

Not all brawn, but some brain. Strength gains after training alters kinematic motor abundance in hopping

Bernard X.W. Liew^{Corresp. 1}, Andrew Morrison², Hiroaki Hobara³, Susan Morris⁴, Kevin Netto⁴

¹ Centre of Precision Rehabilitation for Spinal Pain (CPR Spine), School of Sport, Exercise and Rehabilitation Sciences, College of Life and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom

² Sport and Exercise Sciences, Faculty of Science and technology, Anglia Ruskin University, Cambridge, United Kingdom

³ Human Informatics Research Institute, National Institute of Advanced Industrial Science and Technology (AIST), Tokyo, Japan

⁴ School of Physiotherapy and Exercise Sciences, Curtin University of Technology, Perth, Western Australia, Australia

Corresponding Author: Bernard X.W. Liew

Email address: LiewB@adf.bham.ac.uk

Background. The effects of resistance training on a muscle's neural, architectural, and mechanical properties are well established. However, whether resistance training can positively change the coordination of multiple motor elements in the control of a well-defined lower limb motor performance objective remains unclear. Such knowledge is critical given that resistance training is an essential and ubiquitous component in gait rehabilitation. This study aimed to investigate if strength gains of the ankle and knee extensors after resistance training increases kinematic motor abundance in hopping.

Methods. The data presented in this study represents the pooled group results of a sub-study from a larger project investigating the effects of resistance training on load carriage running energetics. 30 healthy adults performed self-paced unilateral hopping, and strength testing before and after six weeks of lower limb resistance training. Motion capture was used to derive the elemental variables of planar segment angles of the foot, shank, thigh, and pelvis, and the performance variable of leg length. Uncontrolled manifold analysis (UCM) was used to provide an index of motor abundance (IMA) in the synergistic coordination of segment angles in the stabilization of leg length. Bayesian Functional Data Analysis was used for statistical inference, with a non-zero crossing of the 95% Credible Interval (CrI) used as a test of significance.

Results. Depending on the phase hop stance, there were significant main effects of ankle and knee strength on IMA, and a significant ankle by knee interaction effect. For example at 10 % hop stance, a 1 Nm/kg increase in ankle extensor strength increased IMA by 0.37 (95% CrI 0.14 to 0.59), a 1 Nm/kg increase in knee extensor strength decreased IMA by 0.29 (95% CrI 0.08 to 0.51), but increased the effect of ankle strength on IMA by 0.71 (95% CrI 0.10 to 1.33). At 55% hop stance, a 1 Nm/kg increase in knee extensor strength increase IMA by 0.24 (95% CrI 0.001 to 0.48), but reduced the effect of ankle strength on IMA by 0.71 (95% CrI 0.13 to 1.32).

Discussion. Resistance training not only improves strength, but also the structure of coordination in the control of a well-defined motor objective. The role of resistance training on motor abundance in gait should be investigated in patient cohorts, other gait patterns, and its translation into functional improvements.

- 1 **Article title:** Not all Brawn, but some Brain. Strength gains after training alters kinematic motor
- 2 abundance in hopping.

Authors

Bernard X.W. Liew, BSc (Hon) ^{1,4}

Andrew Morrison, PhD²

Hiroaki Hobara, PhD³

Susan Morris, PhD⁴

Kevin Netto, PhD ⁴

Affiliations

¹ Centre of Precision Rehabilitation for Spinal Pain (CPR Spine), School of Sport, Exercise and Rehabilitation Sciences, College of Life and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom.

² Sport and Exercise Sciences, Faculty of Science and technology, Anglia Ruskin University, Cambridge, United Kingdom.

³ Human Informatics Research Institute, National Institute of Advanced Industrial Science and Technology (AIST), Tokyo, Japan.

⁴School of Physiotherapy and Exercise Sciences, Curtin University, Perth, Western Australia, Australia.

Address author

- 3 Dr Bernard Liew, School of Sport, Exercise and Rehabilitation Sciences, Centre of Precision
- 4 Rehabilitation for Spinal Pain (CPR Spine), College of Life and Environmental Sciences,
- 5 University of Birmingham, Birmingham, United Kingdom; E-mail: LiewB@adf.bham.ac.uk;
- 6 liew_xwb@hotmail.com. Tel: +44 121 415 8526

Trial registration (Date of registration): ANZCTR (ACTRN12616000023459) (14 Jan 2016)

8 **ABSTRACT.**

9 **Background.**

10 The effects of resistance training on a muscle's neural, architectural, and mechanical properties
11 are well established. However, whether resistance training can positively change the
12 coordination of multiple motor elements in the control of a well-defined lower limb motor
13 performance objective remains unclear. Such knowledge is critical given that resistance training
14 is an essential and ubiquitous component in gait rehabilitation. This study aimed to investigate if
15 strength gains of the ankle and knee extensors after resistance training increases kinematic motor
16 abundance in hopping.

17 **Methods.**

18 The data presented in this study represents the pooled group results of a sub-study from a larger
19 project investigating the effects of resistance training on load carriage running energetics. 30
20 healthy adults performed self-paced unilateral hopping, and strength testing before and after six
21 weeks of lower limb resistance training. Motion capture was used to derive the elemental
22 variables of planar segment angles of the foot, shank, thigh, and pelvis, and the performance
23 variable of leg length. Uncontrolled manifold analysis (UCM) was used to provide an index of
24 motor abundance (IMA) in the synergistic coordination of segment angles in the stabilization of
25 leg length. Bayesian Functional Data Analysis was used for statistical inference, with a non-zero
26 crossing of the 95% Credible Interval (CrI) used as a test of significance.

27 **Results.**

28 Depending on the phase hop stance, there were significant main effects of ankle and knee
29 strength on IMA, and a significant ankle by knee interaction effect. For example at 10 % hop

30 stance, a 1 Nm/kg increase in ankle extensor strength increased IMA by 0.37 (95% CrI 0.14 to
31 0.59), a 1 Nm/kg increase in knee extensor strength decreased IMA by 0.29 (95% CrI 0.08 to
32 0.51), but increased the effect of ankle strength on IMA by 0.71 (95% CrI 0.10 to 1.33). At 55%
33 hop stance, a 1 Nm/kg increase in knee extensor strength increase IMA by 0.24 (95% CrI 0.001
34 to 0.48), but reduced the effect of ankle strength on IMA by 0.71 (95% CrI 0.13 to 1.32).

35 **Discussion.**

36 Resistance training not only improves strength, but also the structure of coordination in the
37 control of a well-defined motor objective. The role of resistance training on motor abundance in
38 gait should be investigated in patient cohorts, other gait patterns, and its translation into
39 functional improvements.

40

41 INTRODUCTION

42 Regular participation in walking and running has important health benefits (Lee et al. 2014), and
43 is commonly undertaken along irregular surfaces. Normally, humans have no problems
44 maintaining dynamic postural control and energy efficiency during gait despite these surface
45 irregularities, ensuring a smooth center of mass (COM) trajectory. Excessive COM trajectory
46 disturbance in gait can be energetically costly and potentially destabilizing to postural control
47 (Andrada et al. 2013; Geyer et al. 2006).

48 Perturbation to the COM trajectory can be minimized over irregular surfaces by adjusting the
49 length of a simplified virtual leg (henceforth termed as leg), spanning the COM to the center of
50 pressure (COP) (Andrada et al. 2013; Geyer et al. 2006). Leg length is regulated by four major
51 segments (foot, shank, thigh, and pelvis), along which flexion-extension occurs. The excess of
52 segments required to control a single leg, means that the body has an abundance of solutions to
53 flexibly combine segment angles to achieve the same leg length (Auyang et al. 2009). Greater
54 motor abundance in leg length regulation affords the body greater adaptability to rapidly react to
55 irregular surfaces to minimize COM trajectory perturbation. In the context of quantifying motor
56 abundance in leg length regulation, the Uncontrolled Manifold (UCM) analysis has been used to
57 investigate the motor control of unilateral hopping (Auyang et al. 2009). UCM provides a ratio
58 of two variances: one where the variance in angles (motor elements) does not change leg length
59 (performance variable) - Goal-Equivalent Variance (GEV), to a variance in angles which change
60 leg length - Non Goal Equivalent Variance (NGEV) (Auyang et al. 2009).

