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Title: **Contraction type influences the human ability to utilise the available torque capacity of skeletal muscle during explosive efforts**

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Running title: Explosive torque and type of contraction

1 **Abstract**

2 The influence of contraction type on the human ability to utilise the torque capacity of
3 skeletal muscle during explosive efforts has not been documented. Fourteen male
4 participants completed explosive voluntary contractions of the knee extensors in four
5 separate conditions: concentric (CON) and eccentric (ECC); and isometric at two
6 knee angles (101°, ISO101; and 155°, ISO155). In each condition torque was
7 measured at 25-ms intervals up to 150-ms from torque onset, and then normalised to
8 the maximum voluntary torque (MVT) specific to that joint angle and angular
9 velocity. Explosive voluntary torque after 50-ms in each condition was also expressed
10 as a percentage of torque generated after 50-ms during a supramaximal 300-Hz
11 electrically evoked octet in the same condition. Explosive voluntary torque
12 normalised to MVT was >60% larger in CON than any other condition after the initial
13 25-ms. The percentage of evoked torque expressed after 50-ms of the explosive
14 voluntary contractions was also greatest in CON (ANOVA; $P < 0.001$), suggesting
15 higher concentric volitional activation. This was confirmed by greater agonist EMG
16 normalised to M_{\max} (recorded during the explosive voluntary contractions) in CON.
17 These results provide novel evidence that the ability to utilise the muscle's torque
18 capacity explosively is influenced by contraction type, with concentric contractions
19 being more conducive to explosive performance due to a more effective neural
20 strategy.

21

22 Keywords: Rate of torque development, neural activation, concentric
23 contractions, eccentric contractions, isometric contractions

24

25 **Introduction**

26 The capacity of the human neuromuscular system for explosive force/torque
27 production, typically measured as rate of torque development (RTD), is considered
28 functionally more important than maximal voluntary torque (MVT) during explosive
29 movements such as sprinting, jumping, or restabilising the body following a loss of
30 balance (1-3). An understanding of the neural and mechanical factors that limit
31 explosive torque production will therefore have important implications for both health
32 and sports performance. The influence of contraction type (i.e. isometric, concentric
33 or eccentric) on MVT *in-vivo* has been documented extensively via the MVT-velocity
34 relationship (4-9); however, little is known about the capability for explosive torque
35 production during different types of contractions.

36

37 The majority of past studies have investigated RTD during isometric contractions (1-
38 3,10), and occasionally during the acceleration phase of isoinertial dynamic
39 contractions (11,12). However, the latter provides an experimentally inconsistent
40 situation, as the movement dynamics (acceleration, velocity and displacement) are not
41 controlled and combine with the inertial properties of the system in a non-linear
42 manner, giving rise to torques that vary within and between trials and participants,
43 and confound RTD measurements. In contrast, performing explosive concentric and
44 eccentric contractions at a constant acceleration from stationary may provide a more
45 controlled situation in which to investigate RTD during the acceleration phase of
46 dynamic contractions.

47

48 A further complication with measuring dynamic RTD is that joint angle will change
49 throughout the effort, and this change is in opposite directions for concentric and

50 eccentric contractions. Consequently, it is not possible to match joint angle
51 throughout the different types of contractions, apart from at a single time point/angle.
52 The discrete influence of joint angle on explosive torque production can be evaluated
53 by comparing isometric contractions at different angles; however, isolating the
54 influence of the type of contraction is problematic. One approach is to normalise the
55 explosive torque produced at any time point during the different types of contractions
56 to the MVT available at that specific joint angle and angular velocity. This also
57 enables us to investigate whether explosive torque production changes in proportion
58 to MVT. Another approach is to normalise explosive voluntary torque to the
59 maximum capacity for explosive torque production elicited during an evoked octet
60 contraction (8 supramaximal pulses at 300 Hz; (2,13)) in identical contractile
61 conditions. This provides an experimental approach that can dissociate between the
62 neural and peripheral limitations of explosive torque production during different types
63 of contraction.

64

65 Whilst normalising explosive torque (via the above methods) will control for
66 differences in joint kinematics between the different types of contraction, the
67 behaviour of the series elastic component (SEC) may decouple the association
68 between joint kinematics and muscle fibre behaviour (Roberts and Azizi, 2011).
69 Muscle modelling can be used to assess whether any measured effects of contraction
70 type on explosive torque production are representative of muscle fibre performance,
71 or due to the influence of the SEC.

72

73 There is limited evidence of the effect of joint angle on human RTD. During the
74 initial 40 ms of explosive isometric contractions in humans torque production has

75 been reported to change with joint angle, but only in proportion to MVT (2). In
76 contrast, animal studies have found a faster time to peak force with decreasing muscle
77 length (15-17), although this appears to primarily affect the later phases of explosive
78 contractions (15,16). Clearly, further work is required to understand the influence of
79 joint angle on explosive torque production.

80

81 The primary aim of this study was to compare explosive torque production during
82 concentric, eccentric and isometric contractions, and examine the neural and
83 peripheral limitations to explosive torque production in these different contractile
84 conditions. Two isometric angles were also studied to examine the discrete influence
85 of joint angle on explosive torque production.

