque angle may not always coincide with the 299 peak MVC torque angle. However, it is likely that VA is less susceptible to timing errors as during maximal effort trials (STIM or MVC) subjects are meant to be maximally 300 301 active and therefore the twitch increment will still be relative to maximum effort. 302 Another potential limitation of using triplet stimulation is the level of discomfort felt by 303 subjects. This may also explain the lower values for MVT via a fear avoidance reduction of 304 volitional effort over and above the potential neural inhibition (Button & Behm, 2008). 305 This was predominantly observed during isometric contractions where three of the six subjects recorded STIM values that were significantly lower than their respective MVC 306 307 values. Given subject comments and that a typical twitch response can be seen that does 308 not drive the torque value towards the MVC, this was likely due to increased whole body 309 tension and degree of co-contraction of the antagonist (Figure 4).

At the end of the short term high velocity dynamometer training protocol subjects achieved a significant increase in overall torque output during both concentric and eccentric contractions, in agreement with our hypothesis. Regarding the effect of the training protocol on neural activation and the action of the tension limiting mechanism, a significant increase in the %VA post-training was achieved, as well as a significant increase in the peak torque outputs, during eccentric contractions at 350°/s with respect to torque outputs from 150°/s. These results are indicative of increased neuromuscular activation post-training and a possible reduction in the inhibitive action of the tension limiting mechanism. These results are in, at least partial, agreement with previous isovelocity training studies that also reported significant increases in the torque output during eccentric/concentric contractions of the quadriceps after isovelocity strengthening protocols (Caiozzo et al., 1981; Coyle et al., 1981; Hortobàgyi et al., 1996; Higbie et al., 1996).

322 The current study also sought to address the nature of the underlying reason behind increased 323 torque output post-training, and more specifically whether this was due to an increase in 324 neuromuscular activation. The significant increase in the %VA value post-training suggests 325 an increase in the neuromuscular activation of the quadriceps muscle. This is in line with 326 findings by Hortobàgyi et al. (1996), Higbie et al. (1996) and Aagaard et al. (2000) who 327 reported increased iEMG activity of the quadriceps muscle post-training. However, since 328 post-training increases in quadriceps cross-sectional area and number of type II fibres were also reported (Higbie et al., 1996; Hortobàgyi et al., 1996), it is not clear whether the 329 330 observed increases in iEMG values were solely due to increased neuromuscular activation or 331 also due to increased muscle hypertrophy. In the current study only 8 training sessions in three weeks took place, thus it is likely that the observed increase in the torque output post-332 333 training can be attributed almost exclusively to neural factors, such as increased muscle 334 neuromuscular activation, more efficient recruitment and decreased neural inhibition (Staron et al., 1994; Colliander & Tesch, 1990). 335

Increased neuromuscular activation would manifest itself through a greater increase in torque
output during eccentric compared to concentric contractions post-training and a reversal of
the torque suppression during eccentrics at high velocities *in vivo* (Westing et al., 1990, 1991;
Dudley et al., 1990; Webber & Kriellaars, 1997; Seger & Thorstensson, 2005). The observed
torque increase in this study was not higher post-training during eccentric compared to

341 concentric contractions. However, the results of the repeated measures ANOVA showed that 342 whereas the subjects' torque outputs tended to plateau at 150°/s during eccentric contractions 343 pre-training they do not appear to do so post-training. This is possibly a significant finding as 344 it offers an indication that the neural inhibition may, indeed be reversible. At the same time it must be noted that, unlike Phase 1, there was no clear increasing trend in eccentric peak 345 346 torque values with increasing angular velocities suggesting that some level of neural inhibition was possibly still present post-training. If this is indeed the case then, a complete 347 348 reversal of neural inhibition may need longer periods of training to emerge if the inhibition is 349 present to act against overloading the musculoskeletal system. To safely increase eccentric strength concomitant increases in resistance to loading of the tendons, bones, and other 350 351 structural tissues would be necessary and take longer to adapt.