61 The manifestation of normal abundance in motor task may depend on the task's physical demand
62 relative to an individual's physiological strength capacity (Greve et al. 2013; Olafsdottir et al.
63 2008; Park et al. 2015; Shim et al. 2008; Yen & Chang 2010). Greater motor abundance may

64 emerge when the task's relative physical demand increases (Greve et al. 2013). For example,
65 older adults with lower maximal strength have non-significantly greater motor abundance in sit-
66 to-stand compared to younger adults with greater maximal strength (Greve et al. 2013). When an
67 external load was added to walking, there was a significant increase in the motor abundance of
68 joint angle co-variation in the control of the COM trajectory in the frontal plane, and a non-
69 significant increase in abundance in the control of the COM trajectory in the sagittal plane (Qu
70 2012). It is reasonable to expect that if one muscle is operating near its physiological limit,
71 additional muscles would be recruited to achieve successful performance.

72 In contrast, prospective resistance training studies of the upper limb demonstrated that greater
73 wrist and finger strength was associated with greater abundance in finger force coordination
74 tasks (Olafsdottir et al. 2008; Park et al. 2015; Shim et al. 2008). Resistance training may
75 augment motor abundance via several mechanisms: (1) by increasing reciprocal inhibition of co-
76 varying muscle groups via heteronomous spinal pathways (Geertsen et al. 2008), (2) increasing
77 the role of bi-articular muscles in inter-segmental kinematic co-variation (Cleather et al. 2015),
78 and (3) increasing the number of muscle modes available for co-variation (Hashiguchi et al.
79 2016).

80 Although prospective study designs (Olafsdottir et al. 2008; Park et al. 2015; Shim et al. 2008)
81 already provide a higher level of evidence base than a cross-sectional design (Greve et al. 2013;
82 Qu 2012), the relationship between physiological strength and motor abundance may still have
83 been confounded by other factors. First, different mathematical formulation of the variance ratios
84 of motor abundance may have contributed to the conflicting evidence (Greve et al. 2013;
85 Olafsdottir et al. 2008). For example, Olafsdottir et al. (2008) defined motor abundance using the
86 ratio of $\frac{GEV - NGEV}{GEV + NGEV}$, whilst Greve et al. (2013) used a simple ratio of $\frac{GEV}{NGEV}$. Second, differences

87 may lie in the hierarchical level of analysis as it pertains to the neural control of motor
88 abundance. Greve et al. (2013) investigated the covariation of joint-level kinematics to whole-
89 body performance variables, such as ground reaction force. The analysis by Greve et al. (2013)
90 thus did not consider an intermediary level of hierarchical control – that is in the stabilization of
91 limb-level performance variables (Toney & Chang 2016). In contrast, Olafsdottir et al. (2008)
92 investigated the covariation of limb-level (finger) force in the stabilization of the total force
93 generated by four fingers. To this end, a prospective study design that quantifies lower limb
94 motor abundance within a hierarchical control framework would increase the evidence base
95 behind using resistance training to improve motor abundance.

96 Resistance training is an essential component in gait rehabilitation (Papa et al. 2017). Whether a
97 gain in physiological strength capacity benefits or harms motor abundance is an essential
98 question to answer, as it directly implicates the role of resistance training in gait rehabilitation.
99 The aim of this study was to investigate if lower limb strength gains after resistance training
100 influenced lower limb motor abundance. Hopping represents an excellent model of forward gait
101 patterns to fulfill the present study's aim. First, lower limb spring-mass dynamics in hopping is
102 present in walking and running (Geyer et al. 2006). Second, leg length is a regulated
103 performance variable in hopping using UCM analysis (Auyang et al. 2009). Given that leg length
104 mechanics contributes to COM trajectory (Moritz & Farley 2003), greater motor abundance in
105 leg length stabilization in hopping may translate into more available motor solutions to minimize
106 COM trajectory perturbation when walking or running over irregular surfaces. Third, normal
107 inter-segmental kinematic and kinetic coordination in hopping, quantified using UCM and vector
108 coding, varies depending on the task's relative physical demand (Auyang et al. 2009; Smith et al.
109 2014; Yen & Chang 2010), Similar to the effects of finger muscle strengthening on finger

110 pressing motor abundance (Olafsdottir et al. 2008), the hypothesis of this study was that greater
111 strength gains after resistance training would increase kinematic motor abundance in leg length
112 regulation during hopping.

113 **MATERIALS AND METHODS.**

114 **Participants**

115 The data presented in this manuscript represents the pooled group results of a sub-study from a
116 larger project investigating the effects of resistance training on load carriage running energetics
117 (Liew et al. 2017). (Liew et al. 2017). Healthy adult recreational runners between 18 to 60 years
118 old were invited to participate in the study. Participants had to be actively engaged in running or
119 running-related sports with a minimum cumulated total duration of 45 minutes per week to be
120 considered for inclusion. Exclusion criteria included: 1) self-reported medical conditions which
121 precluded the safe performance of running, jumping, hopping activities and heavy resistance
122 exercises; 2) self-reported running related injuries currently and within the past three months; 3)
123 surgeries within the past year; and 4) females who were pregnant at time of recruitment Thirty
124 participants volunteered for this study (16 male, 14 female). This study was approved by the
125 Curtin University Human Research Ethics Committee (RD-41-14). Informed written consent was
126 sought and gained prior to study enrolment.

127 **Intervention**

128 The two training programs were developed to improve load carriage running energetics (Table
129 S1 in supplementary material). One group performed “conventional” heavy-resistance isoinertial
130 training on the bilateral leg press, unilateral calf raises, and lunge exercises. These exercises have
131 been routinely adopted in conventional load-carriage military training (Knapik et al. 2012). The

132 other group performed “load carriage specific” resistance training targeting the specific
133 biomechanical requirements of load carriage running (Liew et al. 2017). Exercises in this group
134 comprised of externally loaded single-leg hopping to increase leg stiffness, countermovement
135 jumps to increase knee power generation, and hip flexor pull to increase pre-swing running
136 energetics (Liew et al. 2017). Greater leg stiffness, knee power generation, and pre-swing hip
137 energetics were previously shown to be required to sustain constant running velocity during load
138 carriage (Liew et al. 2016a; Silder et al. 2015). Despite the differences between the training
139 programs, the present study was only interested in accounting for the between time (pre-post)
140 change in strength (ankle extensor = mean increase 0.34 Nm/kg [95% Confidence Interval (CI)
141 0.25 to 0.42 Nm/kg]; knee extensor = mean increase 0.24 Nm/kg [95% CI 0.11 to 0.37 Nm/kg])
142 (Liew et al. 2017), in predicting alterations in hopping motor abundance.