86

87 **Methods**

88 **Participants**

89 Fourteen healthy male participants (age, 24 ± 6 yrs; height, 1.78 ± 0.05 m; and mass,
90 75 ± 5 kg), ranging from elite explosive power athletes to low/moderately active
91 individuals, gave informed consent to participate in the study, which was approved by
92 the Loughborough University ethical advisory committee.

93

94 **Overview**

95 Participants visited the laboratory on 3 occasions separated by 3-5 days to complete a
96 series of voluntary and evoked contractions of the knee extensors on an isovelocity
97 dynamometer. Session 1 involved: a series of isometric maximal voluntary
98 contractions (MVCs) at different knee joint angles; electrically evoked concentric,

99 eccentric and isometric octet contractions; and familiarisation with explosive
100 voluntary concentric, eccentric and isometric contractions. In session 2 surface EMG
101 was collected from the three superficial quadriceps muscles whilst participants
102 completed explosive voluntary concentric, eccentric and isometric contractions, and
103 during electrically evoked supramaximal twitch contractions to elicit compound
104 muscle action potentials (M-waves). In session 3 participants completed a series of
105 concentric and eccentric isovelocity MVCs.

106

107 The isometric and isovelocity MVCs were used to determine joint angle and angular
108 velocity specific MVT, for normalisation of explosive voluntary torque measured
109 under concentric, eccentric and isometric conditions. Likewise, concentric, eccentric
110 and isometric explosive voluntary torque were also normalised to electrically evoked
111 octet torque in the same contractile conditions. Finally, the M-waves recorded in
112 session 2 were used for normalisation of surface EMG data collected during the
113 concentric, eccentric and isometric explosive contractions of the same session.

114

115 **Measurements**

116 *Dynamometer and Surface EMG*

117 Shoulder and waist straps secured participants firmly in the seat of the dynamometer
118 (Con-Trex; CMV AG, Switzerland) with the hip angle fixed at 95°. Single differential
119 surface EMG electrodes (Delsys Bagnoli-4, Boston, USA) were placed: over the belly
120 of the rectus femoris (RF), vastus lateralis (VL), and vastus medialis (VM); parallel to
121 the presumed orientation of the muscle fibres; and at ~50% (RF), 55% (VL), and 80%
122 (VM) of the distance between the greater trochanter and lateral femoral condyle.
123 Analogue torque and crank angle (representing knee angle) signals from the

124 dynamometer, and amplified EMG signals (x100, differential amplifier 20-450 Hz),
125 were sampled at 2000 Hz with an analogue to digital converter and PC utilising Spike
126 2 software (CED micro 1401, CED, Cambridge, UK). Using a 4th order zero-lag
127 Butterworth digital filter, torque and angle signals were low pass filtered at 21 and 12
128 Hz, respectively, and EMG signals were band-pass filtered (6-500 Hz). Knee angular
129 velocity was derived from the knee angle signal by numerical differentiation with a 1
130 ms epoch. Biofeedback was provided via a computer monitor.

131

132 *Concentric, Eccentric and Isometric Explosive Voluntary Contractions*

133 Explosive voluntary contractions were performed in four conditions; concentric
134 (CON), eccentric (ECC), and isometrically at 101° (ISO101) and 155° (ISO155) knee
135 joint angles (Fig. 1). During the concentric and eccentric conditions the crank arm
136 was slowly moved ($\sim 10^\circ \cdot s^{-1}$) through the range of motion (94-161°) to the start
137 position for CON (94°) or ECC (161°). On reaching the start position the crank arm
138 accelerated from stationary, at a constant $2000^\circ \cdot s^{-2}$, to a peak velocity of $450^\circ \cdot s^{-1}$,
139 moving 52° (94-146° in CON and 161-109° in ECC) in 225 ms, before rapidly
140 decelerating ($-6000^\circ \cdot s^{-2}$) to stop 15° later (Fig. 1 and 2). In the CON and ECC
141 conditions participants performed ~ 15 explosive voluntary contractions (separated by
142 ~ 30 s), when they were instructed to push as ‘fast and hard’ as possible at the start of
143 the acceleration phase, from a completely relaxed state, and to keep pushing for the
144 entire range of motion. The crank angle signal was displayed on the computer monitor
145 with a cursor placed at the start position to indicate when the participant should start
146 pushing. During extensive pilot testing we found that participants typically started
147 generating torque 50-70 ms into the acceleration phase due to a delayed response to
148 the biofeedback. During three passive trials (no muscle activation) of the CON and

149 ECC conditions, torque due to the acceleration and weight of the shank was recorded.
150 In offline analysis (using Matlab; The MathWorks inc., Natick, MA, USA), the
151 average torque-time curve of the three passive trials in each condition were time
152 aligned with, and subtracted from, each active trial in the same condition, to calculate
153 the torque due to muscle activation (Fig. 2).