Limitations of this study include the difficulty of eliciting consistent electrical pulses at high 352 353 isovelocities during stimulated contractions, the use of two different stimulation protocols 354 due to subject discomfort, and possible learning effects from the repeated use of the 355 dynamometer by the subjects. The change to using doublet ITT to look at voluntary 356 activation via twitch responses prevents some direct comparisons between Phase 1 and Phase 2 results but still reflects the activation changes. The familiarization session protocol was 357 358 designed to minimize learning effects and their confounding influence (Madsen, 2006; Lund 359 et al., 2005) and should not be a major factor.

This is the first time triplet nerve stimulation has been used to assess eccentric suppression during fast dynamic contractions and produced very similar results to muscle stimulation studies whilst also allowing the application of dynamic doublet ITT to eccentric and concentric knee extensions. Performing a short, strength training protocol, consisting of 8 training sessions, on an isovelocity dynamometer over a range of angular velocities produced notable increases in torque output for all velocities and types of contraction. This is

- 366 attributed to an increase in muscle activation and, a decrease in the inhibitive action of the
- 367 tension-limiting mechanism observed during fast eccentric contractions of the quadriceps.

368 Disclosure of conflict of interest

369 There is no conflict of interest.

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371 **References**

Aagaard, P., Simonsen, E. B., Andersen, J. L., Magnusson, S. P., Dyhre-Poulsen, P., HalkjærKristensen, J., 2000. Neural inhibition during maximal eccentric and concentric
quadriceps contraction: effects of resistance training. Journal of Applied Physiology, 89,
2249-2257.

376

Aagaard, P., Andersen, J. L., Dyhre-Poulsen, P., Leffers, A. M., Wagner, A., Magnusson, S.
P., Halkjær-Kristensen, J., & Simonsen, E. B., 2001. A mechanism for increased
contractile strength of human pennate muscle in response to strength training: changes in
muscle architecture. Journal of Physiology, 534, 613-623.

381

Amiridis, I. G., Martin, A., Morlon, B., Martin, L., Cometti, G., Pousson, M., van Hoecke, J.,
1996. Co-activation and tension-regulating phenomena during isokinetic knee extension in
sedentary and highly skilled humans. European Journal of Applied Physiology, 73, 149156.

386

Behm, D. G., St-Pierre, D. M. M., Perez, D., 1996. Muscle inactivation: assessment of
interpolated twitch technique. Journal of Applied Physiology, 81, 2267-2273.

389

Beltman, J. G. M., Sargeant, A. J., van Mechelen, W., de Haan, A. 2004. Voluntary activation
level and muscle fiber recruitment of human quadriceps during lengthening contractions.
Journal of Applied Physiology, 97, 619-626.

393

Button, D. C., Behm, D. G., 2008. The effect of stimulus anticipation on the interpolated
twitch technique. Journal of Sports Science and Medicine, 7, 520-524.

396	Caiozzo, V. J., Perrine, J. J., Edgerton, V. R., 1981. Training-induced alterations of the in
397	vivo force-velocity relationship of human muscle. Journal of Applied Physiology, 51, 750-
398	754.
399	

Cohen, J., 1992. Statistical power analysis. Current Directions in Psychological Science, 1,
98-101.

402

403 Corriander, E., B., & Tesch, P., A., 1990. Effects of eccentric and concentric muscle actions
404 in resistance training. Acta Physiologica Scandinavica, 140, 31-39.

405

- 406 Coyle, E. F., Feiring, D. C., Rotkis, T. C., Cote III, R. W., Roby, F. B., Lee, W., Wilmore, J.
- 407 H., 1981. Specificity of power improvements through slow and fast isokinetic training.
 408 Journal of Applied Physiology, 51, 1437-1442.
- 409
- 410 Délèze, J.B., 1961. The mechanical properties of the semitendinosus muscle at lengths
 411 greater than its length in the body. Journal of Physiology, 158, 154–164.