143 **Three dimension motion capture on hopping (combined group analysis)**

144 Participants performed unilateral hopping, on both sides, at a self-selected frequency lasting
145 approximately 15s. During hopping, the arms were held in a 90° abducted position, to allow
146 visualization of the lateral pelvic markers. The only instruction provided was to hop at a
147 “comfortable pace”. In the post hoc analysis stage, only hops maintained within 10% of the
148 individual’s mean hop frequency was kept for further analysis (termed as successful trials). This
149 10% frequency window was deemed appropriate given that a previous study reported a variation
150 of up to 20 % for adults hopping at their preferred frequency (Beerse & Wu 2016). A between
151 side standing rest period of one minute was provided. An 18 camera motion capture system
152 (Vicon T-series, Oxford Metrics, UK) (250 Hz), with synchronized in-ground force plates
153 (AMTI, Watertown, MA) (2000 Hz) were used to collect marker trajectories and force data
154 (Vicon Nexus, v2.3, Oxford Metrics, UK). Force data were used to detect initial contact and toe-

155 off, with a 20 N vertical force threshold used. The marker placements were based on a previous
156 study (Liew et al. 2016b). A seven-segment lower-limb biomechanical model was created in
157 Visual 3D (C-motion, Germantown, MD) (Liew et al. 2016a). Joint centers of the hip were
158 derived using a regression equation (Bell et al. 1989), whilst those of the knee and ankle were
159 derived as the midpoint between the medial and lateral femoral condyles, and malleoli,
160 respectively. Segment inertial and geometric properties were based on Visual 3D's default
161 routines. The biomechanical model's position and orientation was derived using inverse
162 kinematics. Each joint had three rotational degrees of freedom, with the model having a total of
163 18 degrees of freedom. The laboratory and joint coordinate system used had the following
164 sequence: X axis – mediolateral with positive pointing to the right, Y axis – postero-anterior with
165 positive pointing anteriorly, and Z axis – vertical with positive pointing proximally. Marker
166 trajectories were low pass filtered at 12 Hz (zero lag, 4th order, Butterworth).

167 **Isokinetic strength measurement**

168 Isokinetic concentric strength testing of the bilateral knee and ankle extensors was performed in
169 a dynamometer (HUMAC NORM, Computer Sports Medicine Inc., Stoughton, MA), collecting
170 data at 100 Hz and set up according to the manufacturer's guidelines (Liew et al. 2017). For each
171 muscle group tested, participants first performed 10 repetitions of warm-up contractions at 90°/s,
172 and two sets of six maximal concentric-concentric contractions at 60°/s. Each set was
173 interspersed with one minute of seated rest in-situ. Between muscle group and side rest periods
174 of three minutes were provided.

175 **Uncontrolled manifold analysis**

176 A modified sagittal plane forward kinematic model mapping segment angles to leg length used in
177 a previous study was adopted in the present study (Auyang et al. 2009) (Figure 1). Leg length

178 was presently defined by the vector between the centre of pressure (COP) to the proximal end of
 179 the pelvic segment, instead of the toe and anterior superior iliac spine markers, respectively
 180 (Auyang et al. 2009). The X-coordinate of landmarks used to create the planar segments was set
 181 to zero. The foot, shank, thigh, and pelvic planar segments were defined by the line vectors in the
 182 YZ plane between 1) COP to ankle joint centre, 2) ankle to knee joint centre, 3) knee to hip joint
 183 centre, and 4) hip joint to proximal end of the pelvic inertial segment. Trial-to-trial variability in
 184 leg length can be influenced by variable changes to segment lengths, given the presence of soft
 185 tissue artefact. This effect was minimized by using landmarks modeled after the biomechanical
 186 model was optimized using inverse kinematic. Sagittal planar angles of each segment in the YZ
 187 plane were defined relative to the laboratory's horizontal plane, using the Right Hand Rule. All
 188 segment planar angles and leg length were time-normalized to 100 data points in the stance
 189 period for UCM analysis.

190 The UCM analysis was carried out using a previously published method (Auyang et al. 2009),
 191 for each of the 100 stance data points.

$$192 \quad NGEV = \frac{\text{trace}(\text{orth}(J^t) \cdot C \cdot \text{orth}(J^t))}{d} \dots(1)$$

$$193 \quad GEV = \frac{\text{trace}(\text{null}(J)^t \cdot C \cdot \text{orth}(J))}{n - d} \dots(2)$$

$$194 \quad IMA = \frac{GEV - NGEV}{GEV + NGEV} \dots(3)$$

195 In equations (1) to (3), non-goal equivalent variance (NGEV) represented the variance of all
 196 segment angle combinations that contributed to leg length changes while goal equivalent
 197 variance (GEV) represented the variance of all segment angle combinations that did not change

198 leg length. The index of motor abundance (IMA) represented the ratio of two variance measures
199 (Auyang et al. 2009). Thus an $IMA > 0$ characterized variation in segment angles which
200 minimized leg length variation (i.e. motor abundance), and an $IMA < 0$ characterized variation in
201 segment angles that maximized leg length variation (Auyang et al. 2009). In the equation, J is the
202 Jacobian matrix mapping infinitesimally small changes in segment angles to changes in leg
203 length; C is the co-variance matrix in the deviation of the segment angles from the mean
204 reference segment angles at each datum; d is the degree of freedom in the performance variable
205 ($d = 1$ in this study); and n is the degree of freedom in the elemental variables ($n = 4$).

206 **Statistical analysis (combined group inference)**

207 A previous study reported that the standard deviation of the GEV and NGEV was lowest with at
208 least 20 trials (Latash et al. 2010). Hence, UCM analysis and subsequent functional regression
209 analyses was performed only on participants with ≥ 20 successful trials. Simple linear regression
210 was used to quantify differences in age, height, weight, running frequency (times/week) and
211 cumulated distance (km/week) over the past six weeks, baseline ankle and knee extensor strength
212 between participants with and without ≥ 20 successful trials.

213 Descriptive scalar variables of post-pre change in hopping frequency and stance duration, and
214 baseline (pre-training) waveform variables of leg length, foot, shank, thigh, and pelvic segment
215 angles, IMA, GEV, and NGEV were reported for participants with ≥ 20 successful hopping
216 trials. The dependent variable was the between time change in waveform IMA. The predictor
217 variables were the between time change (post-pre) in ankle, knee strength and their interaction,
218 and the regression coefficients were adjusted for three covariates: 1) change (post-pre) in
219 hopping frequency, 2) side (right vs left); and (3) total number (post + pre) of hopping trials were
220 included in the statistical model. These statistical adjustments were made given that changes in

221 IMA between pre- and post-testing could be due to (1) changes in hopping frequency, (2) limb
222 dominance, and (3) the number of trials used for UCM analysis; and we wish to isolate the
223 estimate of strength gains on IMA changes. Bayesian regression functional analysis was
224 performed in R software (Goldsmith & Kitago 2016). Recent investigations in sports science
225 have advocated the avoidance of frequentist null-hypothesis significance testing, and instead to
226 focus on estimating the probabilities associated with observing an effect size. Fixed effect
227 parameters for ankle and knee strength, frequency, side, trial number, and non-parametric
228 smooth functions (modelled with 15 B-splines) were estimated using a Gibbs sampler with a
229 burn-in of 1000 and drawing 15000 inference samples. The residual covariance structure was
230 estimated using Bayesian functional principle components. A significant effect was defined by a
231 non-zero crossing of the Bayesian 95% credible interval (CrI).

232 **RESULTS**

233 Twenty-five participants had ≥ 20 successful trials (Figure 2). No significant differences in
234 baseline characteristics between participants with and without ≥ 20 successful trials, were
235 detected (Table 1). For the 25 participants with ≥ 20 successful trials, the number of hop trials
236 used for UCM analysis per participant ranged from 20 to 57.

237 Baseline hopping kinematics, IMA, GEV, NGEV are reported in Figure 3 and 4. For the 25
238 participants with ≥ 20 successful trials, the mean (standard deviation) change in hopping
239 frequency was a 0.15 (0.25) Hz increase, and change in stance duration was a 0.01 (0.03) s
240 decrease post-testing, relative to a baseline of 2.24 (0.26) Hz and 0.31 (0.04) s, respectively.

