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Raphaël Hamard, François Hug, Nicole Kelp, Romain Feigean, Jeroen Aeles, et al.. Inclusion of image-based in vivo experimental data into the Hill-type muscle model affects the estimation of individual force-sharing strategies during walking.. *Journal of Biomechanics*, 2022, 135, pp.111033. 10.1016/j.jbiomech.2022.111033 . hal-03618632

HAL Id: hal-03618632

<https://hal.science/hal-03618632>

Submitted on 22 Jul 2024

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1 **Inclusion of image-based *in-vivo* experimental data into the Hill-type muscle model**
2 **affects the estimation of individual force-sharing strategies during walking**

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13 **Keywords:** B-mode ultrasound, Electromyography, Gastrocnemius, MRI, Muscle
14 coordination

15 **Word count:** 3494

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24 **ABSTRACT**

25 The study of muscle coordination requires knowledge of the force produced by individual
26 muscles, which can be estimated using Hill-type models. Predicted forces from Hill-type
27 models are sensitive to the muscle's maximal force-generating capacity (F_{\max}), however, to
28 our knowledge, no study has investigated the effect of different F_{\max} personalization methods
29 on predicted muscle forces. The aim of this study was to determine the influence of two
30 personalization methods on predicted force-sharing strategies between the human
31 gastrocnemii during walking. Twelve participants performed a walking protocol where we
32 estimated muscle activation using surface electromyography and fascicle length, velocity, and
33 pennation angle using B-mode ultrasound to inform the Hill-type model. F_{\max} was determined
34 using either a scaling method or experimental method. The scaling method used
35 anthropometric scaling to determine both muscle volume and fiber length, which were used to
36 estimate the F_{\max} of the gastrocnemius medialis and lateralis. The experimental method used
37 muscle volume and fascicle length obtained from magnetic resonance imaging and diffusion
38 tensor imaging, respectively. We found that the scaling and the experimental method
39 predicted similar gastrocnemii force-sharing strategies at the group level (mean over the
40 participants). However, substantial differences between methods in predicted force-sharing
41 strategies was apparent for some participants revealing the limited ability of the scaling
42 method to predict force-sharing strategies at the level of individual participants. Further
43 personalization of muscle models using *in vivo* experimental data from imaging techniques is
44 therefore likely important when using force predictions to inform the diagnosis and
45 management of neurological and orthopedic conditions.

46 1. INTRODUCTION

47 Knowledge of the forces that individual muscles produce provides important insights into
48 muscle coordination, and this information can be used to improve the diagnosis and
49 management of many neurological and orthopedic conditions (Hug and Tucker, 2017).
50 However, directly measuring human muscle force requires highly invasive techniques (Finni
51 et al., 1998; Gregor et al., 1987; Komi, 1990), which are not feasible in clinical environments
52 and remain limited in most research settings. To overcome this limitation, muscle models for
53 predicting muscle forces have been developed.

54 The Hill-type model is the most ubiquitous muscle model in biomechanics (Eq. 1; Zajac,
55 1989). It takes into account most of the known determinants of muscle force, i.e. the
56 activation, the instantaneous length and velocity of the contracting muscle fibers, and the
57 maximal force-generating capacity (F_{\max}). The Hill-type model can be personalized with
58 subject-specific data, such as time-varying muscle activation assessed using surface
59 electromyography (EMG) (Perreault et al., 2003) or time-varying fascicle length, fascicle
60 velocity, and pennation angle recorded using ultrasound imaging (Dick et al., 2017). An
61 important determinant of muscle force is F_{\max} (Bujalski et al., 2018; Scovil and Ronsky,
62 2006), for which the vast majority of studies rely on scaled data using different methods. For
63 example, muscle volume, a determinant of F_{\max} , has been personalized through values scaled
64 to the participant's body mass (Dick et al., 2017). Furthermore, optimal muscle fiber length,
65 which is another determinant of F_{\max} , is often scaled from generic musculoskeletal models
66 (Millard et al., 2013). An important limitation of these approaches is that they use the same
67 underlying equations to scale all individuals. This conceals the well-described inter-individual
68 variability in the distribution of F_{\max} across muscles (Crouzier et al., 2018; Hug et al., 2015).

