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1 **Prolonged depression of knee extensor torque complexity following eccentric exercise**

2

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18 **Author contributions:** JP, KW, SW and MB were each involved in the conception and design  
19 of the study and contributed to the writing and critical revisions of the manuscript. JP and KW  
20 collected the data; SW wrote the MATLAB code to process the data. All authors were involved  
21 in the analysis and interpretation of the data.

22

23 **Running head:** Complexity and eccentric exercise

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25 **Word count:** 8739

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35 **Abstract**

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37 Neuromuscular fatigue reduces the temporal structure, or complexity, of muscle torque output.  
38 Exercise-induced muscle damage reduces muscle torque output for considerably longer than  
39 high-intensity fatiguing contractions. We hypothesised that muscle damaging eccentric  
40 exercise would lead to a persistent decrease in torque complexity, whereas fatiguing exercise  
41 would not. Ten healthy participants performed five isometric contractions (6 s contraction, 4 s  
42 rest) at 50% maximal voluntary contraction (MVC) before, immediately after, 10, 30 and 60  
43 minutes, and 24 hours after eccentric (muscle damaging) and isometric (fatiguing) exercise.  
44 These contractions were also repeated 48 hours and one week after eccentric exercise. Torque  
45 and surface EMG signals were sampled throughout each test. Complexity and fractal scaling  
46 were quantified using approximate entropy (ApEn) and the detrended fluctuation analysis  $\alpha$   
47 exponent (DFA  $\alpha$ ). Global, central and peripheral perturbations were quantified using MVCs  
48 with femoral nerve stimulation. Complexity decreased following both eccentric (ApEn, mean  
49 (SD), from 0.39 (0.10) to 0.20 (0.12),  $P < 0.001$ ) and isometric exercise (from 0.41 (0.13) to  
50 0.09 (0.04);  $P < 0.001$ ). After eccentric exercise ApEn and DFA  $\alpha$  required 24 hours to recover  
51 to baseline levels, but only 10 minutes following isometric exercise. MVC torque remained  
52 reduced (from 233.6 (74.2) to 187.5 (64.7) N.m) 48 hours after eccentric exercise, with such  
53 changes only evident up to 60 minutes following isometric exercise (MVC torque, from 246.1  
54 (77.2) to 217.9 (71.8) N.m). The prolonged depression in maximal muscle torque output is  
55 therefore accompanied by a prolonged reduction in torque complexity.

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57 **Abbreviations:** ApEn, approximate entropy; DFA detrended fluctuation analysis; MVC  
58 maximal voluntary contraction.

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69 **New findings**

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71 **What is the central question?**

72 Does eccentric exercise leading to prolonged knee extensor torque depression also result in a  
73 prolonged loss of knee extensor torque complexity?

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75 **What is the main finding of importance?**

76 The recovery of the loss of torque complexity following eccentric exercise took 24 hours,  
77 whereas after acute muscle fatigue it took 10 minutes, thus the depression of torque complexity  
78 following eccentric exercise was prolonged.

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80 **Keywords:** eccentric; fatigue; non-linear dynamics; complexity; fractal scaling.

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103 **Introduction**

104

105 Human movement is characterized by inherent variability and fluctuations (Hamilton et al.,  
106 2004; Stergiou and Decker, 2011). Such fluctuations have typically been quantified according  
107 to their magnitude, using measures such as the standard deviation (SD) and coefficient of  
108 variation (CV; Jones et al., 2002; Taylor et al., 2003). However, these fluctuations also possess  
109 an irregular temporal structure, or complexity (Lipsitz and Goldberger, 1992), which refers to  
110 the relationship between successive data points and the predictability of a time-series (Pincus,  
111 1991; Slifkin and Newell, 2000). Complex outputs are thought to be a hallmark of healthy  
112 physiological systems (Peng et al., 2009), and can be observed in, inter alia, normal heart rate,  
113 gait and muscle torque output (Hausdorff et al., 1995; Goldberger, 1996; Slifkin and, Newell,  
114 1999). A loss of physiological complexity appears to be a ubiquitous response to ageing and/or  
115 pathology (Lipsitz and Goldberger, 1992).

116

117 In the context of muscle torque output, it is thought that complexity reflects the adaptability of  
118 the neuromuscular system (i.e., the ability to modulate motor output rapidly and accurately in  
119 response to perturbations; Vaillancourt and Newell, 2003). Any loss of muscle torque  
120 complexity therefore has the potential to negatively affect co-ordination, impact motor task  
121 performance and exercise tolerance (Cortes et al., 2014; Pethick et al., 2016). We have recently  
122 demonstrated that neuromuscular fatigue reduces the complexity of muscle torque output  
123 during both maximal and submaximal isometric contractions (Pethick et al., 2015). We  
124 subsequently demonstrated that this fatigue-induced loss of complexity is only evident during  
125 contractions performed above the critical torque (Pethick et al., 2016) and that such losses can  
126 be slowed by the ingestion of caffeine (Pethick et al., 2018a). These studies have demonstrated  
127 that the loss of torque complexity is tightly coupled to the fatigue process, with complexity  
128 declining in tandem with the loss of force-generating capacity. However, whether this effect is  
129 specific to the development of fatigue during high-intensity contractions is not known. If the  
130 fatigue-induced loss of torque complexity is related to the loss of force-generating capacity in  
131 the neuromuscular system per se, then interventions that reduce this capacity independently of  
132 metabolite-mediated fatigue should also diminish torque output complexity.

133

134 Unaccustomed eccentric exercise, which involves the active lengthening of muscle fibres  
135 (Enoka, 1996), has been repeatedly demonstrated to lead to muscle damage, attributed to  
136 mechanical disruption of the sarcomeres, in the days after exercise (Asmussen, 1956; Fridén et

137 al., 1981; Clarkson et al., 1992; Proske and Morgan, 2001). In contrast, no such damage is  
138 typically observed following either isometric or concentric exercise (Newham et al., 1983;  
139 Lavender and Nosaka, 2006). A consequence of this eccentric exercise-induced muscle damage  
140 is a decrease in maximal force generating capacity, which lasts considerably longer than after  
141 the performance of either isometric or concentric contractions (Jones et al., 1989; Gibala et al.,  
142 1995; Smith and Newham, 2007). While maximal force typically recovers to >90% of its fresh  
143 value within 60 minutes of isometric contractions (Sahlin and Ren, 1989; Allman and Rice,  
144 2001), significant decrements in maximal force following eccentric exercise have been shown  
145 to persist for several days and, in some cases, for up to two weeks (Cleak and Eston, 1992;  
146 Sayers and Clarkson, 2001). If the loss of torque output complexity during fatigue is directly  
147 linked to the decrement in force generating capacity, then the persistent loss of maximal force  
148 following eccentric exercise should be accompanied by a persistent loss of torque complexity.

149

150 In support of the contention that eccentric exercise may lead to a prolonged decrease in the  
151 complexity of muscle torque output, it has been observed that eccentric actions result in an  
152 increase in the magnitude of torque fluctuations, as measured by the CV, during subsequent  
153 low, moderate and high intensity isometric contractions (Weerakkody et al., 2003; Lavender  
154 and Nosaka, 2006; Semmler et al., 2007; Skurvydas et al., 2010). This effect has typically been  
155 observed an hour after the cessation of exercise, though in some cases has persisted for 24  
156 hours (Leger and Milner, 2001; Dartnall et al., 2008), and has not been observed following  
157 isometric or concentric contractions (Lavender and Nosaka, 2007; Semmler et al., 2007). Thus,  
158 whilst it is known that the magnitude of torque variability can be altered following eccentric  
159 exercise, the effect on the structure of these fluctuations over several days has not yet been  
160 investigated.