241 For simplicity, only effects at a discrete hop phase within a statistically significant temporal
242 period are reported here. At 10 % hop stance, there was a significant interaction between ankle

243 and knee strength gains, and significant main effect of ankle and knee strength gains (Figure 5).
244 A 1 Nm/kg increase in ankle extensor strength increased IMA by 0.37 (95% CrI 0.14 to 0.59), a
245 1 Nm/kg increase in knee extensor strength decreased IMA by 0.29 (95% CrI 0.08 to 0.51), but
246 increased the effect of ankle strength on IMA by 0.71 (95% CrI 0.10 to 1.33) (Figure 5). At 55%
247 hop stance, a 1 Nm/kg increase in knee extensor strength increase IMA by 0.24 (95% CrI 0.001
248 to 0.48), but reduced the effect of ankle strength on IMA by 0.71 (95% CrI 0.13 to 1.32) (Figure
249 5). At 70 % hop stance, a 1 Nm/kg increase in ankle extensor strength reduced IMA by 0.31
250 (95% CrI 0.06 to 0.58) (Figure 5). At 98 % hop stance, a 1 Nm/kg increase in ankle extensor
251 strength increased IMA by 0.39 (95% CrI 0.05 to 0.73) (Figure 5).

252 **DISCUSSION**

253 Leg length regulation is a strategy of coping with irregular surfaces to minimize disturbance to
254 the COM trajectory during gait (Andrada et al. 2013; Geyer et al. 2006). Normally, leg length
255 regulation is achieved by harnessing segmental kinematic motor abundance (Auyang et al. 2009).
256 Even though resistance training has been typically prescribed to treat gait impairments, there is
257 uncertainty as to the relationship between physiological strength capacity and normal motor
258 abundance. This poses a dilemma as to whether resistance training benefits or harms gait motor
259 control rehabilitation. In this study, we prospectively investigated if lower limb strength gains
260 after resistance training, predicted a change in IMA during a simple model of spring-mass gait -
261 unilateral hopping. In partial agreement with our hypothesis, greater strength gains predicted an
262 increase in IMA, but this effect was dependent on the muscles being strengthened. In addition,
263 the effects of ankle strength gained on IMA was opposite to that of knee strength gains.

264 The increase in kinematic motor abundance with an isolated gain in ankle extensor strength after
265 initial contact and toe-off of hopping, was consistent with the findings of previous resistance
266 training studies of the upper limb (Olafsdottir et al. 2008; Park et al. 2015; Shim et al. 2008). The
267 mechanisms linking strength gains to motor abundance improvements was not investigated in the
268 present study, but may speculatively involve mechanical and neural factors. The bi-articular
269 gastrocnemius is mechanically capable of plantar flexing the foot while flexing the knee
270 (Cleather et al. 2015). Greater gastrocnemius strength could augment inter-segmental kinematic
271 co-variation, increasing motor abundance during hopping. Resistance training has also been
272 shown to increase reciprocal inhibition of antagonistic muscles within a joint muscle pair
273 (Geertsen et al. 2008). However, no studies to the authors' knowledge have directly investigated
274 the influence of resistance training on heteronomous reflex pathways, which would enable inter-
275 muscular co-variation and facilitate hopping kinematic motor abundance.

276 It was previously suggested that greater motor abundance will emerge in tasks with greater
277 relative physical demand (Greve et al. 2017; Greve et al. 2013), which contradicts the present
278 findings. It may be that the relationship between physical demand and motor abundance is non-
279 linear with potentially plateauing effects. Both physiological weakening and strengthening may
280 augment motor abundance depending in part on the task's absolute demand on the participants,
281 and the capacity to use available motor elements. Wang et al. reported that older adults have
282 preserved muscle motor abundance but were more delayed at their recruitment during rapid
283 balance recovery, than younger adults (Wang et al. 2017). The tasks used by Greve and
284 Colleagues were either much slower, or required a combination of low muscular force and fast
285 movement speed (Greve et al. 2017; Greve et al. 2013). It is plausible that the speed-force
286 demands in previous studies were low (Greve et al. 2017; Greve et al. 2013), such that muscle

287 groups had sufficient time to stabilize the performance variable(s). In addition, if a muscle is
288 operating at its physiological limit, it can no longer compensate for the reduction in activation of
289 other muscles. In this instance, co-variation may still occur but only between muscles with
290 adequate physiological strength reserve. The relationship between task demand and motor
291 abundance may be better understood by investigating abundance at the level of muscle
292 activations, including UCM analysis in a reduced subset of motor elements (Toney & Chang
293 2016).

294 The period surrounding mid-stance in hopping is critical of leg length regulation for peak
295 muscular force minimization (Auyang et al. 2009), which minimizes the energy expenditure and
296 joint contact loads during hopping. If knee strength gain occurred in isolation, an increase in
297 motor abundance at 55% stance was observed. However, if strength gains occurred at the ankle
298 and knee, due to the statistical interaction, motor abundance was reduced. The detrimental effect
299 of additional ankle strength gain could be due to the foot segment angle around mid-stance being
300 nearly invariant (Figure 3) (Joao et al. 2014). If the foot functions as a punctum fixum around
301 mid-stance (Joao et al. 2014), the gastrocnemius is only able to flex and extend the thigh
302 segment, without compensatory foot kinematics to stabilize overall leg length. The invariant
303 foot-segment angle may instead shift the joint-level mediator of leg length stabilization to the
304 knee during the period of mid-stance.

305 Greater knee extensor strength reduced motor abundance after initial contact, but augmented the
306 incremental effect ankle strength gain had on abundance for leg length control. It may be that the
307 influence of knee extensor strength gain on motor abundance was shifted to the control of leg
308 orientation (angle between the leg and ground) (Auyang et al. 2009). Leg orientation at initial

309 contact may be critical as it determines the overall position of the force application relative to the
310 COM in stance.

311 The reduction in kinematic motor abundance predicted by an increase in knee extensor strength
312 after initial contact differed from a study investigating walking in individuals with and without
313 knee osteoarthritis (OA) (Tawy et al. 2018). Several reasons could account for the disagreement.
314 Tawy et al. (2018) did not directly quantify the relationship between knee extensor strength and
315 motor abundance. The occurrence of knee OA is associated with a range of neuromuscular
316 deficits (Mills et al. 2013), and the importance of knee extensor strength to motor abundance
317 cannot be ascertained from a between-groups comparison. Second, Tawy et al. (2018) used COM
318 trajectory, while the present study used leg length, as the performance variable for UCM
319 analysis. It must be emphasized that using both the COM and leg length as performance
320 variables are equally valid. The organization of motor control may involve a hierarchical
321 structure (Latash 2010), where segment-level variation serve to stabilize limb-level outcomes,
322 and inter-limb variation stabilizes whole-body outcomes. Thus, the present study focused only on
323 limb-level motor control, while Tawy et al. (2018) performed UCM analysis across two layers of
324 hierarchical control.

325 Several aspects of the present study's methodology need to be discussed in lieu of differences in
326 reported IMA of the present study, with that of a previous work (Auyang et al. 2009). First, the
327 number of hop cycles included in the present study was much lower than the 170 cycled used in
328 Auyang et al. (2009). This may explain the difference in IMA values between studies. Second,
329 leg length was defined starting from the COP in the present study, but from the toe marker in
330 Auyang et al. (2009). COP accuracy may be reduced when the magnitude of the GRF is small,
331 which could explain the differences in IMA between the present study and Auyang et al. (2009)

332 during the periods surrounding initial contact and toe-off. However, the effective leg length
333 during human locomotion may be more accurately defined from the point of ground force
334 application, compared to the fixed toe-marker (Coleman et al. 2012). Despite this difference in
335 leg length definition, the overall shape of the IMA reported in this study was similar to Auyang
336 et al. (2009).