412

- de Ruiter, C. J., Kooistra, R. D., Paalman, M. L, de Haan, A., 2004. Initial phase of maximal
 voluntary and electrically stimulated knee extension torque development at different knee
 angles. Journal of Applied Physiology, 97, 1693-1701.
- 416
- 417 Deutekom, M., Beltman, J. G. M., de Ruiter, C. J., Koning, J. J., de Haan, A., 2000. No acute
 418 effects of short-term creatine supplementation on muscle properties and sprint
 419 performance. European Journal of Applied Physiology, 82, 223-229.

420

421	Dudley, G. A., Harris, R. T., Duvoisin, M. R., Hather, B. M., Buchanan, P., 1990. Effect of
422	voluntary vs. artificial activation on the relationship of muscle torque to speed. Journal of
423	Applied Physiology, 69, 2215-2221.
424	
425	Edman, K. A. P., Elzinga, G., Noble, M. I. M., 1978. Enhancement of mechanical
426	performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres.
427	Journal of Physiology, 281, 139-155.
428	
429	Edman, K. A. P., 1988. Double hyperbolic force-velocity relation in frog muscle fibers.
430	Journal of Physiology, 404, 301-321.
431	
432	Enoka R. M., 1997. Neural adaptations with chronic physical activity. Journal of
433	Biomechanics, 30, 447-455.
434	
435	Erdfelder, F. F., Buchner, A., Lang, A. G., 2009. Statistical power analyses using GPower
436	3.1: Tests for correlation and regression analyses. Behavior Research Methods, 41, 1149-
437	1160.
438	
439	Folland, J. P. & Williams, A. G., 2007. Methodological issues with the interpolated twitch
440	technique. Journal of Electromyography and Kinesiology, 17, 317-327.
441	
442	Folland, J. P., Buckthorpe, M. W., Hannah, R., 2014. Human capacity for explosive force
443	production: Neural and contractile determinants. Scandinavian Journal of Medicine and
444	Science in Sports, 24, 894-906.
445	

446	Forrester, S. E. & Pain, M.T.G., 2010. A combined muscle model and wavelet approac				
447	interpreting the surface EMG signals from maximal dynamic knee extensions. Journal of				
448	Applied Biomechanics, 26, 62-72.				

- 450 Forrester, S. E., Yeadon, M. R., King, M. A., Pain, M.T.G., 2011. Comparing different
- 451 approaches for determining joint torque parameters from isovelocity dynamometer

452 measurements. Journal of Biomechanics, 44, 955-961.

453

- Gandevia. S. C., Herbert, R. D., Leeper, J. B., 1998. Voluntary activation of human elbow
 flexor muscles during maximal eccentric contractions. Journal of Physiology, 512, 595602.
- Hortobàgyi, T., Hill, J. P., Houmard, J. A., Fraser, D. D., Lambert, N. J., Israel, R. G., 1996.
 Adaptive responses to muscle lengthening and shortening in humans. Journal of Applied
 Physiology, 80, 765-772.

460

- Higbie, E. J., Cureton, K. J., Warren III, G. L., Prior, B. M., 1996. Effects of concentric and
 eccentric training on muscle strength, cross-sectional area, and neural activation. Journal
 of Applied Physiology, 81, 2173-2181.
- 464
- Katz, B., 1939. The relation between force and speed in muscular contraction. Journal of
 Physiology, 96, 45–64.
- 467
- 468 Lund, H., Søndergaard, K., Zachariassen, T., Christensen, R., Bülow, P., Henriksen, M.,
 469 Bliddal, H., 2005. Learning effect of isokinetic measurements in healthy subjects and