161

162 The purpose of the present study was to investigate the effect of muscle damaging eccentric  
163 exercise on the complexity of knee extensor torque output. To that end, we aimed to compare  
164 the recovery kinetics of torque complexity following eccentric and isometric exercise. The  
165 experimental hypothesis tested was that muscle damaging eccentric exercise would result in a  
166 persistent loss of torque complexity, quantified by decreased approximate entropy (ApEn) and  
167 increased detrended fluctuation analysis  $\alpha$  exponent (DFA  $\alpha$ ), whereas fatiguing isometric  
168 exercise would not.

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170

171 **Materials and methods**

172

173 Participants

174 Ten healthy participants (8 male, 2 female; mean (SD): age 24.8 (6.2) years; height 1.75 (0.08)  
175 m; body mass 69.5 (10.6) kg) provided written informed consent to participate in the study,  
176 which was approved by the ethics committee of the University of Kent (Reference Number:  
177 Prop\_02\_2015\_2016), and adhered to the Declaration of Helsinki, except for registration in a  
178 database. None of the participants had been involved in any lower limb strength training for  $\geq$   
179 3 months. Participants were instructed to arrive at the laboratory in a rested state (having  
180 performed no strenuous exercise in the preceding 24 hours, and not to have consumed any food  
181 or caffeinated beverages in the three hours before arrival. Participants attended the laboratory  
182 at the same time of day ( $\pm$  2 hours) during each visit.

183

184 Experimental design

185 Participants were required to visit the laboratory on seven occasions over a four to six-week  
186 period. During their first visit, participants were familiarised with all testing equipment and  
187 procedures, and the settings for the dynamometer and femoral nerve stimulation were recorded.  
188 The second visit involved performance of fatiguing intermittent isometric knee extension  
189 contractions (“Isometric exercise”; see below); with the third visit, 24 hours later, assessing  
190 recovery. The contractions in these visits were performed with the dominant leg (the leg  
191 participants would instinctively use to kick a football). At least one week after the third visit,  
192 the fourth visit involved performance of intermittent eccentric knee extension contractions  
193 (“Eccentric exercise”; see below); with the fifth, sixth and seventh visits, 24 hours, 48 hours  
194 and one week later, assessing recovery. The contractions in these visits were performed with  
195 the non-dominant leg, in order to maximise the damaging effect of the eccentric exercise. In  
196 each visit, torque output was sampled continuously to allow the quantification of complexity,  
197 muscle activity was measured using the m. vastus lateralis electromyogram (EMG), and MVCs  
198 with supramaximal femoral nerve stimulation were used to quantify global, central and  
199 peripheral fatigue, as detailed below.

200

201 Dynamometry

202 Participants sat in the chair of a Cybex isokinetic dynamometer (HUMAC Norm; CSMi,  
203 Stoughton, MA, USA), initialised and calibrated according to the manufacturer's instructions.  
204 The leg to be used was attached to the lever arm of the dynamometer, with the seating position  
205 adjusted to ensure that the lateral epicondyle of the femur was in line with the axis of rotation  
206 of the lever arm. The lower leg was securely attached to the lever arm above the malleoli with  
207 a padded Velcro strap, while straps secured firmly across both shoulders and the waist  
208 prevented any extraneous movement and the use of the hip extensors during the contractions.  
209 The seating position was recorded during familiarisation and replicated during each subsequent  
210 visit.

211

#### 212 Electromyography and femoral nerve stimulation

213 During all visits, on arrival at the laboratory participants had the leg to be used in that visit  
214 shaved and cleaned using an alcohol swab over the belly of the vastus lateralis and on the  
215 medial aspect of the tibia, at the level of the tibial tuberosity. Two Ag/AgCl electrodes (Nessler  
216 Medizintechnik, Innsbruck, Austria) were placed on the belly of the vastus lateralis in line with  
217 the muscle fibers, and a single electrode was placed on the medial aspect of the tibia at the level  
218 of the tibial tuberosity for EMG acquisition.

219

220 For femoral nerve stimulation, the anode (100 mm x 50 mm; Phoenix Healthcare Products Ltd.,  
221 Nottingham, UK) was placed on the lower portion of the gluteus maximus, lateral to the ischial  
222 tuberosity. The location of the cathode was determined using a motor point pen (Compex; DJO  
223 Global, Guildford, UK), and another Ag/AgCl electrode was placed on that point. The  
224 establishment of the appropriate stimulator current (200  $\mu$ s pulse width) was then determined  
225 as described in Pethick et al. (2015). Current was incrementally increased until knee extensor  
226 torque and the compound motor unit action potential (M-wave) response to single twitches had  
227 plateaued and was verified with stimulation delivered during an isometric contraction at 50%  
228 MVC to ensure a maximal M-wave was also evident during an isometric contraction. The  
229 stimulator current was then increased to 130% of the current producing a maximal M-wave. In  
230 all trials, doublet stimulation (two 200  $\mu$ s pulses with 10 ms interpulse interval) was used, with  
231 stimuli delivered 1.5 seconds into MVCs to coincide with maximal torque and assess the  
232 maximality of the contraction, and 2 seconds after the contraction to provide a potentiated  
233 doublet.

234

235 Protocol



236 Each participant performed two tasks involving isometric contraction of the knee extensors: 1)  
237 MVCs, to assess torque generating capacity; and 2) a constant force task at 50% MVC, to  
238 assess muscle torque complexity. These measures were taken before, immediately after, 10, 30  
239 and 60 minutes after, and 24 hours after the eccentric and isometric exercise. Additional  
240 measures were taken 48 hours and one week after eccentric exercise. Estimates of muscle  
241 damage and soreness were also taken prior to and after the eccentric and isometric exercise.

242  
243 MVC task. Following the instrumentation of the participants, the (re)-establishment of the  
244 correct dynamometer seating position and the establishment of the supramaximal stimulation  
245 response, participants performed a series of brief (3 second) MVCs to establish the maximum  
246 torque of the leg to be used in that visit. These MVCs were separated by a minimum of 60  
247 seconds rest, and continued until three consecutive peak torques were within 5% of each other.  
248 Participants were given a countdown, followed by very strong verbal encouragement to  
249 maximise torque. The first MVC was used to establish the fresh maximal EMG signal, against  
250 which the subsequent EMG signals were normalised (“Data analysis”; see below). The second  
251 and third MVCs were performed with femoral nerve stimulation.

252  
253 Constant force task. Following the establishment of maximal torque, participants rested for 10  
254 minutes and then performed a series of five isometric contractions at a target torque of 50%  
255 MVC, based on the fresh pre-test MVC recorded in visit 2 or 4. These contractions were 6  
256 seconds long and separated by 4 seconds rest.

257  
258 Estimates of muscle damage. Participants were asked to rate their muscle soreness and capillary  
259 whole-blood was sampled from a fingertip. Muscle soreness was measured using a visual  
260 analog scale consisting of a horizontal line 10 cm long, with 0 and 10 marked at each end. On  
261 this scale, zero corresponded to no muscle soreness and 10 corresponded to the most intense  
262 soreness imaginable. Participants performed a squat down to  $\sim 90^\circ$  of knee flexion and were  
263 asked to draw a line marking their subjective soreness, with the distance to the mark (in  
264 centimetres) being used to quantify soreness. A fingertip blood sample was then taken, and  
265 centrifuged for 10 minutes to obtain plasma. Plasma samples were then stored at  $-80^\circ\text{C}$  for  
266 later analysis of creatine kinase (CK). Plasma CK was determined using a commercially  
267 available kit (CKNAC, Randox Laboratories Ltd., Crumlin, County Antrim, UK) and standard  
268 spectrophotometric-colorimetric procedures with a Randox Monza (Randox Laboratories Ltd.,  
269 Crumlin, County Antrim, UK). These measures were obtained prior to exercise, immediately

270 at task failure, 60 minutes after and 24 hours after both the eccentric and isometric conditions.  
271 They were additionally obtained 48 hours and one week after eccentric exercise.