337 Previous studies provided evidence for the benefit of resistance training on finger force motor
338 abundance (Olafsdottir et al. 2008; Park et al. 2015; Shim et al. 2008), and the results of the
339 present study extends the evidence for the same benefit to the lower limb. Findings from the
340 present study carry an optimistic message that strength training may benefit the rehabilitation of
341 gait where movement coordination and strength are impacted upon by the presence of disease
342 (Hashiguchi et al. 2016). By increasing motor abundance to stabilize leg length in hopping,
343 resistance training may increase the adaptability of forward gait patterns over irregular surfaces.
344 It is likely that different gait patterns require different joint-level and limb-level strengthening to
345 benefit kinematic motor abundance, and this should be investigated in future studies. The present
346 study's findings also demonstrate that local strength changes can influence movement
347 coordination across the kinematic chain. Speculatively, this may imply that where strength gains
348 cannot be feasibly achieved using a more functional form of strength training, a more regionally
349 focused form of training (e.g. open-kinetic chain exercises) can still have global functional
350 benefits. Whether different strength training modes differentially influence lower limb motor
351 abundance, remains to be investigated.

352 A limitation of this study was that the analysis predicting motor abundance from alterations in
353 strength gains were analyzed using a prospective, pre-post design. However, we reduced the
354 confounding factor of repeated measurement, by only including the effects of strength changes

355 into the statistical model. A second limitation of this study was that the influence of strength
356 gains on kinematic abundance was analyzed in healthy individuals. This limitation may in fact be
357 a strength, as we were able to isolate the investigation of IMA changes to strength changes.

358 **CONCLUSIONS**

359 In addition to the well-known effects on a muscle's neural, architectural, and mechanical
360 properties, resistance training also influences the coordination of multiple motor elements in the
361 control of a well-defined motor performance objective. The benefits of strength gain on motor
362 abundance was dependent on the site of muscle strengthened and the phase of gait. The role of
363 resistance training on motor abundance should be investigated in patient cohorts, other gait
364 patterns, as well as its translation into functional improvements.

365 **ACKNOWLEDGEMENTS.**

366 The authors of this study would like to thank Nour Faiz Aqil Yacob, Jason Hu, Nicholas
367 Callaghan, Tess Moynihan, Hannah Watt, and Giorgia Alford for delivering the interventions.
368 The results of this study are presented clearly, honestly, and without fabrication, falsification, or
369 inappropriate data manipulation.

370 **References**

- 371 Andrada E, Nyakatura JA, Bergmann F, and Blickhan R. 2013. Adjustments of global and local
372 hindlimb properties during terrestrial locomotion of the common quail (*Coturnix*
373 *coturnix*). *The Journal of Experimental Biology* 216:3906-3916.
374 10.1242/jeb.085399
- 375 Auyang AG, Yen JT, and Chang YH. 2009. Neuromechanical stabilization of leg length and
376 orientation through interjoint compensation during human hopping. *Experimental Brain*
377 *Research* 192:253-264. 10.1007/s00221-008-1582-7

- 378 Beerse M, and Wu J. 2016. Vertical stiffness and center-of-mass movement in children and
379 adults during single-leg hopping. *Journal of Biomechanics* 49:3306-3312.
380 <http://dx.doi.org/10.1016/j.jbiomech.2016.08.014>
- 381 Bell AL, Brand RA, and Pedersen DR. 1989. Prediction of hip joint centre location from external
382 landmarks. *Human Movement Science* 8:3-16. [http://dx.doi.org/10.1016/0167-](http://dx.doi.org/10.1016/0167-9457(89)90020-1)
383 [9457\(89\)90020-1](http://dx.doi.org/10.1016/0167-9457(89)90020-1)
- 384 Cleather DJ, Southgate DFL, and Bull AMJ. 2015. The role of the biarticular hamstrings and
385 gastrocnemius muscles in closed chain lower limb extension. *Journal of Theoretical*
386 *Biology* 365:217-225. <https://doi.org/10.1016/j.jtbi.2014.10.020>
- 387 Coleman DR, Cannavan D, Horne S, and Blazevich AJ. 2012. Leg stiffness in human running:
388 Comparison of estimates derived from previously published models to direct kinematic-
389 kinetic measures. *Journal of Biomechanics* 45:1987-1991.
390 10.1016/j.jbiomech.2012.05.010
- 391 Geertsen SS, Lundbye-Jensen J, and Nielsen JB. 2008. Increased central facilitation of antagonist
392 reciprocal inhibition at the onset of dorsiflexion following explosive strength training.
393 *Journal of applied physiology (Bethesda, Md : 1985)* 105:915-922.
394 10.1152/jappphysiol.01155.2007
- 395 Geyer H, Seyfarth A, and Blickhan R. 2006. Compliant leg behaviour explains basic dynamics of
396 walking and running. *Proceedings of the Royal Society of London Series B - Biological*
397 *Sciences* 273:2861-2867. 10.1098/rspb.2006.3637
- 398 Goldsmith J, and Kitago T. 2016. Assessing systematic effects of stroke on motorcontrol by
399 using hierarchical function-on-scalar regression. *Journal of the Royal Statistical Society*
400 *Series C, Applied statistics* 65:215-236. 10.1111/rssc.12115

- 401 Greve C, Hortobagyi T, and Bongers RM. 2017. Old adults preserve motor flexibility during
402 rapid reaching. *European Journal of Applied Physiology* 117:955-967. 10.1007/s00421-
403 017-3584-2
- 404 Greve C, Zijlstra W, Hortobagyi T, and Bongers RM. 2013. Not all is lost: old adults retain
405 flexibility in motor behaviour during sit-to-stand. *PLoS ONE [Electronic Resource]*
406 8:e77760. 10.1371/journal.pone.0077760
- 407 Hashiguchi Y, Ohata K, Kitatani R, Yamakami N, Sakuma K, Osako S, Aga Y, Watanabe A, and
408 Yamada S. 2016. Merging and Fractionation of Muscle Synergy Indicate the Recovery
409 Process in Patients with Hemiplegia: The First Study of Patients after Subacute Stroke.
410 *Neural Plasticity* 2016:5282957. 10.1155/2016/5282957
- 411 Joao F, Veloso A, Cabral S, Moniz-Pereira V, and Kepple T. 2014. Synergistic interaction
412 between ankle and knee during hopping revealed through induced acceleration analysis.
413 *Human Movement Science* 33:312-320. 10.1016/j.humov.2013.10.004
- 414 Knapik JJ, Harman EA, Steelman RA, and Graham BS. 2012. A systematic review of the effects
415 of physical training on load carriage performance. *Journal of Strength & Conditioning*
416 *Research* 26:585-597. 10.1519/JSC.0b013e3182429853
- 417 Latash ML. 2010. Motor Synergies and the Equilibrium-Point Hypothesis. *Motor Control*
418 14:294-322.
- 419 Latash ML, Levin MF, Scholz JP, and Schöner G. 2010. Motor Control Theories and Their
420 Applications. *Medicina (Kaunas)* 46:382-392.
- 421 Lee DC, Pate RR, Lavie CJ, Sui X, Church TS, and Blair SN. 2014. Leisure-time running
422 reduces all-cause and cardiovascular mortality risk. *Journal of the American College of*
423 *Cardiology* 64:472-481. 10.1016/j.jacc.2014.04.058