154

155 [INSERT FIG. 1 AND 2 HERE]

156

157 In both ISO101 and ISO155 participants completed ≥ 6 voluntary explosive
158 contractions (separated by ~ 30 s), where they were instructed to push as ‘fast and
159 hard’ as possible for 1 s, from a completely relaxed state. These specific joint angles
160 were selected as they occurred during the early phase (~ 75 ms into the acceleration
161 phase) of CON and ECC explosive contractions to consider if joint angle effects were
162 influencing the comparison of CON and ECC conditions.

163

164 Contractions performed in the CON and ECC conditions were disregarded if they did
165 not meet the following criteria: baseline torque within ± 2 Nm; a change in baseline
166 torque < 2 Nm in the 200 ms prior to torque onset; and torque onset occurred 20-75
167 ms from the start of the acceleration phase. Contractions performed in the ISO101 and
168 ISO155 conditions were disregarded if torque baseline changed by > 1 Nm in the 200
169 ms prior to torque onset. The three valid contractions in each condition with the
170 greatest proportion of MVT (see below) at 100 ms from torque onset were chosen for
171 further analysis, which involved measuring torque at 25 ms intervals up to 150 ms.
172 Torque onset was defined as the point at which the first derivative of the torque-time
173 curve crossed zero for the last time.

174

175 For comparison of explosive voluntary torques across the different types of
176 contraction absolute torques were normalised, firstly to maximal voluntary torque
177 (MVT): ISO101 and ISO155 torque values were normalised to measured isometric
178 MVT at the same knee angle (see below); CON and ECC torque values were
179 normalised to interpolated dynamic MVT at the same knee angle and angular velocity
180 (interpolated from a dynamic MVT function; see below). Secondly, voluntary
181 explosive torque at 50 ms from torque onset in each condition was normalised to
182 evoked explosive torque at 50 ms (see below) in the same condition
183 (voluntary/evoked). Furthermore, the voluntary/evoked ratio was established after
184 each had been normalised to the relevant interpolated or measured MVT value, to
185 control for any discrepancies in joint kinematics at the 50 ms time point between the
186 voluntary and evoked trials.

187

188 During the explosive voluntary contractions agonist activation was assessed by
189 measuring the root mean square (RMS) amplitude of the EMG signal of each muscle
190 in three consecutive 50 ms time windows (0-50, 50-100, and 100-150 ms) from EMG
191 onset. Agonist (RF, VL, and VM) RMS EMG values were normalised to M_{\max} (see
192 below) and averaged across the three muscles to give a mean agonist value. EMG
193 onset was detected manually as detailed previously (3). All explosive voluntary torque
194 and EMG variables were averaged across the three contractions chosen for analysis in
195 each condition.

196

197 *Electrical Stimulation*

198 Using previously published methods (Tillin et al., 2010, Tillin et al., 2011), the
199 femoral nerve was electrically stimulated (DS7AH, Digitimer Ltd., UK) with square
200 wave pulses (0.1 ms duration) whilst participants were voluntarily passive to elicit
201 explosive octet contractions (via 8 pulses at 300 Hz) and compound muscle action
202 potentials (M-waves; via a single pulse). At a knee angle of 101° a series of single
203 pulses were elicited at incremental current intensities until a maximal current intensity
204 (simultaneous plateau in torque and M-wave response of each muscle) was achieved.
205 Thereafter, supramaximal octet contractions and M-waves were elicited at 20% above
206 the maximal current intensity.

207

208 Three supramaximal octet ('evoked') contractions were elicited in both isometric
209 conditions, and at 4° (~60 ms) into the acceleration phase of CON and ECC, so that
210 evoked torque onset would occur at a similar knee angle and angular velocity to that
211 expected in the voluntary explosive contractions. Corrected, evoked torque in each
212 condition was measured at 25 ms intervals up to 75 ms (75 ms was the shortest time
213 to peak torque - CON). In ISO101 and ISO155 torque at 100 ms, peak torque, time-to-
214 peak torque and half relaxation time were also recorded. For these isometric
215 conditions, evoked torque at each time point was normalised to evoked peak torque.
216 Measurements were averaged across the three evoked contractions in each condition.

217

218 The peak-to-peak amplitude of supramaximal M-waves (M_{\max}) is affected by joint
219 angle (18). Therefore, three M_{\max} were elicited at both 101 and 155° knee angles, and
220 the average M_{\max} at each angle was used to normalise volitional agonist EMG in these
221 conditions. Three M_{\max} were also elicited at 3°, 11°, and 25° into the acceleration

222 phase of CON and ECC conditions. Extensive pilot work had shown that these
223 positions were typically in the centre of the consecutive 50 ms time windows after
224 volitional EMG onset, and thus average M_{\max} at each position was used to normalise
225 volitional agonist EMG during the 0-50, 50-100, 100-150 ms time windows,
226 respectively.

227

228 *Isometric Maximal Voluntary Contractions*

229 Participants completed 3 isometric MVCs (separated by ≥ 90 seconds) at each of 4
230 different knee angles; 101, 119, 136, and 155° (12 MVCs overall). The instruction in
231 each MVC was to push as hard as possible for 3-5 s. The largest measured extensor
232 torque at each knee angle was defined as MVT at that angle. These measurements
233 were used to establish a torque – angle relationship (defined by a quadratic function)
234 that set the estimates and bounds of the dynamic MVT function (see below).