272

273 Isometric and eccentric exercise

274

275 Isometric contractions (ISO). Participants performed intermittent isometric knee extension  
276 contractions at a target torque of 50% MVC until task failure in their second visit to the lab.  
277 The target torque of 50% MVC was based on the highest instantaneous torque recorded during  
278 the pre-test MVCs. The duty cycle for the contractions was 0.6; with contractions lasting 6  
279 seconds and being followed by 4 seconds rest. The contractions were performed until task  
280 failure, the point at which the participant failed to reach the target torque on three consecutive  
281 occasions, despite strong verbal encouragement. Participants were not informed of the elapsed  
282 time during the trials, but were informed of each “missed” contraction. After the third missed  
283 contraction, participants were instructed to immediately produce an MVC, which was  
284 accompanied by femoral nerve stimulation.

285

286 Eccentric exercise (ECC). Eccentric knee extension actions with the non-dominant leg were  
287 used to induce a minimum 40% reduction of isometric MVC torque (Prasartwuth et al., 2006;  
288 Dartnall et al., 2008) in visit four. This protocol was used to induce a similar amount of muscle  
289 damage in all participants, compared to the large variation in strength loss that can be seen  
290 following a fixed number of eccentric contractions (Hubal et al., 2007). Participants were  
291 seated with their non-dominant leg strapped to the dynamometer, and raised their leg to an  
292 angle of 20° extension (with full extension being 0°). The dynamometer then flexed the  
293 participant’s knee to an angle of 90° extension, at a constant angular velocity of 60°·s<sup>-1</sup>, whilst  
294 the participant resisted this motion by attempting to maximally extend their knee. Each  
295 eccentric contraction was separated by a minimum of 3 seconds rest. Contractions were  
296 performed in sets of 10, followed by a 1 minute rest period. At the start of each 1 minute rest  
297 period, participants performed an isometric MVC. The eccentric exercise continued until there  
298 was a reduction in isometric MVC torque exceeding 40%. At this point, participants performed  
299 another isometric MVC, this time accompanied by femoral nerve stimulation.

300

301 Data acquisition and participant interface

302 Data acquisition was performed in the same manner as described in Pethick et al. (2015). All  
303 peripheral devices were connected via BNC cables to a Biopac MP150 (Biopac Systems Inc.,

304 California, USA) and a CED Micro 1401-3 (Cambridge Electronic Design, Cambridge, UK)  
305 interfaced with a personal computer. All signals were sampled at 1 kHz. The data were  
306 collected in Spike2 (Version 7; Cambridge Electronic Design, Cambridge, UK). A chart  
307 containing the instantaneous torque was projected onto a screen placed ~1 m in front of the  
308 participant. A scale consisting of a thin line (~1 mm thick) was superimposed on the torque  
309 chart and acted as a target, so that participants were able to match their instantaneous torque  
310 output to the target torque.

311

#### 312 Data analysis

313 All data were processed and analysed using code written in MATLAB R2013a (The  
314 MathWorks, Massachusetts, USA). The analysis focused on three main areas: 1) measures of  
315 torque and EMG; 2) measures of global, central and peripheral fatigue; and 3) measures of  
316 torque variability and complexity.

317

318 Torque and EMG. The mean and peak torque for each isometric contraction at 50% MVC (i.e.  
319 from the constant force tasks and isometric fatigue test) were determined. The mean torque was  
320 calculated based on the steadiest five seconds of the contraction, identified by MATLAB code  
321 as the five seconds containing the lowest standard deviation. To determine task failure in the  
322 isometric condition, the mean contraction torque produced in the first minute of contractions  
323 was calculated, and task failure deemed to have occurred when participants' mean torque  
324 output failed to achieve that in the first minute by more than 5 N·m for three consecutive  
325 contractions, with the first of these contractions being the point of task failure (Pethick et al.,  
326 2015).

327

328 The EMG signal from the vastus lateralis from the isometric contractions at 50% MVC was  
329 filtered (10-500 Hz) and full-wave rectified with a gain of 1000. The average rectified EMG  
330 (arEMG) for each contraction was then calculated and normalised by expressing arEMG as a  
331 fraction of the arEMG obtained during an MVC from fresh muscle.

332

333 Global, central and peripheral fatigue. Global fatigue was assessed as the fall in MVC torque.  
334 Measures of central and peripheral fatigue were calculated based on the stimuli delivered to  
335 the femoral nerve during and after the pre-test and recovery MVCs. Peripheral fatigue was  
336 evidenced by a fall in the peak potentiated doublet torque, and central fatigue by the decline in  
337 voluntary activation (VA; Behm et al., 1996):

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$$\text{Voluntary activation (\%)} = (1 - \text{superimposed doublet/potentiated doublet}) \times 100 \quad [1]$$

where the superimposed doublet was that measured during the contraction of interest and the potentiated doublet was measured 2 seconds after the contraction.

Variability and complexity. All measures of variability and complexity were calculated using the steadiest five seconds of each isometric contraction at 50% MVC, identified as the five seconds containing the lowest standard deviation (SD; Forrest et al., 2014). The magnitude of variability in the torque output of each contraction was measured using the SD and the CV. These provide measures of the absolute magnitude of variability in a time series, and the magnitude of variability in a time series normalised to the mean of the time series, respectively.

The temporal structure, or complexity, of torque output was quantified using multiple time domain analyses, as recommended by Goldberger et al. (2002). To determine the regularity of torque output, we calculated approximate entropy (ApEn; Pincus, 1991), and to estimate the temporal fractal scaling of torque the detrended fluctuation analysis (DFA)  $\alpha$  exponent was used (Peng et al., 1994). ApEn and DFA  $\alpha$  were calculated as in our previous studies (Pethick et al., 2015; Pethick et al., 2016; Pethick et al., 2018a), with these calculations briefly detailed below.

ApEn quantifies the negative natural logarithm of the conditional probability that a template of length  $m$  (set at 2) is repeated during a time series (Pincus, 1991). Matching templates that remain arbitrarily similar (i.e. within the tolerance,  $r$ , set at  $0.1SD$ ; Pincus, 1991) are counted, with the number of matches to the  $i$ th template of length  $m$  designated  $B_i$ . The number of these matches that remain similar for the  $m + 1$ th point is then counted, with this number for the  $i$ th template designated  $A_i$ . The conditional probability that the template including the  $m + 1$ th data point matches given the template of length  $m$  is then calculated for each template match. The negative logarithm of the condition probability is calculated for all templates and the results averaged. If the data are highly ordered, then templates that are similar for  $m$  points are likely to also be similar for  $m + 1$  points. The conditional probability will be close to 1, and the negative log, and therefore the entropy, will be close to zero. This will reflect low complexity and high predictability.

$$ApEn(m,r,N) = \frac{1}{N-m} \sum_{i=1}^{N-m} \log \frac{A_i}{B_i} \quad [2]$$

372 where: N is the number of data points in the time series, m is the length of the template,  $A_i$  is  
 373 the number of matches to the  $i$ th template of length  $m + 1$  data points, and  $B_i$  is the number of  
 374 matches to the  $i$ th template of length  $m$  data points.

375

376 In the DFA algorithm, the time series is first integrated and the vertical characteristic scale of  
 377 this integrated time series is measured. The integrated time series is then divided into boxes of  
 378 length  $n$  and a least-squares line is fitted, representing the trend in each box. The  $y$  co-ordinate  
 379 of the straight-line segment of length  $n$  in the  $k$ th box is denoted by  $y_n(k)$ , and the integrated  
 380 time series is detrended by subtracting the local trend in each box. For a given box size,  $n$ , the  
 381 characteristic size of fluctuation for the integrated and detrended time series is given by:

382

$$F(n) = \sqrt{\frac{1}{N} \sum_{k=1}^N [y(k) - y_n(k)]^2} \quad [3]$$

383

384

385 This computation is repeated over all time scales of box sizes to provide a relationship between  
 386 box size and  $F(n)$ . We used 57 boxes, ranging from 1250 to 4 data points. The slope of the log-  
 387 log plot of  $n$  and  $F(n)$  determines the scaling parameter  $\alpha$ . When  $\alpha = 0.5$ , every value will be  
 388 completely independent of the values of previous observations. When  $\alpha \neq 0.5$ , each observation  
 389 is not completely independent and is correlated, to some extent, with the values of previous  
 390 observations. When  $0 < \alpha < 0.5$  power law anti-correlations are present, and when  $0.5 < \alpha < 1$   
 391 power law correlations are present. When  $\alpha > 1$  correlations exist but cease to be of a power  
 392 law form. Brownian noise is indicated by  $\alpha = 1.5$ .