- 424 Liew B, Morris S, and Netto K. 2017. The biomechanics of running with load PhD. Curtin
425 University; .
- 426 Liew BX, Morris S, and Netto K. 2016a. Joint power and kinematics coordination in load
427 carriage running: Implications for performance and injury. *Gait & Posture* 47:74-79.
- 428 Liew BX, Morris S, Robinson MA, and Netto K. 2016b. Performance of a lateral pelvic cluster
429 technical system in evaluating running kinematics. *Journal of Biomechanics*.
430 10.1016/j.jbiomech.2016.05.010
- 431 Mills K, Hunt MA, Leigh R, and Ferber R. 2013. A systematic review and meta-analysis of
432 lower limb neuromuscular alterations associated with knee osteoarthritis during level
433 walking. *Clin Biomech (Bristol, Avon)* 28:713-724. 10.1016/j.clinbiomech.2013.07.008
- 434 Moritz CT, and Farley CT. 2003. Human hopping on damped surfaces: strategies for adjusting
435 leg mechanics. *Proceedings of the Royal Society of London Series B - Biological Sciences*
436 270:1741-1746. 10.1098/rspb.2003.2435
- 437 Olafsdottir HB, Zatsiorsky VM, and Latash ML. 2008. The effects of strength training on finger
438 strength and hand dexterity in healthy elderly individuals. *Journal of applied physiology*
439 (*Bethesda, Md : 1985*) 105:1166-1178. 10.1152/jappphysiol.00054.2008
- 440 Papa EV, Dong X, and Hassan M. 2017. Resistance training for activity limitations in older
441 adults with skeletal muscle function deficits: a systematic review. *Clinical interventions*
442 *in aging* 12:955-961. 10.2147/cia.s104674
- 443 Park J, Han D-W, and Shim JK. 2015. Effect of Resistance Training of the Wrist Joint Muscles
444 on Multi-Digit Coordination. *Perceptual and Motor Skills* 120:816-840.
445 10.2466/25.26.PMS.120v16x9
- 446 Qu X. 2012. Uncontrolled manifold analysis of gait variability: effects of load carriage and
447 fatigue. *Gait Posture* 36:325-329. 10.1016/j.gaitpost.2012.03.004

- 448 Shim JK, Hsu J, Karol S, and Hurley BF. 2008. Strength training increases training-specific
449 multifinger coordination in humans. *Motor Control* 12:311-329.
- 450 Silder A, Besier T, and Delp SL. 2015. Running with a load increases leg stiffness. *Journal of*
451 *Biomechanics* 48:1003-1008. 10.1016/j.jbiomech.2015.01.051
- 452 Smith JA, Popovich JM, Jr., and Kulig K. 2014. The influence of hip strength on lower-limb,
453 pelvis, and trunk kinematics and coordination patterns during walking and hopping in
454 healthy women. *Journal of Orthopaedic & Sports Physical Therapy* 44:525-531.
455 10.2519/jospt.2014.5028
- 456 Tawy GF, Rowe P, and Biant L. 2018. Gait variability and motor control in patients with knee
457 osteoarthritis as measured by the uncontrolled manifold technique. *Gait & Posture*
458 59:272-277. <https://doi.org/10.1016/j.gaitpost.2017.08.015>
- 459 Toney ME, and Chang YH. 2016. The motor and the brake of the trailing leg in human walking:
460 leg force control through ankle modulation and knee covariance. *Experimental Brain*
461 *Research* 234:3011-3023. 10.1007/s00221-016-4703-8
- 462 Wang Y, Watanabe K, and Asaka T. 2017. Aging effect on muscle synergies in stepping forth
463 during a forward perturbation. *European Journal of Applied Physiology* 117:201-211.
464 10.1007/s00421-016-3514-8
- 465 Yen JT, and Chang YH. 2010. Rate-dependent control strategies stabilize limb forces during
466 human locomotion. *Journal of the Royal Society, Interface* 7:801-810.
467 10.1098/rsif.2009.0296
- 468

Figure 1

Planar kinematic model

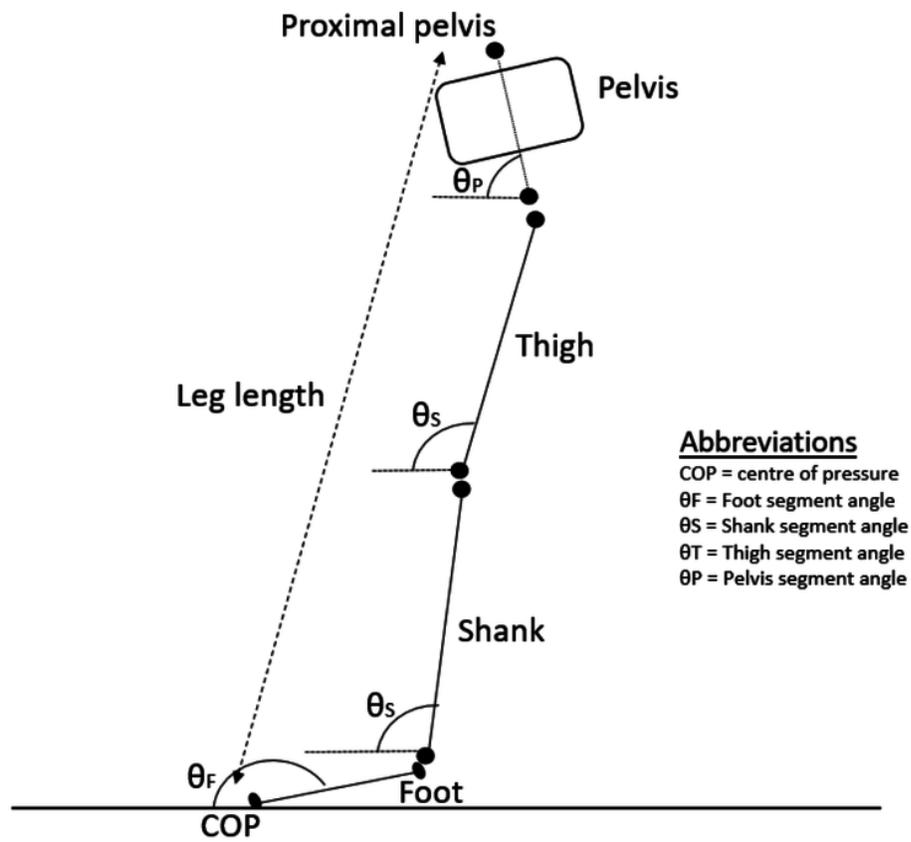


Figure 2 (on next page)