235

236 *Dynamic Maximal Voluntary Torque Function*

237 To establish dynamic MVT as a function of joint angle and angular velocity,
238 participants completed a cycle of four reciprocal eccentric-concentric isovelocit
239 MVCs at three angular velocities; 100, 250, and 400°.s⁻¹. This protocol is thought to
240 ensure maximal voluntary activation, and thus MVT, throughout the entire range of
241 motion (6,9,19,20), which was set at ~100° (70-170°), providing an isovelocit
242 of ~75, 62, and 40° at 100, 250 and 400°.s⁻¹, respectively. Following familiarisation at
243 each velocity, participants were instructed to extend their knee as hard as possible
244 throughout the entire cycle. If peak eccentric torque of at least two eccentric efforts in
245 one cycle were not $\geq 90\%$ of the largest recorded isometric MVT for that participant,
246 the cycle was repeated. Active torque values were corrected for the effects of gravity

247 using a 6th order polynomial to describe the passive torque-angle relationship. For
248 each velocity the largest gravity corrected torque per degree of isovelocity movement
249 was input into a nine parameter mathematical model (Forrester et al., 2011) to
250 establish a dynamic MVT function, defined as the product of torque - angular velocity
251 (9), differential activation - angular velocity (9) and torque - angle (24) functions. The
252 nine parameters were obtained by minimising the weighted RMS difference between
253 interpolated and measured values using a simulated annealing algorithm (21). A
254 weighting for the RMS difference score function forced ~85% of the measured values
255 below the surface representing the dynamic MVT function (Fig. 3) was used, as errors
256 in the measured data were thought to be predominantly one-sided (i.e., due to
257 submaximal effort; (22)). The average weighted RMS difference of all participants
258 was 6 ± 2 Nm ($1.3 \pm 0.3\%$ of maximum eccentric torque).

259

260 [INSERT FIG. 3 HERE]

261

262 *Generic Muscle Model*

263 To assess whether any observed effects of contraction type on explosive torque
264 production during the dynamic conditions were indicative of muscle fibre
265 performance the torque and kinematic data from CON, ECC, and the dynamic MVCs,
266 was collapsed across all participants and input into a generic Hill-type muscle model
267 (Pain and Forrester, 2009). This model consisted of a SEC and contractile component,
268 and calculated fibre force, length and velocity of the RF, VL, and VM during CON,
269 ECC, and the dynamic MVCs. Force in each muscle and at each 25 ms interval from
270 force onset was normalised to maximal voluntary force at the same muscle length and
271 velocity, and averaged across the three muscles.

272

273 **Statistical Analysis**

274 The influence of condition (CON, ECC, ISO101, and ISO155) on all dependent
275 variables measured in explosive voluntary and evoked contractions was analysed with
276 a repeated measures ANOVA (4 conditions). Paired t-tests and a stepwise Bonferroni
277 correction were then used to determine paired differences between conditions at
278 specific time points. Statistical analysis was completed using SPSS version 17, and
279 the significance level was set at $P < 0.05$.

280

281 **Results**

282 **Kinematics of the Explosive Contractions**

283 During the dynamic explosive contractions, voluntary torque onset in the CON and
284 ECC conditions occurred at similar angular displacements and angular velocities
285 (Table 1). In both CON and ECC explosive voluntary torque onset typically occurred
286 5-10 ms earlier in the acceleration phase than evoked torque onset, as denoted by the
287 overall tendency for angular displacement and velocity to be greater at torque onset in
288 the evoked contractions (Table 1). Voluntary EMG onset occurred at an angle of $96 \pm$
289 1° and an angular velocity of $74 \pm 21^\circ \cdot s^{-1}$ during the CON trials and at $159 \pm 1^\circ$ and -
290 $60 \pm 39^\circ \cdot s^{-1}$ during the ECC trials. Relative to these onsets M_{max} was recorded at $22 \pm$
291 11 , 65 ± 11 , and 121 ± 10 ms into the CON trials, and 16 ± 25 , 65 ± 18 , and 128 ± 22
292 ms into the ECC trials. This confirmed that M_{max} was typically recorded in the centre
293 of each of the three consecutive 50 ms time windows from voluntary EMG onset in
294 both CON and ECC conditions.

295

296

[INSERT TABLE 1 HERE]

297

298 **Volitional Parameters**

299 Absolute explosive voluntary torque was affected by condition at each of the six
300 measured time points from torque onset (ANOVA, $P < 0.001$; Fig. 4A). These effects
301 are consistent with the different joint kinematics of the separate conditions. ISO101
302 was performed at a joint angle close to θ_{opt} , and thus recorded the highest torque
303 values after the initial 50 ms. CON torque was greater than ISO101, ISO155 and ECC
304 in the initial 50 ms when angular velocity was relatively low, and joint angle was near
305 θ_{opt} . ECC torque was greater than ISO155 and CON in the later phase of the
306 contraction (>100 ms), as angular velocity increased and the joint angle moved closer
307 to θ_{opt} .