393

394 Statistics

395 All data are presented as means (SD) unless otherwise stated, and results were deemed  
 396 statistically significant when  $P < 0.05$ . No comparisons were made between the ISO and ECC  
 397 conditions due to the fact that the limbs used in each condition were selected rather than  
 398 randomised. Consequently, the time courses in each condition were analysed. To that end, one-  
 399 way ANOVAs with repeated measures were used to test for differences between time points  
 400 for MVC torque, arEMG, potentiated doublet torque, voluntary activation, measures of

401 variability, measures of complexity, muscle soreness and plasma creatine kinase in ISO and  
402 ECC. When main effects were observed, Bonferroni-adjusted 95% confidence intervals were  
403 then used to determine specific differences.

404

405

## 406 **Results**

407

### 408 Preliminary measures

409 The contractile properties of the knee extensors, along with muscle soreness and plasma CK,  
410 measured prior to ISO and ECC are shown in Table 1. The variability and complexity of torque  
411 output prior to ISO and ECC are shown in Table 2. These tables show that there were no  
412 significant differences between the conditions prior to exercise for any of the variables.

413

### 414 Plasma creatine kinase and muscle soreness

415 As shown in Table 1, plasma CK increased in ECC ( $F = 19.68, P < 0.001$ ). CK peaked 24 hours  
416 after exercise ( $893 (388) \text{ U.L}^{-1}$ ; 95% paired samples confidence intervals (CIs) 299, 1144  $\text{U.L}^{-1}$ )  
417 and remained significantly elevated 48 hours after exercise (CIs 203, 998  $\text{U.L}^{-1}$ ). It had  
418 recovered and was not significantly different from its pre-test value one week after exercise  
419 (CIs  $-161, 71 \text{ U.L}^{-1}$ ). There were no significant differences between time points for plasma CK  
420 in ISO.

421

422 Self-reported muscle soreness increased following both ECC ( $F = 27.48, P < 0.001$ ) and ISO  
423 ( $F = 13.42, P < 0.001$ ; Table 1). By the end of ECC, soreness had increased from 0.4 (0.4) to  
424 6.9 (3.0) cm (CIs 3.4, 9.7 cm) and remained significantly elevated over the next 48 hours (CIs  
425 3.3, 6.5 cm), before recovering to its pre-test level one week after exercise (CIs  $-0.7, 0.2$  cm).  
426 At the end of ISO, soreness had increased from 0.5 (0.4) to 5.0 (2.3) cm (CIs 2.2, 6.8 cm). It  
427 decreased over the next 24 hours, though remained significantly elevated at this time point (CIs  
428 0.3, 2.2 cm).

429

### 430 Torque and EMG

431 Both ECC ( $F = 64.37, P < 0.001$ ) and ISO ( $F = 93.21, P < 0.001$ ) had significant effects on  
432 MVC torque (Figure 1; Table 1). Task end in ECC occurred when an isometric MVC  
433 performed at the end of a set had decreased by 40%. This occurred after  $182 \pm 24$  contractions  
434 and resulted in a change in MVC torque from 233.6 (74.2) to 137.7 (45.6)  $\text{N}\cdot\text{m}$ ; a decrease of

435 41.0 (5.2)% (CIs -46.7, -35.2%). MVC torque slowly recovered over the next 48 hours, but  
436 remained significantly depressed at this time point, by 19.7 (9.4)% (CIs -30.1, -9.3%). MVC  
437 torque had recovered and was not significantly different from its pre-test value one week after  
438 exercise (CIs -6.1, 10.2%). Task failure in ISO occurred when participants were no longer able  
439 to achieve the target torque (123.0 (38.6) N·m) despite a maximal effort. This occurred after  
440 4.3 (1.7) minutes and resulted in a change in MVC torque from 246.1 (77.2) to 130.6 (36.2)  
441 N·m; a decrease of 46.2 (4.5)% (CIs -50.9, -41.5%). MVC torque exhibited partial recovery  
442 throughout the subsequent 60 minutes, though still remained significantly depressed, by 11.9  
443  $\pm$  2.1%, at the end of this period (CIs -18.8, -5.0%). MVC torque had recovered and was not  
444 significantly different from its pre-test value 24 hours after exercise (CIs -0.3, 4.3%).

445  
446 The mean arEMG, normalised to a fresh pre-test MVC, during the contractions at 50% MVC  
447 changed in ECC ( $F = 24.59$ ,  $P < 0.001$ ; Table 1). ECC resulted in an increase in arEMG from  
448 51.2 (6.9) to 66.5 (13.1)% (CIs 1.1, 29.2%). Throughout the subsequent 60 minutes this  
449 increased further, reaching 89.7 (7.9)% at the end of this period. arEMG remained significantly  
450 elevated after 48 hours (68.4 (11.2)%; CIs 4.5, 30.0%) and had recovered, and was not  
451 significantly different, from its pre-test value one week after exercise (CIs -13.2, 4.9%). The  
452 mean arEMG also changed in ISO ( $F = 18.33$ ,  $P < 0.001$ ; Table 1). ISO resulted in an increase  
453 in arEMG from 52.9 (6.4) to 88.3 (18.4)% (CIs 18.5, 52.2%). arEMG decreased over the  
454 subsequent 60 minutes, but still remained significantly elevated at the end of this period (66.2  
455 (8.5)%; CIs 7.3, 19.2%). It had recovered and was not significantly different from its pre-test  
456 value 24 hours after exercise (CIs -10.9, 7.1%).

457

#### 458 Peripheral and central perturbations

459 Both ECC ( $F = 33.22$ ,  $P < 0.001$ ) and ISO ( $F = 26.52$ ,  $P < 0.001$ ) resulted in significant  
460 reductions in potentiated doublet torque (Figure 1; Table 1), indicating the presence of  
461 peripheral perturbations. In ECC, potentiated doublet torque decreased from 109.2 (28.7) to  
462 84.8 (24) N·m (CIs -34.0, -14.9 N·m) and continued to decrease in the subsequent 60 minutes,  
463 reaching 70.8 (18.1) N·m at the end of this period. It had recovered and was not significantly  
464 different from its pre-test value 48 hours after exercise (CIs -2.6, 29.1 N·m). In ISO,  
465 potentiated doublet torque decreased from 107.9 (26.2) to 63.3 (16.8) N·m (CIs -69.0, -20.2  
466 N·m). Throughout the subsequent 60 minutes it exhibited partial recovery, but still remained  
467 significantly decreased at the end of this period (CIs -31.7, -9.0 N·m). It had recovered and

468 was not significantly different from its pre-test value 24 hours after exercise (CIs -5.8, 13.9  
469 N·m).

470

471 Both ECC ( $F = 16.05$ ,  $P < 0.001$ ) and ISO ( $F = 12.70$ ,  $P < 0.001$ ) also resulted in significant  
472 reductions in voluntary activation (Figure 1; Table 1), indicating the presence of central  
473 perturbations. In ECC, voluntary activation decreased from 92.0 (2.5) to 68.3 (16.8)% (CIs -  
474 37.3, -10.0%). It remained significantly decreased after 30 minutes of recovery (CIs -18.8, -  
475 1.2%), but had recovered and was not significantly different from its pre-test value 60 minutes  
476 after exercise (CIs -2.4, 8.6%). In ISO, voluntary activation decreased from 91.7 (1.9) to 77.3  
477 (10.2)% (CIs -25.5, -3.3%). It remained significantly decreased after 30 minutes of recovery  
478 (CIs -15.4, -0.3%), but had recovered and was not significantly different from its pre-test value  
479 60 minutes after exercise (CIs -1.3, 9.7%).