69 The aim of this study was to compare two different personalization methods of a Hill-type
70 model to predict human gastrocnemii forces during level and incline walking. The first
71 personalization method, herein referred to as the “scaling method”, used anthropometric
72 scaling to determine both muscle volume and muscle fiber length to estimate F_{\max} of the
73 gastrocnemius medialis (GM) and lateralis (GL). The second method, named hereafter the
74 “experimental method”, used muscle volume and fascicle length obtained from magnetic
75 resonance imaging (MRI) and diffusion tensor imaging (DTI), respectively. We specifically
76 investigated the force-sharing strategy between the two gastrocnemii muscles. Because the
77 scaling method inevitably conceals interindividual variability in the distribution of F_{\max}

78 between the GM and GL, we expected to observe substantial differences between methods
79 when comparing the gastrocnemii force-sharing strategy at the individual level. However, we
80 hypothesized that the two methods would predict similar force-sharing strategies at the group
81 level.

82 **2. MATERIALS AND METHODS**

83 **2.1. Participants**

84 Twelve adults with no recent (< 6 months) lower limb pain or injury gave informed written
85 consent to participate in the study (5 females, 7 males, age: 25 ± 3.5 years, body mass: $75.4 \pm$
86 16.4 kg, height: 1.71 ± 0.10 m; mean \pm standard deviation). This study was approved by the
87 institutional ethics review committee at The University of Queensland (#2013001448).

88 **2.2. Experimental data acquisition**

89 Data were collected over two experimental sessions. The first session consisted of two
90 consecutive scanning sequences of the participant's dominant leg: a T1-weighted MRI scan to
91 determine muscle volume, and a DTI scan to determine muscle fascicle lengths.

92 For the second session, participants walked on a treadmill (Nautilus Trimline T345, TX,
93 USA) at their preferred walking speed (1.1 ± 0.1 m.s⁻¹), which was determined at the
94 beginning of the protocol (Dal et al., 2010). During walking, we recorded surface EMG and
95 B-mode ultrasound of the GM and GL of the dominant leg to measure muscle activation and
96 fascicle behavior, respectively. Foot position was measured using motion capture to identify
97 phases of the gait cycle. Participants walked under two conditions presented in a randomized
98 order: (i) 0% treadmill grade (level walking) and (ii) 10% treadmill grade (incline walking).
99 They performed two trials at each walking condition and repeated each condition a second
100 time, first to record EMG and second to measure fascicle behavior. The EMG and the
101 ultrasound recordings were conducted in separate trials to ensure that the measures were taken
102 on the same mid-region of the muscle belly. Participants also performed three isometric
103 plantar flexion maximal voluntary contractions (MVCs), with 120 s rest between contractions,
104 to determine maximal GM and GL EMG amplitude for EMG normalization. The EMG and
105 ultrasound data have been published elsewhere (Hamard et al., 2021).

106 **2.2.1. *MRI***

107 Participants were placed in a 3T MRI scanner (Magnetom Prisma, Siemens, Germany) in a
108 supine position. The dominant foot was secured into a custom-built MRI-compatible foot
109 plate with the hip extended and the ankle positioned in a 90° angle. The dominant knee was
110 positioned in slight flexion (< 5°) by using a foam wedge under the knee. Details on the MRI
111 parameters have been described elsewhere (Pinel et al., 2021). The T1-weighted MRI images
112 were analyzed using a combination of semi-automated (Sashimi V1.1; Bolsterlee, 2020) and

113 manual segmentation software (ITK-SNAP v3.8.0, NIH, USA). We calculated total muscle
114 volume for the GM and GL as the sum of the volume of all voxels in each muscle (ITK-
115 SNAP v3.8.0, NIH, USA). These muscle volumes were included in the Hill-type model (see
116 2.3) for the experimental method.

117 **2.2.2. DTI**

118 DTI scans were performed with the same scanner as for the MRI. Detailed information on the
119 DTI parameters, processing and data analyses has been described elsewhere (Aeles et al.,
120 2021). Briefly, the muscle was divided into smaller muscle regions in the local muscle frontal
121 plane. Then, fascicles were assigned to the muscle region that contained the fascicle midpoint
122 and the median muscle fascicle length was calculated for each region. Finally, the mean of all
123 muscle regions was calculated and used as an input for optimal fiber length.