308

309 Normalised explosive voluntary torque (relative to measured/interpolated MVT at the
310 relevant joint angle and angular velocity) was also influenced by condition at each
311 measured time point from torque onset (ANOVA, $P < 0.001$; Fig. 4B; Table 2).
312 Normalised CON torque was $>60\%$ larger than all other conditions at all measured
313 time points after 25 ms. Remarkably, after 125 ms explosive voluntary CON torque
314 equalled MVT, and had exceeded MVT by 150 ms, being 119% MVT. The
315 considerably greater normalised torque in CON appears to be indicative of muscle
316 fibre performance, as the generic muscle model results emulate the joint torque results
317 (Fig. 5). In fact the difference between the CON and ECC conditions appears to be to
318 be just as large, if not larger, than those measured on a whole joint level. Normalised
319 torque was similar in the ISO101, ISO155, and ECC conditions during the initial 75

320 ms of these explosive contractions, but during the later stages of contraction ISO155
321 was greater than ECC (75-150 ms), and ISO101 (125-150 ms).

322

323 [INSERT FIG. 4, FIG. 5, AND TABLE 2 HERE]

324

325 Absolute voluntary/evoked torque at 50 ms after torque onset was dependent upon the
326 contractile condition (ANOVA, both $P < 0.001$). Paired comparisons revealed that
327 voluntary/evoked torque in CON ($77 \pm 17\%$) was substantially greater than all other
328 conditions ($P < 0.001$; Fig. 6); ISO101 ($46 \pm 14\%$) tended to be greater than ISO155
329 ($36 \pm 13\%$; $P = 0.054$), and both isometric conditions were greater than ECC ($23 \pm$
330 9% ; $P \leq 0.002$). These results were identical when voluntary and evoked torques were
331 both first normalised to MVT prior to calculating the voluntary/evoked percentage.

332

333 [INSERT FIG. 6 HERE]

334

335 There was also a condition effect on the agonist normalised EMG during each 50-ms
336 time window (0-50, 50-100, 100-150 ms) and over the whole 0-150 ms (ANOVA,
337 $P < 0.001$). Over the whole 0-150 ms agonist normalised EMG was 10.1 ± 1.7 (CON),
338 9.0 ± 1.3 (ISO101), 7.3 ± 1.3 (ISO155), and 4.7 ± 1.5 (ECC) % M_{\max} , and all
339 conditions were significantly different from each other (Paired t-tests, $P < 0.032$).
340 Paired comparisons for the first 50 ms time window were similar to those for
341 voluntary/evoked torque at 50 ms, where agonist normalised EMG differed between
342 all of the conditions and was greatest in the CON followed by ISO101, ISO155, and
343 ECC ($P < 0.05$; Fig. 7). Paired differences between conditions during the 50-100 and

344 100-150 ms time windows were less pronounced, but agonist normalised EMG
345 remained greatest in CON and ISO101, and lowest in ECC.

346

347 [INSERT FIG. 7 HERE]

348

349 **Evoked Parameters**

350 As expected given the different joint kinematics in each condition, absolute evoked
351 torque at 25, 50 and 75 ms after torque onset was affected by condition (ANOVA,
352 $P < 0.001$; Fig. 8), with evoked ECC and ISO101 torque greater than ISO155 and CON
353 at all measured time points. Evoked torque in ISO101 and ISO155 normalised to
354 evoked peak torque in the same condition was similar over the first 50 ms, but greater
355 in ISO155 at 75 (+5%; Paired t-test, $P = 0.004$) and 100 ms (+14%; Paired t-test,
356 $P < 0.001$) after torque onset (Fig. 9). Despite greater peak torque in ISO101, time-to-
357 peak torque and half relaxation time were shorter in ISO155 (Table 3).

358

359 [INSERT FIG. 7, FIG. 8, AND TABLE 3 HERE]

360

361 **Discussion**

362 The results of the current study provide novel evidence that the ability of humans to
363 utilise the available torque capacity of a muscle in an explosive situation is influenced
364 by the type of contraction. Whether expressed relative to the available MVT or the
365 maximum capacity for RTD during evoked contractions explosive voluntary
366 performance was clearly superior during concentric than isometric or eccentric
367 actions. The proportion of MVT expressed during explosive concentric efforts was

368 >60% larger than for isometric or eccentric conditions after the first 25 ms of the
369 contraction. Furthermore, participants achieved concentrically 77% of their evoked
370 torque after 50 ms, compared to 36-46% isometrically and 23% eccentrically. This
371 greater concentric ability to utilise the available contractile capacity of the muscle
372 indicates enhanced agonist activation and this was supported by the higher EMG
373 amplitude throughout the explosive contraction.