480

#### 481 Variability and complexity

482 ECC had a significant effect on the amount of variability, as measured by the SD and CV  
483 during the contractions at 50% MVC (SD,  $F = 8.39$ ,  $P < 0.001$ ; CV,  $F = 7.88$ ,  $P < 0.001$ ). In  
484 ECC, the SD increased from 3.5 (1.5) to 8.0 (5.0) N·m (CIs 0.09, 9.3 N·m), while the CV  
485 increased from 2.8 (0.6) to 7.4 (5.0)% (CIs 0.05, 9.0%). The CV remained significantly higher  
486 10 minutes after exercise (CIs 0.1, 6.0%). ISO also had a significant effect on the SD and CV  
487 during the contractions at 50% MVC (SD,  $F = 19.39$ ,  $P < 0.001$ ; CV,  $F = 24.70$ ,  $P < 0.001$ ;  
488 Table 2). In ISO, the SD increased from 3.3 (1.5) to 10.4 (5.4) N·m (CIs 1.9, 12.4 N·m), while  
489 the CV increased from 2.6 (0.4) to 9.6 (4.2)% (CIs 2.5, 11.4%). Both had recovered and were  
490 not significantly different from the pre-test values after 10 minutes of recovery (SD, CIs -0.7,  
491 0.7 N·m; CV, CIs -0.5, 0.4%).

492

493 The torque profiles of contractions in a representative participant in both conditions are shown  
494 in Figure 3. Complexity, as measured by ApEn, changed over time in both ECC ( $F = 17.16$ ,  $P$   
495  $< 0.001$ ) and ISO ( $F = 28.27$ ,  $P < 0.001$ ) for the contractions at 50% MVC (Figure 2; Table 2).  
496 In ECC, ApEn decreased from 0.39 (0.10) to 0.20 (0.12) (CIs -0.3, -0.08) and remained  
497 significantly depressed 60 minutes after exercise (0.25 (0.13); CIs -0.2, -0.07). It had  
498 recovered and was not significantly different from the pre-test value 24 hours after exercise  
499 (CIs -0.06, 0.2). In ISO, ApEn decreased from 0.41 (0.13) to 0.09 (0.04) (CIs -0.4, -0.2). It  
500 had recovered and was not significantly different from the pre-test value 10 minutes after  
501 exercise (0.36 (0.13), CIs -0.1, 0.1).



502

503 DFA  $\alpha$  changed over time in both ECC ( $F = 16.21, P < 0.001$ ) and ISO ( $F = 32.45, P < 0.001$ )  
504 for the contractions at 50% MVC (Figure 2; Table 2). In ECC, DFA  $\alpha$  increased from 1.43  
505 (0.07) to 1.55 (0.11) (CIs 0.04, 0.2) and remained significantly elevated 60 minutes after  
506 exercise (1.56 (0.09); CIs 0.04, 0.2). It had recovered and was not significantly different from  
507 its pre-test value 24 hours after exercise (CIs  $-0.1, 0.03$ ). In ISO, DFA  $\alpha$  increased from 1.39  
508 (0.10) to 1.64 (0.07) (CIs 0.2, 0.3). It was still significantly elevated 10 minutes after exercise  
509 (1.46 0.09); CIs 0.02, 0.1), but had recovered and was not significantly different from its pre-  
510 test value 30 minutes after exercise (CIs  $-0.1, 0.02$ ).

511

512

### 513 **Discussion**

514

515 The major novel finding of the present study was that, consistent with our hypothesis, eccentric  
516 exercise resulted in a prolonged loss of torque complexity, which was of greater duration than  
517 that induced by fatiguing isometric exercise. Both the eccentric and isometric conditions were  
518 associated with a loss of MVC torque and the development of significant central and peripheral  
519 perturbations, which were accompanied by increasingly Brownian fluctuations in torque output  
520 (DFA  $\alpha = 1.50$ ). Importantly, recovery of MVC torque and torque complexity were  
521 significantly delayed following eccentric exercise. Torque complexity recovered back to  
522 baseline levels after 10 minutes of recovery in the isometric condition, but required 24 hours  
523 recovery in the eccentric condition. These results provide the first evidence that eccentric  
524 exercise reduces torque complexity during subsequent isometric contractions, demonstrating  
525 that such a loss of complexity is not unique to the effects of neuromuscular fatigue. The  
526 prolonged depression of complexity following eccentric exercise, which occurred in concert  
527 with the prolonged loss of maximal torque-generating capacity, suggests that torque  
528 complexity may reflect the functional capacity and adaptability of the neuromuscular system.

529

#### 530 Effect of eccentric exercise on torque complexity, MVC torque and EMG

531 It has long been established that eccentric exercise results in a prolonged decrement in force-  
532 generating capacity (Davies and White, 1981; Newham et al., 1987; Jones et al., 1989). More  
533 recently, it has been shown that eccentric exercise also results in a prolonged increase in the  
534 magnitude of torque variability (Semmler et al., 2007; Dartnall et al., 2008). The present study

535 is the first study to demonstrate that such responses also apply to torque complexity (Table 2).  
536 Eccentric exercise resulted in a reduction in isometric knee extension torque complexity, as  
537 measured by significantly decreased ApEn (indicating increased signal regularity) and  
538 significantly increased DFA  $\alpha$  (indicating increasingly Brownian fluctuations). Over the next  
539 60 minutes, complexity exhibited no recovery and remained at the same level as at the cessation  
540 of exercise. It was only after 24 hours that complexity had recovered back to its baseline level.  
541 Such findings are similar to those investigating the magnitude of variability, which have shown  
542 increased CV during the 60 minutes following eccentric exercise (Lavender and Nosaka, 2006;  
543 Semmler et al., 2007; Skurvydas et al., 2010). It has been suggested that the complexity of a  
544 physiological output reflects the underlying system's ability to adapt to environmental  
545 challenges (Lipsitz and Goldberger, 1992; Goldberger et al., 2002; Pethick et al., 2017). If so,  
546 our results demonstrate that eccentric exercise results in a prolonged narrowing of system  
547 responsiveness and loss of adaptability in motor control, which could increase the risk of failing  
548 a motor task, such as dropping objects, failing to correct a fall, or, in the present experiments,  
549 failing to produce the required joint torque (Pethick et al., 2018b).

550

551 The present study revealed that the recovery kinetics of both fatigue-related variables and of  
552 torque complexity were substantially delayed following eccentric exercise compared to  
553 fatiguing isometric exercise. Recovery of MVC torque has been shown to be ~90% complete  
554 60 minutes after isometric exercise (Sahlin and Ren, 1989; Allman and Rice, 2001), but takes  
555 several days to recover following eccentric exercise (Jones et al., 1989; Sayers and Clarkson,  
556 2001). The present study provides further support for such recovery kinetics: MVC torque  
557 reached ~88% of its fresh value after 60 minutes recovery from isometric exercise, but was still  
558 decreased after 48 hours recovery from eccentric exercise (Figure 1; Table 1). As previously  
559 observed (Pethick et al., 2015; Pethick et al., 2016; Pethick et al., 2018a), torque complexity  
560 significantly decreased over the course of isometric exercise performed to task failure. In  
561 contrast to the eccentric exercise, recovery of torque complexity following isometric exercise  
562 was complete 10 minutes after the cessation of exercise (Table 2). Given that both the eccentric  
563 and isometric conditions resulted in significant global, central and peripheral perturbations, it  
564 is possible that the losses in complexity in each condition have, to some extent, similar causes.  
565 However, that complexity recovers almost immediately upon the cessation of isometric  
566 exercise, but takes 24 hours following eccentric exercise suggests a specific effect of eccentric  
567 exercise is responsible for this delayed recovery. It has been speculated that the delayed  
568 recovery of the magnitude of variability following eccentric exercise is of central origin, and

569 could be due to increased motor unit recruitment and rate coding to compensate for losses from  
570 damaged motor units or due to enhanced motor unit synchronisation (Semmler et al., 2007;  
571 Dartnall et al., 2008); both of which have been associated with the fatigue-induced loss of  
572 complexity observed previously (Pethick et al., 2015; Pethick et al., 2016).