124 **2.2.3. 3D motion capture**

125 3D motion capture (Flex 13, OptiTrack, Corvallis, OR, USA) was used to record a static
126 calibration trial with 8 marker clusters and 16 individual markers placed bilaterally on the
127 lower limbs and pelvis to scale a musculoskeletal model (Rajagopal et al., 2016) for each
128 participant (OpenSim v3.3). Then, during the walking protocol, we used the markers attached
129 bilaterally to the calcaneus and the fifth metatarsophalangeal joint to determine the timing of
130 the heel-strike and toe-off events using custom-written scripts based on foot vertical velocity
131 (O'Connor et al., 2007). Motion capture data were collected at 120 Hz (Motive, OptiTrack,
132 Corvallis, OR, USA) and raw marker positions were filtered using a second-order low-pass
133 Butterworth filter with a cut-off frequency of 10 Hz.

134 **2.2.4. Electromyography**

135 We shaved, abraded and cleaned the participant's skin with alcohol to reduce the skin-
136 electrode impedance. We placed surface electrodes (Trigno Delsys Inc., Natick, USA; 10 mm
137 inter-electrode distance) over the GM and GL muscle bellies, aligned along the direction of
138 the muscle fascicles, determined using B-mode ultrasound. The EMG signals were amplified,
139 digitized at 2048 Hz, band-pass filtered (20-500 Hz), and recorded in Spike2 (V7, CED Ltd,
140 Cambridge, UK). During post-processing, the MVC and walking EMG signals were band-
141 pass filtered using a second-order Butterworth filter (20-500 Hz), rectified, and low-pass
142 filtered at 12 Hz. The maximal value of the EMG signal measured during the MVC trials was
143 considered as the maximal EMG amplitude (EMG_{max}). Then, the EMG signals from 15 gait

144 cycles were normalized to EMG_{max} . Finally, we interpolated the data from each gait cycle to
 145 100 data points. We averaged all the cycles within a trial and then we averaged the resulting
 146 two mean cycles from each trial to finally obtain a single mean cycle for each condition and
 147 participant.

148 **2.2.5. B-mode ultrasound**

149 To image the GM and GL during walking, we placed two linear ultrasound probes (5-8 MHz,
 150 60 mm field-of-view, LV8-5L60N-2, ArtUS, Telemed, Vilnius, Lithuania) on the same
 151 location as used for the EMG electrodes. The probe orientation was optimized to be aligned in
 152 the fascicle plane and secured with elastic bandages. Ultrasound data were recorded at 120 Hz
 153 for 15 s of walking. Post data collection, we analyzed five gait cycles of ultrasound data per
 154 trial using a validated (Cronin et al., 2011; Gillett et al., 2013) semi-automated tracking
 155 algorithm (UltraTrack; Farris and Lichtwark, 2016), combined with manual corrections (for
 156 details, see Hamard et al., 2021). Ultrasound data were low-pass filtered at 12 Hz and fascicle
 157 velocity was calculated as the first time derivative of fascicle length. We normalized fascicle
 158 length to the mean fascicle length at heel-strike during level walking (L_{HS} ; average group
 159 value: 56.6 ± 8.0 mm and 65.4 ± 10.1 mm for the GM and GL, respectively). Similarly,
 160 fascicle velocity was expressed as the normalized fascicle length per second. Ultrasound data
 161 from each gait cycle were interpolated to 100 data points and we averaged the cycles within a
 162 trial and then between both trials to create a mean cycle for each condition and participant.

163 **2.3. Estimation of time-varying muscle force during walking**

164 We estimated the time-varying forces produced by the GM and GL muscles during walking
 165 using a Hill-type model (Zajac, 1989):

$$166 \quad F_m = F_{max}[\hat{a}(t)\hat{F}_a(\hat{l}_f)\hat{F}_a(\hat{v}) + \hat{F}_p(\hat{l}_f)]\cos\beta. \quad (1)$$

167 The muscle force F_m (N) was calculated from the maximal force-generating capacity F_{max} ,
 168 expressed in N, the time-varying normalized activation $\hat{a}(t)$, the normalized active ($\hat{F}_a(\hat{l}_f)$)
 169 and passive ($\hat{F}_p(\hat{l}_f)$) forces as determined from the force-length relationship, the normalized
 170 force $\hat{F}_a(\hat{v})$ as determined from the force-velocity relationship and the cosine of the time-
 171 varying pennation angle β ($^\circ$).