374

375 *Effects of Contraction Type*

376 The absolute voluntary and evoked torque-time curves appear to conform to the
377 torque – angle – angular velocity relationship. Overall absolute torque development
378 was highest for ECC during the evoked contractions, but highest for ISO101 during
379 the volitional contractions. This discrepancy is likely to reflect the differences
380 typically observed between the torque/force – velocity relationships measured *in-vitro*
381 and voluntarily *in-vivo* (i.e. eccentric to isometric torque/force for the same muscle
382 length is normally >1.5 *in-vitro* and 0.9-1.1 *in-vivo* (4,6,8)). Clearly the absolute
383 voluntary and evoked torque-time curves are primarily determined by the joint
384 kinematics of each condition, and should therefore be normalised to a reference
385 torque specific to that mechanical situation, in order to make a meaningful
386 comparison between the different types of contraction.

387

388 Explosive voluntary torque normalised to joint angle and angular velocity specific
389 MVT was consistently >60% larger in CON than during the isometric or eccentric
390 conditions, after the initial 25 ms. In fact, MVT was achieved after only 125 ms in
391 CON, whilst torque in the other conditions did not exceed 73% of MVT even after
392 150 ms. Previous studies have reported that it takes >300 ms to achieve MVT in

393 explosive isometric contractions performed from rest (1,14), and it is likely that this
394 would have been the case in both the isometric and ECC conditions of the current
395 study, had it been possible to measure torque beyond 150 ms. However, our results
396 provide unique evidence that during explosive concentric contractions MVT can be
397 achieved in <125 ms.

398

399 Whilst the whole joint approach of this study makes its results directly relevant to
400 functional human movement, caution should be taken when inferring muscle fibre
401 performance from whole joint mechanics, due to compliance of the SEC. The greater
402 concentric ability to utilise the available torque generating capacity that we observed
403 appears to be indicative of muscle fibre performance for two main reasons: (i) the
404 generic muscle model which accounted for SEC compliance produced very similar
405 results; and (ii) the percentage of evoked torque achieved voluntarily after 50 ms was
406 also considerably greater in CON than any other condition (CON, 77%; ISO101,
407 46%; ISO155 36%; ECC, 23%). As these values are relative to the maximal
408 involuntary explosive torque capacity in the same contractile conditions they are
409 indicative of substantial differences in neural drive to the agonist muscle. The greater
410 agonist normalised EMG over the first 50 ms, as well as over the whole 150 ms from
411 EMG onset, for CON supports this notion. The mechanistic explanation for this effect
412 requires further investigation, but may be associated with neural inhibition during the
413 isometric and ECC conditions that prevents full utilisation of the high, and potentially
414 harmful, rates of loading available in these contractions. Moreover, the condition
415 effects on agonist activation we have observed occurred within the first 50 ms of
416 crank arm acceleration, which is considered to be the minimum latency period for a
417 reflex response to mechanical perturbation (25). Therefore, our results support earlier

418 evidence that the neural strategy employed at the start of the muscle contraction is
419 pre-defined by the central nervous system according to the type of contraction (26).

420

421 The more effective neural strategy in CON appears to explain why this condition was
422 considerably more conducive to explosive performance than any other condition.
423 MVT was also exceeded by up to 19% in the voluntary CON condition, suggesting
424 that the greatest peak torque response in maximum voluntary concentric contractions
425 is achieved when the focus is on producing explosive, rather than sustained maximal
426 torque. This was an unexpected finding that was not replicated in any of the other
427 conditions, and appears to be a consequence of the more effective neural strategy
428 observed in the CON condition.

429

430 Whilst this is the first study to compare agonist activation during different types of
431 explosive contractions, previous studies have assessed agonist activation at MVT and
432 reported greater activation in concentric than eccentric contractions (5-7,27,28), and
433 in isometric than dynamic conditions (22,28). Any differences in agonist activation at
434 MVT between contraction types in this study could clearly have influenced the
435 comparison of explosive voluntary torques when normalised to MVT. This may
436 explain the marginal differences in normalised explosive torque between ECC and the
437 isometric conditions (particularly ISO101), despite distinct levels of agonist activation
438 indicated by both voluntary/evoked torque and EMG.

439

440 *Effects of Joint Angle*

441 Absolute explosive voluntary and evoked torque-time curves for ISO101 and ISO155
442 conformed to the MVT-angle relationship, where torque at all measured time points

443 from torque onset was greater in ISO101 (nearer θ_{opt}). However, when normalised to
444 MVT at the same knee angle, voluntary torque was similar in ISO101 and ISO155
445 during the initial phase of the contraction (first 100 ms), but greater in ISO155 beyond
446 100 ms. Normalised explosive voluntary torque was also greater during the later
447 stages of ISO155 (75 ms and onwards) compared to ECC. This is further evidence of
448 an effect of knee angle during the later phase of the rising torque-time curve, given
449 that ECC was accelerating into a more flexed knee position. These results suggest that
450 differences in joint angle did not confound comparisons between the type of
451 contraction in the first 100 ms, but may have contributed to greater normalised torque
452 in the later phase of CON compared to ECC, when the knee was accelerating into
453 more extended (CON) or flexed (ECC) positions.