573

574 An important and unexpected observation in the present study was that the recovery kinetics  
575 of MVC and potentiated doublet torque, in both conditions, differed from those of complexity.  
576 Torque generating capacity recovered appreciably more slowly than torque complexity (Table  
577 1; Table 2). Following fatiguing isometric contractions, decrements in MVC and potentiated  
578 doublet torque were still evident after 60 min of recovery. In contrast, torque complexity  
579 recovered within 10-30 minutes. A similar pattern was seen in the eccentric condition:  
580 complexity recovered after 24 hours, but MVC and the potentiated doublet required at least 48  
581 hours to return to control values. Thus, while the loss of torque complexity appears to be tightly  
582 coupled to the neuromuscular fatigue process during exercise (Pethick et al., 2016; Pethick et  
583 al., 2018a), the same is not true during recovery from exercise. The cause of this uncoupling  
584 of torque complexity from the functional capacity of the muscle is not clear. However, it is  
585 possible that in recovery from both fatigue and muscle damage, the restoration of functional  
586 capacity reaches a point at which motor control, which complexity measures reflect, is  
587 effectively restored even though maximal torque-generating capacity remains depressed. In  
588 short, the neuromuscular system's complexity during submaximal contractions appeared to be  
589 restored more rapidly than its maximal torque-generating capacity in both of our experimental  
590 conditions.

591

592 Previous research has indicated that eccentric exercise results in an increase in the amplitude  
593 of submaximal EMG during recovery (Semmler et al., 2007; Dartnall et al., 2008). In the  
594 present study, EMG amplitude following isometric exercise was significantly increased at task  
595 failure, but decreased throughout the subsequent 60 minutes of recovery. However, following  
596 eccentric exercise the EMG amplitude continued to increase throughout that 60 minutes (Table  
597 1) and it was not until 60 minutes after eccentric exercise that EMG amplitude reached its peak.  
598 That EMG starts to recover immediately upon cessation of isometric exercise, but continues to  
599 increase during the 60 minutes following eccentric exercise may be of importance to the  
600 recovery of complexity. Specifically, increased motor unit synchronisation has been observed  
601 immediately following eccentric exercise (Dartnall et al., 2008), with this increase lasting as  
602 long as one week (Dartnall et al., 2011). Several computer simulation studies have suggested

603 that increased motor unit synchronisation substantially increases EMG amplitude (Yao et al.,  
604 2000; Zhou and Rymer, 2004). Moreover, motor unit synchronisation has previously been  
605 speculated to be a potential cause of the fatigue-induced loss of torque (Pethick et al., 2016;  
606 Pethick et al., 2018a) and EMG (Mesin et al., 2009; Beretta-Piccoli et al., 2015) complexity.

607

608 Physiological bases for changes in torque complexity with eccentric exercise

609 Eccentric exercise is well known for impairing neuromuscular function through peripheral  
610 mechanisms, i.e. the muscle damage it induces (Allen, 2001). These mechanisms include those  
611 directly related to myofibrillar damage, and those related to damage to sarcolemmal  
612 membranes (Allen et al., 2005). The muscle damage brought about by eccentric exercise results  
613 in some muscle fibres contributing little to force production (Proske and Morgan, 2001). Thus,  
614 in order to compensate for losses from damaged motor units, increased recruitment and rate  
615 coding would be necessary to achieve the target torque (Semmler et al., 2007), as indicated by  
616 the increasing EMG during the first 60 minutes of recovery (Table 1). Such an increased  
617 activation of the motor unit pool may potentially contribute to the observed prolonged  
618 reduction in complexity, since knee extensor torque complexity appears to decrease as  
619 contractile intensity increases (Pethick et al., 2016). However, the muscle damage experienced  
620 and decreased force generating capability persist for longer than the decreased complexity.  
621 Furthermore, during recovery from isometric exercise the continued presence of peripheral  
622 fatigue would likely indicate fibres contributing less to force production, necessitating greater  
623 activation of the motor unit pool, yet complexity recovers within 10 minutes of the cessation  
624 of exercise. It may be that measures of complexity during contractions at 50% MVC are  
625 insensitive to small differences in neuromuscular system adaptability produced by fatigue as  
626 the muscle recovers; higher intensity contractions might be required to reveal a closer  
627 correspondence between the recovery from fatigue or muscle damage and that of torque  
628 complexity.

629

630 Previous studies have observed increased motor unit synchronisation immediately after and 24  
631 hours after eccentric exercise (Dartnall et al., 2008; Dartnall et al., 2011) and this has been  
632 speculated to be a cause of the increased EMG amplitude and torque variability seen after such  
633 exercise (Saxton et al., 1995; Semmler et al., 2007; Dartnall et al., 2008). The increasing EMG  
634 amplitude (Table 1) and increased amount of variability (Table 2) observed in the 60 minutes  
635 following eccentric exercise are both typical of increased motor unit synchronisation (Yao et  
636 al., 2000; Zhou and Rymer, 2004) and suggest a role for adjustments in motor unit activation

637 (Dartnell et al. 2008). Common synaptic input to muscles, and motor unit synchronisation,  
638 have been proposed to be major determinants of force variability (Dideriksen et al., 2012;  
639 Farina and Negro, 2015) and have been demonstrated to increase with fatigue (Castronovo et  
640 al., 2015). We have, therefore, previously speculated a link between motor unit synchronisation  
641 and torque complexity (Pethick et al., 2016; Pethick et al., 2018a). However, direct  
642 measurement of individual motor units via high-density surface EMG electrodes will be  
643 necessary to confirm a link between motor unit synchronisation and torque complexity, rather  
644 than the analysis of motor unit action potential trains recorded using bipolar EMG, as was  
645 utilised in the present study.

646

647 Two limitations of the present design were the lack of randomisation of the legs used in each  
648 condition, and the non-randomised order of conditions themselves. However, there were strong  
649 physiological reasons for choosing this design: it was necessary to ensure that there were no  
650 spillover effects to or from the eccentric condition, and this meant that the non-dominant leg  
651 was chosen for this condition, and the dominant leg for the isometric condition that preceded  
652 it. Conducting the isometric condition first was necessary to ensure that any adaptation  
653 following the eccentric exercise-induced damage did not affect the response to isometric  
654 exercise. Given the rationale for the present design, the most important effect of the lack of  
655 randomisation was on the assumptions of the statistical tests used to directly compare the two  
656 conditions. Consequently, no such statistical tests were conducted or reported, and we have  
657 instead drawn our conclusions from the separate analysis of the time course of the dependent  
658 variables in each condition. It is possible that having shown the effect of unmitigated eccentric  
659 induced damage in the present study, a future study could be conducted employing  
660 randomisation. However, the long washout time that would be required in such a study would,  
661 we believe, most likely compromise the between-condition comparison and negatively affect  
662 participant compliance.

663

## 664 Conclusion

665 In summary, the present study has demonstrated that muscle-damaging eccentric exercise  
666 results in a decrease in isometric knee extensor torque complexity, as measured using ApEn  
667 and DFA  $\alpha$ , with this decrement being considerably more prolonged than that resulting from  
668 fatiguing isometric exercise. Eccentric exercise was also associated with more prolonged  
669 decreases in MVC torque and peripheral perturbations than isometric exercise, which are  
670 attributed to the effects of muscle damage. As torque complexity recovered rapidly following

671 isometric exercise, the prolonged reduction in complexity following eccentric exercise was also  
672 likely due to an effect of this muscle damage. Whether this was due to the mechanical  
673 disruption itself or due to the mechanical disruption impairing and/or influencing neural drive  
674 is yet to be fully elucidated, though adjustments in motor unit activation appear to be a strong  
675 candidate mechanism. These results suggest that the effects of eccentric exercise are not limited  
676 to the periphery, but also extend to the central nervous system and the ability to control torque  
677 output.