172 The normalized active force-length curve (Otten, 1987), was modelled as:

173
$$\hat{F}_a(\hat{l}_f) = e^{-\left(\frac{\hat{l}_f^{0.6}-1}{0.3}\right)^{2.3}}. \quad (2)$$

174 The normalized passive force-length curve (Otten, 1987) was modelled as:

175
$$\hat{F}_p = 2.64\hat{l}_f^2 - 5.30\hat{l}_f + 2.66 \quad \text{for} \quad \hat{l}_f > 1, \quad (3)$$

176
$$\hat{F}_p(\hat{l}_f) = 0 \quad \text{for} \quad \hat{l}_f \leq 1, \quad (4)$$

177 Where \hat{l}_f is the time-varying normalized fascicle length measured during walking.

178 The normalized force-velocity curve was modelled as:

179
$$\hat{F}_a(\hat{v}) = \frac{1+\left(\frac{\hat{v}}{\hat{v}_0}\right)}{1-\left(\frac{\hat{v}}{\hat{v}_0}\right)} \quad \text{for} \quad \hat{v} \leq 0, \quad (5)$$

180
$$\hat{F}_a(\hat{v}) = 1.5 - 0.5 \frac{1-\left(\frac{\hat{v}}{\hat{v}_0}\right)}{1+\left(\frac{7.56\hat{v}}{\hat{v}_0}\right)} \quad \text{for} \quad \hat{v} > 0, \quad (6)$$

181 Where \hat{v} is the time-varying normalized fascicle velocity recorded during walking. α
 182 describes the curvature of the force velocity relationship and v_0 is the maximum unloaded
 183 shortening velocity. We used intermediate values accounting for slow and fast muscle fibers
 184 from numerous terrestrial species of 0.235 and -7.5 s^{-1} for α and \hat{v}_0 , respectively (Wakeling
 185 et al., 2012).

186 Finally, F_{\max} is a function of the muscle's volume Vol , the optimal fiber length $l_{f,\text{opt}}$ and the
 187 maximum isometric stress of a muscle fiber σ_0 .

188
$$F_{\max} = \left(\frac{Vol}{l_{f,\text{opt}}}\right) \sigma_0. \quad (7)$$

189 σ_0 was estimated from the literature (22.5 N.cm⁻², Powell et al., 1984; Roy et al., 1982;
 190 Spector et al., 1980). For the scaling method, $l_{f,\text{opt}}$ was estimated from a subject-specific
 191 musculoskeletal model (Delp et al., 2007; Rajagopal et al., 2016). This 37 degrees of freedom
 192 model with 97 muscle-tendon complex actuators was scaled to the individual anthropometry
 193 of the participants based on the mass of the participant and markers positions recorded during
 194 the static trial. For the scaling method, muscle volume was calculated using the regression
 195 equations from Handsfield et al. (2014):

196
$$Vol = b1 \times BM + b2 \quad (8)$$

197 Where Vol (cm^3) is a function of body mass, BM (kg) and two coefficients b_1 and b_2 .
198 Coefficient b_1 is 3.41 and 2.19 for the GM and GL, respectively, and b_2 is 12.60 and -7.59
199 for GM and GL, respectively (Handsfield et al., 2014). Concerning the experimental method,
200 we used, as a substitute for the $l_{f,opt}$, the mean muscle fascicle length estimated from DTI and
201 we used the muscle volume measured from MRI for the GM and GL.

202 **2.4. Statistics**

203 We conducted the statistical analyses in Statistica v8.0 (Statsoft, Tulsa, OK, USA). All data
204 passed the Kolmogorov-Smirnov test for normality. First, we compared the muscle volume,
205 fascicle length and F_{max} between the two methods and the two muscles using 2-way repeated-
206 measures ANOVAs (factor: method [scaling, experimental], muscle [GM, GL]). Additionally,
207 the GM/(GM+GL) ratios of muscle volume, fascicle length and F_{max} were calculated and we
208 used paired t-tests to determine whether these ratios differed between the two methods. We
209 also assessed the relationship between the two estimation methods for muscle volume,
210 fascicle length and F_{max} using Pearson's correlation coefficient. Finally, we used the root
211 mean square error (RMSE) to determine the discrepancy between methods for muscle volume,
212 fascicle length and F_{max} .