CONSORT Diagram

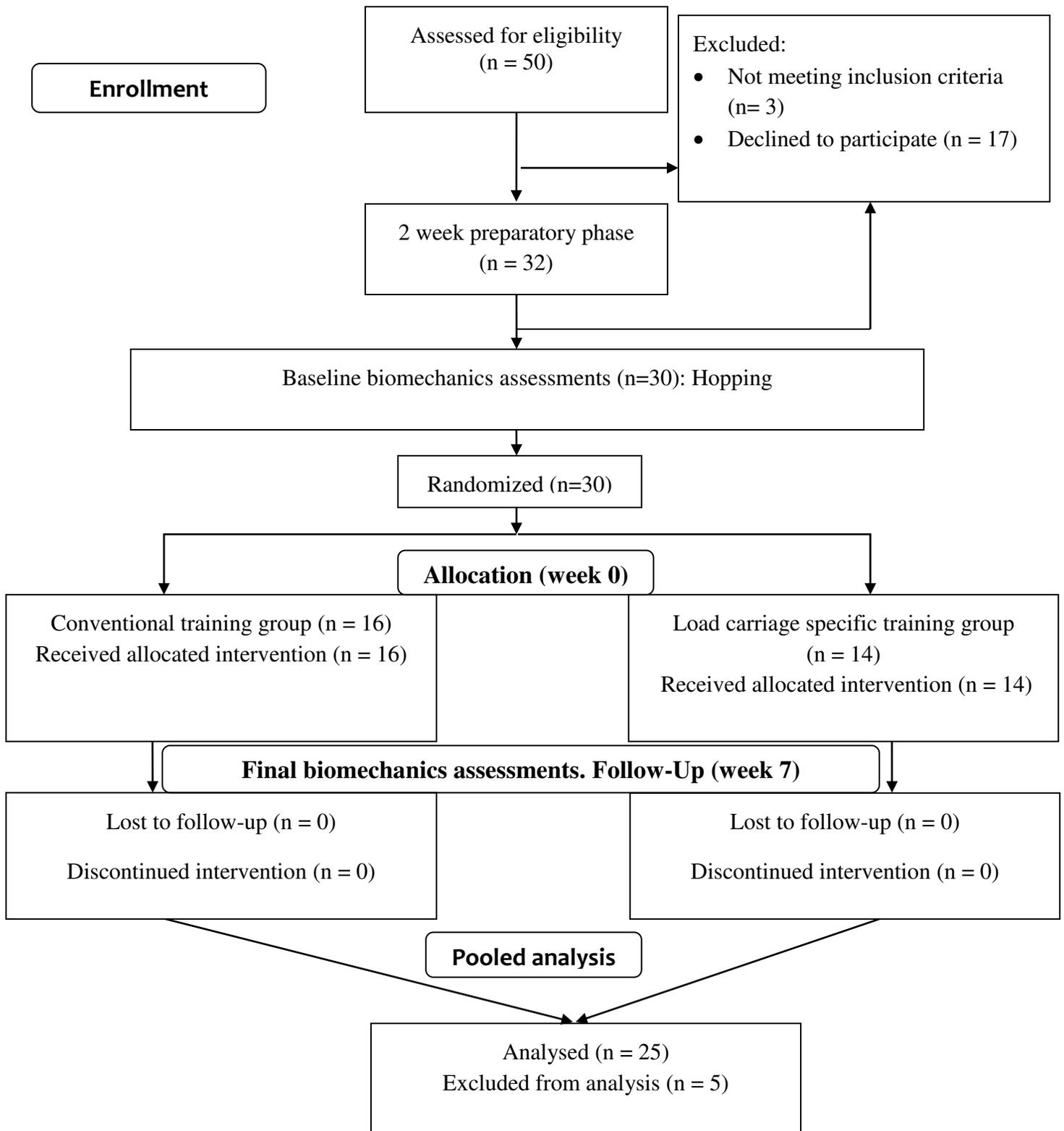


Figure 3

Baseline mean (standard deviation as error clouds) of leg length and segment angles

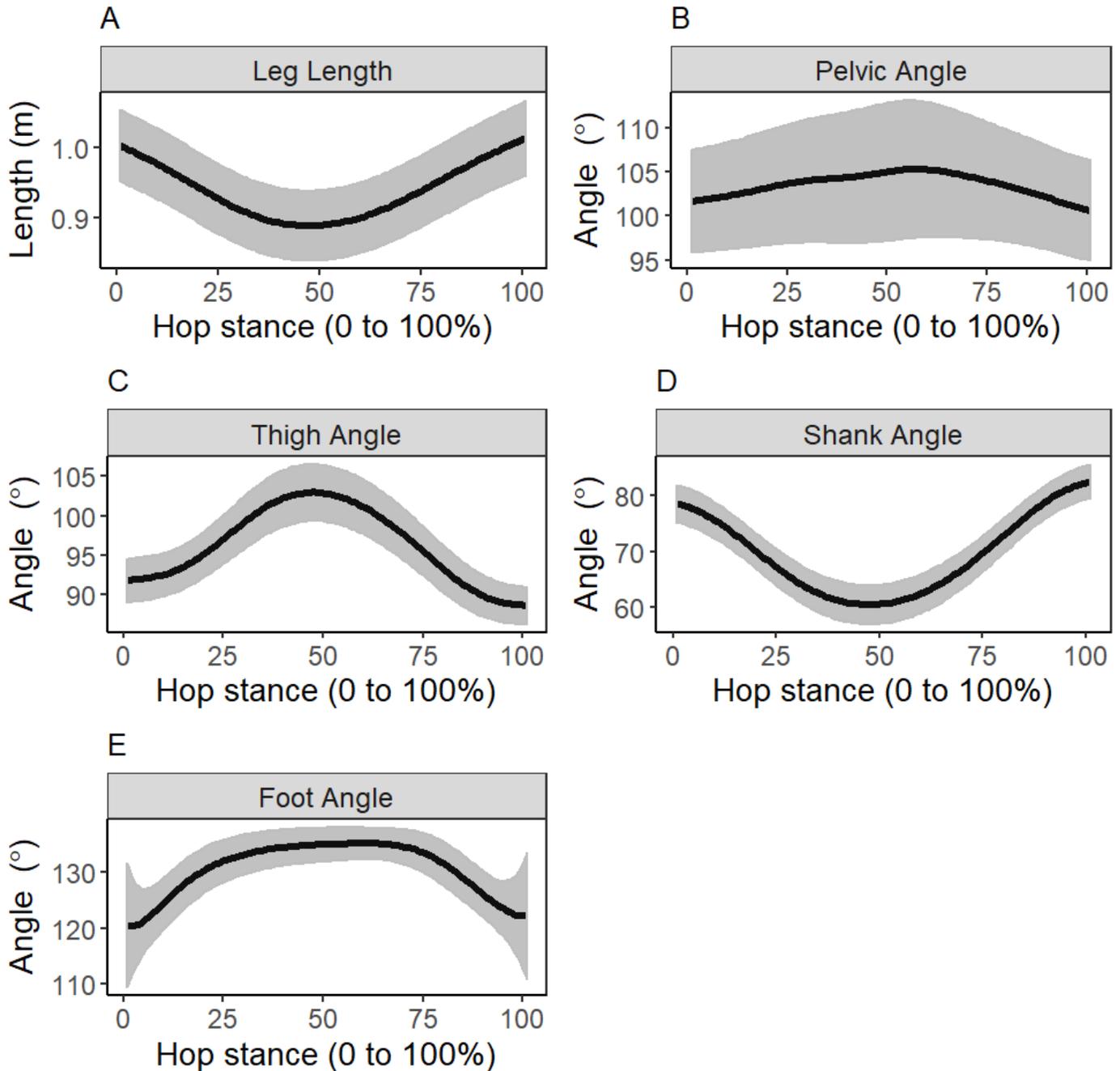


Figure 4

Baseline mean (standard deviation as error clouds) of Index of Motor Abundance (IMA), Non-Goal Equivalent Variance (NGEV) and Goal Equivalent Variance (GEV)