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700

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**Table 1.** Voluntary torque, potentiated doublet torque, voluntary activation, EMG, muscle soreness and plasma creatine kinase responses over the course of the isometric and eccentric tests.

Parameter		Pre	Task end/failure	10 mins post	30 mins post	60 mins post	24 hours post	48 hours post	1 week post
MVC torque, % pre	Iso	100	53.8 (4.5)*	78.0 (11.0)*	79.8 (9.6)*	88.1 (6.6)*	102.0 (2.2)	–	–
	Ecc	100	59.0 (5.2)*	64.6 (8.6)*	68.8 (9.1)*	71.9 (7.4)*	76.1 (9.8)*	80.3 (9.4)*	98.0 (7.4)
Doublet, N·m	Iso	107.9 (26.2)	63.3 (16.8)*	87.2 (22.5)*	87.7 (22.0)*	87.6 (22.0)*	103.9 (26.6)	–	–
	Ecc	109.2 (28.7)	84.8 (24.0)*	73.8 (19.0)*	71.4 (18.7)*	70.8 (18.1)*	91.6 (24.5)*	96.0 (24.2)	100.4 (24.5)
VA, %	Iso	91.7 (1.9)	77.3 (10.2)*	82.2 (8.4)*	83.9 (7.1)*	87.5 (5.6)	91.5 (3.9)	–	–
	Ecc	92.0 (2.5)	68.3 (10.2)*	78.1 (7.4)*	82.0 (8.3)*	84.1 (8.1)	88.9 (5.3)	89.8 (4.1)	91.2 (4.3)
arEMG, % MVC	Iso	52.9 (6.4)	88.3 (18.4)*	72.0 (11.3)*	66.4 (11.4)*	66.2 (9.0)*	54.9 (11.1)	–	–
	Ecc	51.2 (6.9)	66.3 (13.1)*	80.0 (13.1)*	86.7 (18.2)*	89.7 (15.1)*	76.7 (9.5)*	68.4 (11.3)*	55.3 (9.2)
Soreness, cm	Iso	0.5 (0.4)	5.0 (2.3)*	–	–	3.5 (2.6)*	1.7 (1.3)*	–	–
	Ecc	0.4 (0.4)	6.9 ± 3.0*	–	–	6.00 (2.7)*	5.3 (1.4)*	5.3 (1.6)*	0.6 (0.6)
CK, U/L	Iso	166 (108)	168 (110)	–	–	196 (128)	200 (130)	–	–
	Ecc	172 (164)	317 (255)	–	–	378 (202)*	893 (388)*	722 (293)*	217 (101)

Values are means (SD). MVC, maximal voluntary contraction; doublet, potentiated doublet torque; VA, voluntary activation; arEMG, average rectified EMG of the vastus lateralis; CK, plasma creatine kinase; Iso, isometric condition; Ecc, eccentric condition. \* indicates a statistically significant difference from the pre-test value.

**Table 2.** Variability, complexity and fractal scaling responses over the course of the isometric and eccentric tests.

Parameter		Pre	Task end/failure	10 mins post	30 mins post	60 mins post	24 hours post	48 hours post	1 week post
SD, N·m	Iso	3.3 (1.5)	10.4 (5.4)*	3.3 (1.2)	3.2 (1.2)	3.5 (1.2)	3.0 (0.9)	–	–
	Ecc	3.5 (1.5)	8.0 (5.0)*	6.2 (3.3)	5.5 (3.4)	5.0 (2.8)	3.6 (2.0)	3.3 (1.6)	2.9 (1.1)
CV, %	Iso	2.6 (0.4)	9.6 (4.2)*	2.6 (0.5)	2.6 (0.5)	2.9 (0.6)	2.4 (0.3)	–	–
	Ecc	2.8 (0.4)	7.4 (5.0)*	5.9 (3.2)*	5.1 (3.5)	4.4 (2.4)	3.0 (1.5)	2.7 (1.0)	2.4 (0.5)
ApEn	Iso	0.41 (0.13)	0.09 (0.04)*	0.36 (0.13)	0.37 (0.14)	0.35 (0.12)	0.37 (0.09)	–	–
	Ecc	0.39 (0.10)	0.20 (0.12)*	0.19 (0.07)*	0.21 (0.09)*	0.25 (0.13)*	0.33 (0.13)	0.36 (0.15)	0.38 (0.11)
DFA $\alpha$	Iso	1.39 (0.10)	1.64 (0.07)*	1.46 (0.10)*	1.44 (0.10)	1.45 (0.09)	1.42 (0.07)	–	–
	Ecc	1.43 (0.07)	1.54 (0.11)*	1.56 (0.07)*	1.57 (0.07)*	1.55 (0.09)*	1.49 (0.10)	1.45 (0.10)	1.43 (0.11)

Values are means (SD). SD, standard deviation; CV, coefficient of variation; ApEn, approximate entropy; DFA  $\alpha$ , detrended fluctuation analysis; Iso, isometric condition; Ecc, eccentric condition. \* indicates a statistically significant difference from the pre-test value.



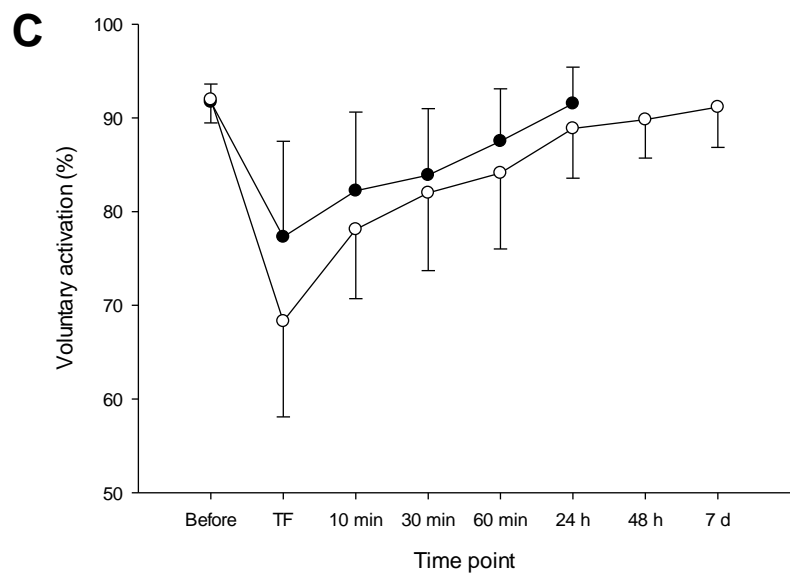
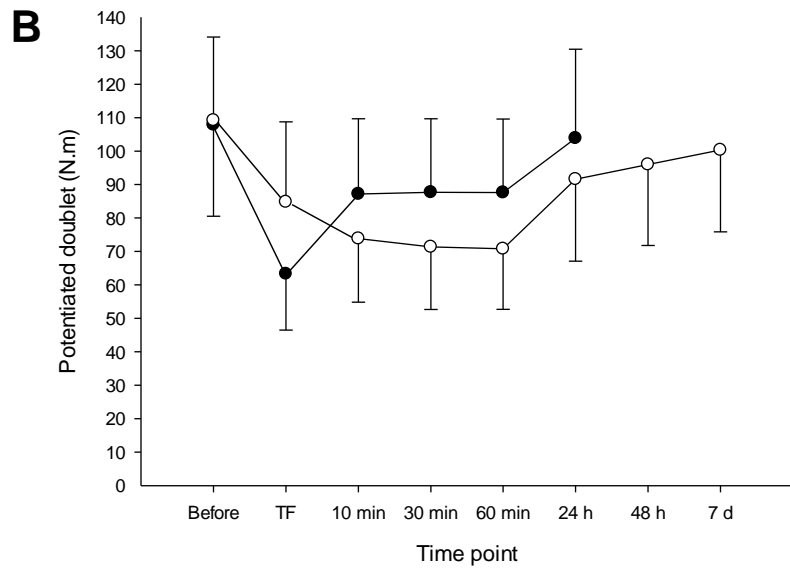
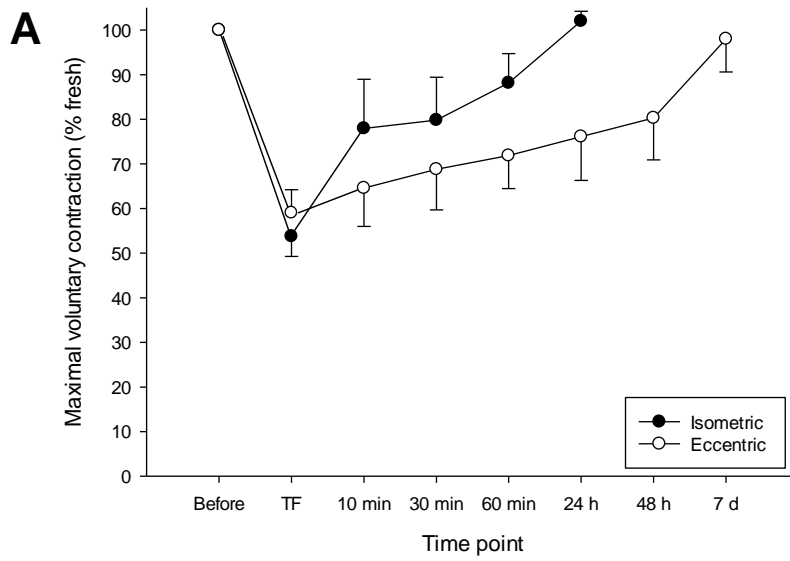
## Figure Legends