470	reliability and comparability of Biodex and Lido dynamometers. Clinical Physiology and
471	Functional Imaging, 25, 75-82.
472	
473	Madsen, O. R., 1996. Torque, total work, power, torque acceleration energy and acceleration
474	time assessed on dynamometer: reliability of knee and elbow extensor and flexor strength
475	measurements. European journal of Applied Physiology, 74, 206-210.
476	
477	Motulski, H., & Christopoulos, A., 2004. Fitting Models to Biological Data using Linear and
478	Nonlinear Regression. Oxford University Press, New York.
479	
480	Paillard, T., Margnes, E., Maitre, J., Chaubet, V., Francois, Y., Gonzalec, G., Borel, L., 2005.
481	Electrical stimulation superimposed onto voluntary muscular contraction. Sports
482	Medicine, 35, 951-966.
483	
484	Pain, M. T. G. & Forrester, S. E., 2009. Predicting maximum eccentric strength from surface
485	EMG measurements. Journal of Biomechanics, 42, 1598-1603.
486	
487	Pain, M. T. G., Young, F., Forrester, S. E., 2013. The torque-velocity relationship in large
488	human muscles: maximum voluntary versus electrically stimulated behaviour. Journal of
489	Biomechanics, 46, 645–650.
490	
491	Place, N., Casartelli, N., Glatthorn, J. F., Maffiuletti, N. A., 2010. Comparison of quadriceps
492	inactivation between nerve and muscle stimulation. Muscle Nerve, 42, 894-900.
493	

494	Seger, J. Y., & Thorstensson, A., 2005. Effects of eccentric versus concentric training on
495	thigh muscle strength and EMG. International Journal of Sports Medicine, 26, 45-52.
496	
497	Shield, A., & Zhou, S., 2004. Assessing Voluntary Muscle Activation with the Twitch

- 498 Interpolation Technique. Sports Medicine, 34, 253-267.
- 499
- Spurway, N. C., Watson, H., McMillan, K., Connoly, G., 2000. The effect of strength training
 on the apparent inhibition of eccentric force production in voluntarily activated human
 quadriceps. European Journal of Applied Physiology, 82, 374-380.
- 503
- 504 Staron, R. S., Karapondo, D. L., Kraemer, W. J., Fry, A. C., Gordon, S. E., Falkel, J. E.,
- Hagerman, F. C., Hikida, R. S., 1994. Skeletal muscle adaptations during the early phase
 of heavy-resistance training in men and women. Journal of Applied Physiology, 76, 12471255.
- 508
- Tillin, N. A., Pain, M. T. G., Folland, J. P., 2011. Short term unilateral resistance training
 affects the agonist-antagonist but not the force-agonist activation relationship. Muscle
 Nerve, 43, 375-384.
- 512
- Voukelatos, D., & Pain, M. T. G., 2015. Modelling suppressed muscle activation by means of
 an exponential sigmoid function: Validation and bounds. Journal of Biomechanics,
 48,712-715.

517 Weber, S., & Kriellaars, D., 1997. Neuromuscular factors contributing to in vivo eccentric
518 moment generation. Journal of Applied Physiology, 83, 40-45.

520	Westing, S. H., 1988. Eccentric and concentric torque-velocity characteristics of the
521	quadriceps femoris in man. European Journal of Applied Physiology, 58, 100-104.
522	
523	Westing, S. H., Seger, J. Y., Thorstensson, A., 1990. Effects of electrical stimulation on
524	eccentric and concentric torque -velocity relationships during knee extension in man. Acta
525	Physiologica Scandinavica, 140, 17-22.
526	
527	Westing, S. H., Cresswell, A. G., Thorstensson, A., 1991. Muscle activation during maximal
528	voluntary eccentric and concentric knee extension. European Journal of Applied
529	Physiology, 62, 104-108.
530	
531	Yeadon, M. R., King, & M. A., Wilson, C., 2006. Modelling the maximum voluntary joint
532	torque/angular velocity relationship in human movement. Journal of Biomechanics, 39,

476-482.

Table 1: Mean peak torque \pm SD values per isovelocity obtained for MVC and stimulated eccentric contractions during Phase 1. It is noted that contrary to the other isovelocities, the stimulated peak torque values were lower than the respective MVC values as some of the subjects were adversely affected by the intensity of the stimulus.