213 From the predicted force output, we extracted the peak force, corresponding to the maximal
214 force value during the gait cycle and the force integral, corresponding to the integral of the
215 time-varying force. To test our first hypothesis, we used 3-way repeated-measures ANOVAs
216 (factor: method [scaling, experimental], muscle [GM, GL] and condition [level, incline]) to
217 determine whether the peak force or the force integral systematically differed between
218 methods, muscles or conditions. Then, the GM/(GM+GL) ratios for peak force and force
219 integral were calculated to estimate the force-sharing strategy between the gastrocnemii. We
220 performed 2-way repeated-measures ANOVAs (factor: method [scaling, experimental] and
221 condition [level, incline]) on these ratios to assess whether they systematically differed
222 between methods and between conditions. Finally, we compared the peak force and force
223 integral between the two methods using the RMSE. For all tests, the level of significance was
224 set at $P < 0.05$.

225 3. RESULTS

226 3.1. Maximal force-generating capacity

227 Fig. 1 depicts the results for volume, fascicle length and F_{\max} . This paragraph, however,
228 presents only the results for F_{\max} as they are more closely related to our aim. There was a
229 main effect of muscle ($P < 0.001$) on F_{\max} , with no main effect of method ($P = 0.744$), nor a
230 muscle \times method interaction ($P = 0.265$). Specifically, the GM had a larger F_{\max} (1072 ± 240
231 N) than the GL (587 ± 166 N) regardless of the method. Moreover, the correlation between
232 F_{\max} estimated from the scaling method and F_{\max} estimated from experimental data was strong
233 for both the GM ($R = 0.871$; $P < 0.001$) and the GL ($R = 0.739$; $P = 0.006$). Even though there was
234 no statistical difference in the GM/(GM+GL) ratio of F_{\max} between the methods ($66.5 \pm 0.5\%$
235 for the scaling method and $63.0 \pm 5.6\%$ for the experimental method; $P = 0.056$), inspection of
236 individual data indicated large differences between methods for some participants, with the
237 difference being up to 12.5% (Fig. 1). We found high RMSE values between methods for the
238 F_{\max} , i.e. 186 N for the GM and 160 N for the GL corresponding to 18.1% and 26.3% of the
239 average F_{\max} , respectively. Moreover, a discrepancy between calculation methods for F_{\max}
240 was also observed for the GM/(GM+GL) ratios as indicated by a RMSE of 6.5%.

241 3.2. Force output

242 When considering the peak force, which occurred during the stance phase (Fig. 2), there was a
243 main effect of muscle ($P < 0.001$) and condition ($P = 0.001$), with no main effect of method
244 ($P = 0.513$), nor any interaction (all $P \geq 0.303$) (Table 1). Similarly, when considering the force
245 integral calculated over the whole gait cycle, we observed a main effect of muscle ($P < 0.001$)
246 and condition ($P = 0.003$), with no main effect of method ($P = 0.557$), nor any interaction (all
247 $P \geq 0.333$). Overall, the GM produced more force compared to the GL during walking ($+170 \pm$
248 96% and $+159 \pm 100\%$ for peak force and force integral, respectively), regardless of the
249 method. In addition, higher peak force ($+34 \pm 18\%$) and force integral ($+27 \pm 14\%$) were
250 predicted during incline walking compared to level walking, regardless of the muscle and
251 method.

252 When considering the peak force ratio (i.e. the force-sharing strategy between muscles), there
253 was a main effect of condition ($P = 0.046$), with no main effect of method ($P = 0.163$) or a
254 method \times condition interaction ($P = 0.984$). Specifically, the ratio of peak force was lower
255 (closer to 50%) during incline walking compared to level walking (Table 2). When

256 considering the ratio of the force integral, there was no main effect of method ($P=0.137$), nor
257 an effect of condition ($P=0.071$) or a method \times condition interaction ($P=0.971$).