454

455 The improved capacity for normalised voluntary torque production in ISO155 does
456 not appear to be due to agonist activation, as agonist normalised EMG in the 100-150
457 ms time window, as well as over the whole 150 ms from EMG onset, was 21-23%
458 greater in ISO101. Earlier studies have also reported reduced agonist activation during
459 voluntary contractions at more extended knee angles (5,20,29,30), and this effect is
460 thought to be a neural mechanism that protects the knee joint near full extension,
461 where loading of the anterior cruciate ligament is greatest (31).

462

463 In a similar pattern to that observed in the normalised voluntary torque-time curves,
464 normalised evoked torque (relative to peak evoked torque) was comparable for the
465 two isometric conditions in the early phase of the contraction, but greater in ISO155
466 in the later phase (after 50 ms). This was associated with a shorter time to peak torque
467 in ISO155, suggesting a mechanical explanation for improved normalised explosive

468 torque in the extended position. Our results are consistent with earlier *in-vitro* studies
469 that found shorter muscle lengths to have a faster time to peak tension (15-17), and a
470 steeper normalised tension-time curve during the later phase of the contraction
471 (15,16). However, this is the first study to measure a similar effect *in-vivo* during both
472 explosive voluntary and evoked contractions. The faster time to peak force at shorter
473 muscle lengths has been attributed to: lower Ca^{2+} release or a reduced affinity of
474 troponin C for Ca^{2+} (15) resulting in less efficient excitation-contraction coupling
475 (17); and/or overlapping of the actin filaments, which would interfere with cross-
476 bridge formation (32). Nevertheless, it is unclear why a faster time to peak torque at
477 shorter muscle lengths would only affect the normalised torque-time curve during the
478 later stages of the contraction.

479

480 In conclusion, the type of contraction influences the ability to utilise the muscles
481 torque producing capacity explosively, with concentric contractions being
482 considerably more conducive to explosive performance than any other type of
483 contraction, due to more effective neural activation. Finally, a faster time to peak
484 torque at more extended knee angles appears to increase the slope of the normalised
485 voluntary and evoked torque-time curves at high, but not low torque levels.
486 Collectively, the novel results of this study further our understanding of the neural and
487 mechanical limitations of explosive torque production, and provide a platform for
488 further research in this area that has important implications for health and sports
489 performance.

490

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496

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- 589
- 590

591 **Tables**

592

593 Table 1. Knee joint angular displacement and angular velocity (kinematic parameters)

594 at torque onset in explosive voluntary and evoked knee extensions completed in

595 concentric (CON) and eccentric (ECC) conditions. P-values for paired differences

596 between voluntary and evoked contractions are reported. Data are means \pm SD (n =

597 14).

Kinematic Parameter	Voluntary	Evoked	P-value
CON Angle ($^{\circ}$)	3.6 \pm 1.2	4.4 \pm 0.8	0.055
CON Velocity ($^{\circ}\cdot s^{-1}$)	117 \pm 24	129 \pm 16	0.037
ECC Angle ($^{\circ}$)	3.1 \pm 1.6	4.8 \pm 1.6	0.708
ECC Velocity ($^{\circ}\cdot s^{-1}$)	-93 \pm 38	-123 \pm 31	0.086

598

599

600 Table 2. Normalised torque at 25 ms intervals from torque onset during explosive
 601 voluntary knee extensions in four conditions: isometric at knee joint angles of 101°
 602 and 155° knee angle (ISO101 and ISO155, respectively); concentric (CON); and
 603 eccentric (ECC). Data are means \pm SD (n = 14). Paired differences are denoted by
 604 capital (P<0.01) or lower case (P<0.05) letters; A (> ISO101 and ISO155), B (> all
 605 other conditions) C (> ECC), or D (> ISO101 and ECC).

Time (ms)	Torque (% MVT)			
	ISO101	ISO155	CON	ECC
25	2 \pm 1	2 \pm 1	3 \pm 1 ^A	4 \pm 2 ^A
50	12 \pm 5	11 \pm 4	23 \pm 6 ^B	11 \pm 4
75	31 \pm 9 ^C	29 \pm 9 ^C	54 \pm 8 ^B	24 \pm 7
100	46 \pm 11	50 \pm 12 ^C	79 \pm 10 ^B	40 \pm 10
125	58 \pm 12	65 \pm 12 ^D	101 \pm 13 ^B	55 \pm 10
150	67 \pm 11	74 \pm 10 ^d	119 \pm 20 ^B	64 \pm 9

606 MVT, maximal voluntary torque as a function of knee
 607 angle and angular velocity
 608

609 Table 3. Torque parameters recorded during the supramaximal evoked isometric knee
610 extensions completed at a knee angle of 101° (ISO101) and 155° (ISO155). Data are
611 means \pm SD (n = 14). The P-value denotes differences between the two conditions

	ISO101	ISO155	P-value
Peak torque (Nm)	148 \pm 25	98 \pm 19	<0.001
Time-to-peak torque (ms)	137 \pm 9	112 \pm 13	<0.001
Half relaxation time (ms)	208 \pm 21	174 \pm 12	<0.001

612

613

614 **Figure Legends**

615 **Fig. 1.** A schematic of the hip and knee angles during explosive knee extensions
616 performed on an isovelocity dynamometer, in four separate conditions; concentric
617 (CON) and eccentric (ECC) and two isometric positions (101° (ISO101) and 155°
618 (ISO155)). During the dynamic conditions the crank arm accelerated at $2000^{\circ} \cdot s^{-1}$ from
619 a knee angle of 94° to 146° (CON) and from 161° (ECC) to 109° (ECC), before
620 decelerating over a further 15° of motion.