ω (°/s)	MVC (Nm)	STIM (Nm)
0	284 ± 22	268 ± 38
50	266 ± 15	291 ± 25
200	257 ± 32	318 ± 39
350	254 ± 24	333 ± 60

538

539

Table 2: Mean peak \pm SD torque values obtained at 0 to $\pm 350^{\circ}$ /s during pre and post-training

541 sessions for both contraction modes.

ω (°/s)	Pre-Training	Torque (Nm)	Post-Training	Torque (Nm)	
	ECC	CONC	ECC	CONC	
0	227	227 ± 46		256 ± 42	
50	240 ± 32	188 ± 26	265 ± 46	207 ± 18	
100	251 ± 39	168 ± 27	254 ± 33	196 ±19	
150	245 ± 27	152 ± 19	$257* \pm 29$	169 ± 19	
250	226 ± 34	128 ± 19	251 ± 41	140 ± 12	
350	247 ± 42	109 ± 20	$280^{*} \pm 46$	127 ± 13	

542 *Significant difference (p < 0.05) in torque output at150 and 350°/s post-training.

543	Table 3: Results obtained from fitting the MVT torque function and a 3 rd degree polynomial
544	to the raw T- ω and %VA- ω data sets respectively. Individual comparisons showed that three
545	out of six subjects recorded significantly higher torque outputs and one subject exhibited
546	significantly higher neuromuscular activation post-training.

	MVC fit		%VA fit	
	F-ratio [†]	Cohen's d	F-ratio [†]	Cohen's d
Subject 1	0.92	0.18	1.35	0.75
Subject 2	5.91*	2.1	1.93	0.24
Subject 3	1.58	0.71	0.67	0.11
Subject 4	4.95*	1.45	4.2*	0.35
Subject 5	12.9*	3.8	3.8	0.86
Subject 6	2.62	0.81	0.94	0.32

547 * p < 0.05

[†] F represents the ratio between the sum of the variances of the pre and post-training MVC /
polynomial fits over the respective combined (global) fit variance. If the two variances are
close then the pre and post curves are almost identical suggesting a minimal training effect.
On the other hand, if the variance of the individual curves is greater than the combined
variance then the two curves are distinct indicating a possible training effect on the torque
output or voluntary activation.

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557 List of figures

Figure 1: Rows 1-2: Passive Torque – angle plots with superimposed stimulation (vertical line) for eccentric (row 1) and concentric contractions (row 2) at 50°/s, 200°/s and 350°/s (columns 1-3 respectively). Rows 3-4: MVC (broken red line) and STIM (blue line) Torque – angle plots with superimposed stimulation (vertical line) for eccentric (row 3) and concentric contractions (row 4) at 50°/s, 200°/s and 350°/s (columns 1-3 respectively). Black broken line shows increasing/decreasing value of joint angle. All plots correspond to the respective isovelocity regions.

565

Figure 2: Example plots from Subject 4 of the pre- and post-training T- ω raw data and separately fitted MVT function for each dataset. The fitted MVT function produced maximal concentric angular velocity values, ω , of 1,550°/s and 1,805°/s for pre and post-training fits respectively. Those values compare very well with the values obtained by Forrester et al., 2011 for three different subjects (1,410-2,000°/s).

571

572 **Figure 3:** Example plots from Subject 1 of the pre- and post-training %VA- ω data and 573 separately fitted 3rd degree polynomials for each dataset.

574

575 **Figure 4:** MVC (broken red line) and STIM (blue line) Torque – angle plots with

576 superimposed stimulation (vertical line) during isometric contraction followed by passive577 twitch.

578 Equation 1:

%VA=
$$\left(1-\frac{\text{superimposed twitch}}{\text{control twitch evoked at rest}}\right) \times 100$$



 θ (deg)

















Figure Click here to download Figure: Figure 2.eps



Figure Click here to download Figure: Figure 3.eps



Figure Click here to download Figure: Figure 4.eps