**Figure 1: Maximal voluntary contraction (panel A), potentiated doublet (panel B), and voluntary activation (panel C) before and following fatiguing isometric contractions and damaging eccentric exercise.** Note that recovery from isometric exercise is complete within 24 hours, whereas eccentric exercise requires at least 24-48 hours. Values are mean  $\pm$  SD.

**Figure 2: complexity of torque output in response to isometric and eccentric exercise.** Panel A shows the responses of approximate entropy (ApEn), and panel B shows the results of the detrended fluctuation analysis. Note the rapid recovery of complexity following isometric contractions (complete within 10-30 min), but the slower recovery following eccentric exercise (recovery requiring 24 hours). Values are mean  $\pm$  SD

**Figure 3: example contractions from a representative participant in each condition.** Note the decrease in complexity at task failure in both conditions. Recovery to, or towards, the complexity observed in a fresh isometric contraction (Before) required 10 minutes (isometric condition) or 24 hours (eccentric condition).

**Figure 1**



**Figure 2**

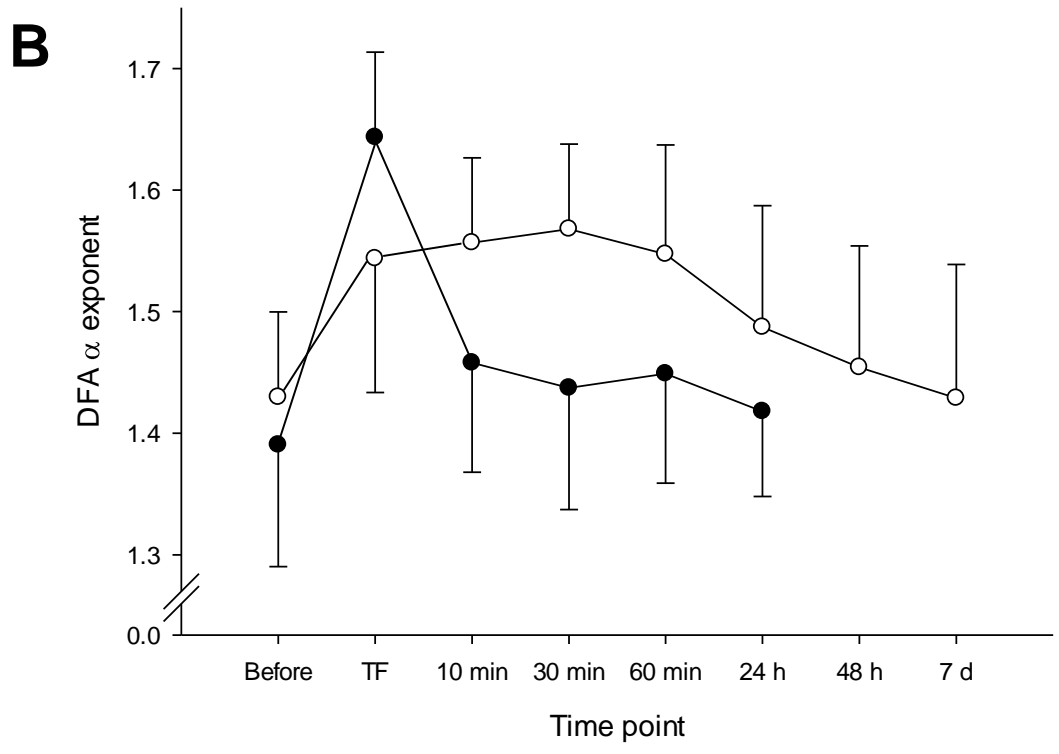
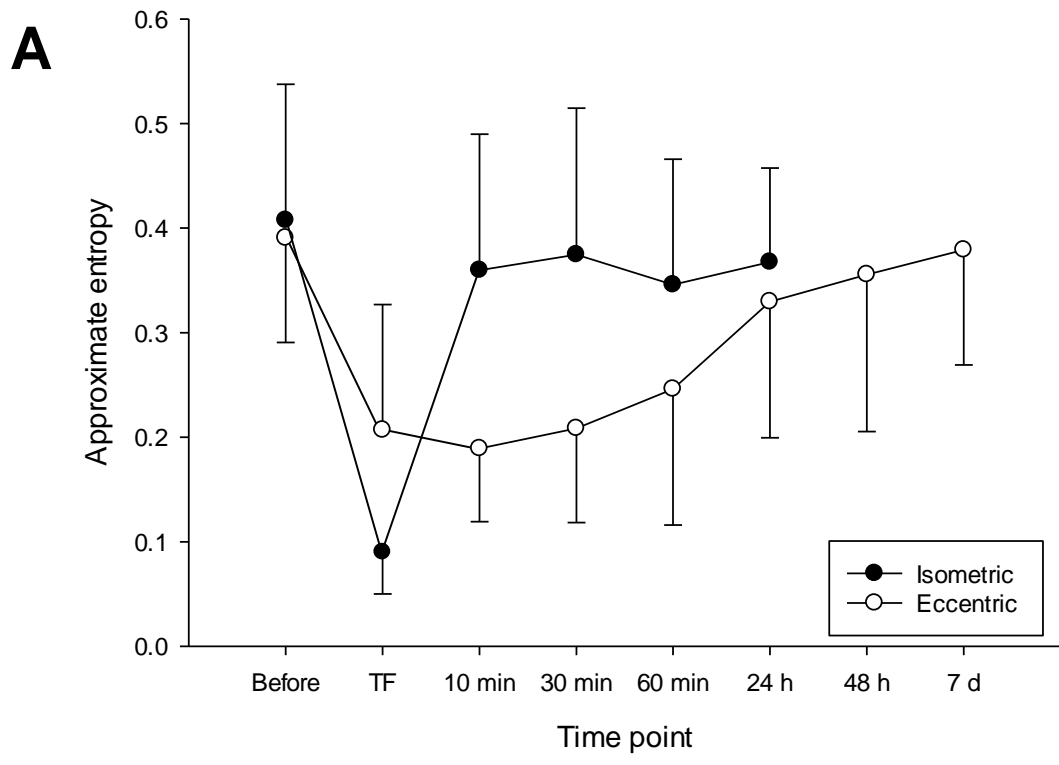


Figure 3