621

622 **Fig. 2.** Kinetic and kinematic data recorded during passive and explosive voluntary
623 concentric contractions of the knee extensors, completed on an isovelocity
624 dynamometer. The crank arm was accelerated at a constant $2000^{\circ} \cdot s^{-2}$ to a peak
625 velocity of $450^{\circ} \cdot s^{-1}$ (A), moving 52° in 225ms (B). During the explosive voluntary
626 contractions participants were instructed to push fast and hard at the start of the
627 acceleration phase, but volitional torque onset typically occurred 50-70 ms later due
628 to a delayed response to the biofeedback. The passive torque-time profile (C) was
629 subtracted from the torque-time profile of the explosive voluntary contractions (D) to
630 calculate the torque due to muscle activation (E). A similar protocol was used for
631 explosive eccentric contractions.

632

633 **Fig. 3.** An example of maximal voluntary torque (MVT) values measured during
634 isovelocity contractions of the knee extensors at six velocities (black circles). The
635 surface of the optimised nine parameter function describing dynamic MVT relative to
636 knee angle and angular velocity was used to interpolate angle and velocity specific
637 MVT values for normalisation of explosive torque values. The RMS difference

638 between measured and interpolated values was weighted so that ~85% of the
639 measured values were forced below the surface.

640

641 **Fig. 4.** Absolute (A) and normalised (B) torque for 150 ms after torque onset during
642 explosive voluntary knee extensions in four conditions: isometric at knee joint angles
643 of 101° and 155° (ISO101 and ISO155, respectively); concentric (CON); and
644 eccentric (ECC). CON and ECC conditions were completed at a constant $2000^{\circ}.s^{-2}$,
645 and torque was corrected for the acceleration and weight of the shank. Normalised
646 torque is expressed as a percentage of maximal voluntary torque (MVT) at the
647 relevant joint angle and angular velocity. Data are means \pm SD on highest and lowest
648 data points (n = 14).

649

650 **Fig. 5.** Average normalised muscle fibre force of the rectus femoris, vastus lateralis,
651 and vastus medialis (F) and normalised knee joint torque (T) during concentric (CON)
652 and eccentric (ECC) explosive voluntary contractions of the knee extensors.
653 Normalised F is a percentage of maximal voluntary fibre force (MVF) at the same
654 fibre length and contractile velocity, whilst normalised T is a percentage of maximal
655 voluntary torque (MVT) at the same joint angle and angular velocity. Data are
656 collapsed across all participants (n = 14).

657

658 **Fig. 6.** Absolute voluntary torque at 50 ms after torque onset as a percentage of
659 absolute evoked torque at the same time point (voluntary/evoked), during explosive
660 knee extensions in four conditions: isometric at knee joint angles of 101° and 155°
661 (ISO101 and ISO155, respectively); concentric (CON); and eccentric (ECC). Data are

662 means \pm SD (n = 14). Paired differences are denoted by capital letters (P<0.01); *B* (>
663 all other conditions), *C* (> ECC).

664

665 **Fig. 7.** Agonist EMG over 0-50 (dark grey bars), 50-100 (light grey bars), and 100-
666 150 ms (white bars) from EMG onset during explosive voluntary knee extensions in
667 four conditions: isometric at a 101 and 155° knee angle (ISO101 and ISO155,
668 respectively); concentric (CON); and eccentric (ECC). Agonist EMG is an average of
669 the three superficial quadriceps muscles once normalised to maximal M-wave (M_{max}).
670 Data are means \pm SD (n = 14). Paired differences for each EMG time window are
671 denoted by capital (P<0.01) or lower case (P<0.05) letters; *B* (> all other conditions),
672 *C* (> ECC), *E* (> ISO155 and ECC).

673

674 **Fig. 8.** Absolute torque recorded during evoked explosive voluntary knee extensions
675 (supramaximal octet, 8 pulses at 300 Hz) in four conditions; isometric at knee joint
676 angles of 101° and 155° (ISO101 and ISO155, respectively), concentric (CON), and
677 eccentric (ECC). CON and ECC conditions were completed at a constant $2000^{\circ}.s^{-2}$,
678 and torque was corrected for the acceleration and weight of the shank. Data are means
679 \pm SD on highest and lowest data points (n = 14).

680

681 **Fig. 9.** Normalised torque during evoked isometric knee extensions (supramaximal
682 octet, 8 pulses at 300 Hz) at a 101° (ISO101) and 155° (ISO155) knee angle,
683 expressed as a percentage of peak torque (PT) during the same contraction. Data are
684 means \pm SD (n = 14). Paired differences are denoted by * (P<0.05) or *** (P<0.001).

685