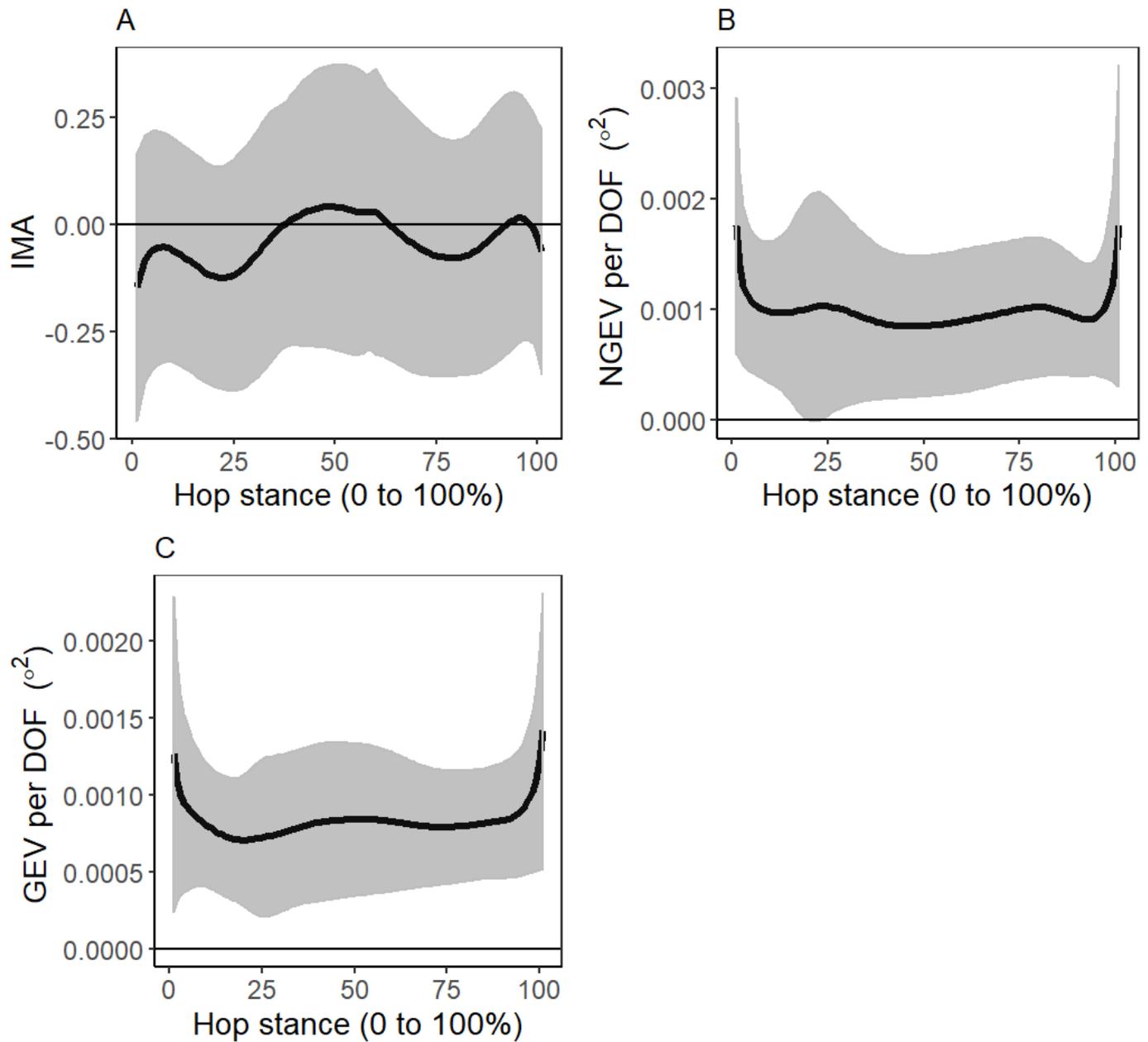


Figure 5

Mean (95% Credible Interval as error clouds) of beta coefficient of 1 Nm/kg increase in ankle extensor strength (A) and knee extensor strength (B), and its interaction (C).

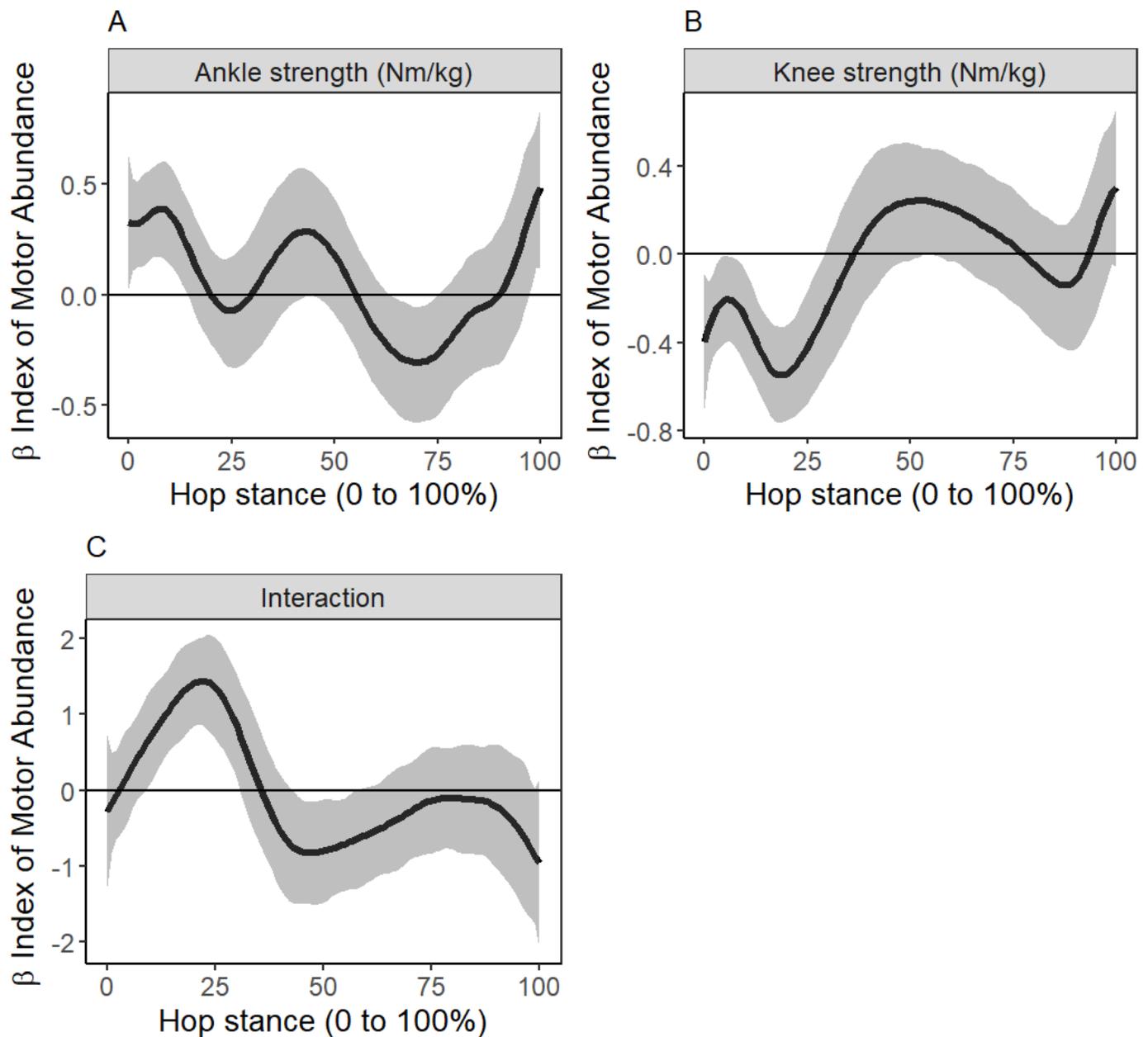


Table 1 (on next page)

Baseline characteristics of participants

1 Table 1

	≥ 20 hop trials for UCM (n = 25)	< 20 hop trials for UCM (n = 5)	p value
Age (years)	30.5 (9.7)	28.6 (6.5)	0.684
Body mass (kg)	67.1 (12.2)	74.9 (11.1)	0.196
Height (cm)	171.3 (7.6)	176.1 (7.5)	0.210
Running frequency over past 6 weeks (times/week)	2.7 (1.4)	2.2 (1.3)	0.423
Running distance over past 6 weeks (km/week)	16.8 (18.8)	15.2 (10.1)	0.852
Ankle strength (Nm/kg)	1.07 (0.19)	1.07 (0.24)	0.978
Knee strength (Nm/kg)	2.05 (0.39)	2.09 (0.42)	0.786

2