258 Even though the group data did not exhibit significant differences between methods,
259 inspection of Fig. 2 and 3 revealed noteworthy differences between methods for some
260 participants. The difference in model-predicted forces between the methods was greater than
261 30% for four participants for GM and for three participants for GL during level walking.
262 When considering the ratios (i.e. the force-sharing strategy between muscles), similar
263 observations were made, i.e. despite the between-methods difference being lower than 1% in
264 four participants for both peak force and force integral, the between-methods difference was
265 substantial (greater than 6%) for four participants. These individual differences led to
266 relatively high RMSE group values. When considering the peak force during level walking,
267 the RMSE between the two methods was 66 N for the GM and 28 N for the GL
268 corresponding to 19.0% and 22.1% of the group-averaged peak force, respectively. We also
269 found high RMSE values for the force integral, i.e. 20 N.s for the GM and 12 N.s for the GL
270 corresponding to 18.0% and 25.9% of the average force integral, respectively. Moreover,
271 discrepancy between methods was also observed for the GM/(GM+GL) ratios of peak force
272 and force integral. The RMSE between methods was 5.4% for peak force and 5.7% for the
273 force integral in level walking.

274 4. DISCUSSION

275 We determined the influence of two different personalization methods on a Hill-type model's
276 predicted force-sharing strategy between the gastrocnemii during walking. We found
277 substantial differences between the scaling method and the experimental method in the
278 predicted force-sharing strategies at the individual level. Therefore, generic scaling methods
279 may be unable to estimate the force-sharing strategy at the level of individual participants.

280 Our main results indicate substantial differences between methods for some participants. This
281 is consistent with previous studies, which highlight that inclusion of subject-specific
282 musculoskeletal geometry (Wesseling et al., 2016) or muscle-tendon origin and insertion
283 (Bosmans et al., 2015) affects a model's force estimation. Furthermore, our results are similar
284 to previous studies that report high inter-individual variability in the distribution of maximal
285 force-generating capacity between synergist muscles from either the triceps surae (Crouzier et
286 al., 2018) or the quadriceps (Hug et al., 2015). However, here we also highlight that the force-
287 sharing strategy varies markedly between individuals during walking - a dynamic task
288 whereby forces are submaximal. Furthermore, during walking, a substantial difference
289 between the scaling method and the experimental method ($> 6\%$) for GM/(GM+GL) ratio of
290 either peak force or the force integral was observed in one third of the participants. Similar
291 levels of differences in the GM/(GM+GL) ratio (+6-10%) were shown in patients with
292 Achilles tendinopathy compared to asymptomatic individuals during submaximal isometric
293 contractions (Crouzier et al., 2019). It is therefore possible that the use of generic scaling
294 methods may reduce the ability to detect pathological force-sharing strategies for individuals
295 who deviate from the generic maximal force-generating capacity distribution, which is often
296 the case in clinical populations (Barber et al., 2011).

297 We compared model-predicted forces when using two different methods to estimate a
298 muscle's maximal force-generating capacity. However, an inherent limitation of such an
299 approach is the inability to evaluate our model against direct measurements of *in vivo* force.
300 We compared our predicted forces with forces previously estimated or measured using
301 different approaches during similar walking conditions. For the GM, we found similar peak
302 force levels (346 N) to those estimated using inverse dynamics analysis combined with
303 moment arm and PCSA calculations (~ 305 N in Farris and Sawicki, 2012). In addition, our
304 predicted forces are in agreement with tendon forces directly measured *in vivo*. Finni et al.
305 (1998) reported a peak Achilles tendon force of 1320 N for the triceps surae during an

306 analogous walking speed ($1.1 \text{ m}\cdot\text{s}^{-1}$). Similar to previous methods (Dick et al., 2016), we
307 combined this peak force with the relative PCSA of the gastrocnemii within the triceps surae
308 ($\sim 26\%$ for the GM and 12% for the GL; Ward et al., 2009) and accounted for the relative
309 gastrocnemii activation levels during walking relative to the triceps surae ($\sim 40\%$ MG, 20%
310 LG; Crouzier et al., 2019) to calculate a peak force of 365 N for the GM and 84 N for the GL
311 – which is consistent with our predicted forces (346 N for the GM and 128 N for the GL for
312 the experimental method).

313 Although our results revealed no difference between methods at the group level, this result is
314 difficult to generalize to other groups such as clinical populations. Moreover, we found a
315 similar estimation of muscle volume for group averages when using a scaling method
316 (Handsfield et al., 2014) versus MRI-derived muscle volumes (Fig. 1A) but, on the other hand,
317 the estimation of fascicle length varied more between the scaling and DTI methods (Fig. 1B).
318 This is likely because the scaling method uses subject-specific musculoskeletal models that
319 provide the theoretical optimal fiber length based on a constant muscle-tendon geometry
320 across all participants, whereas the DTI method provides the resting fascicle length at 90° of
321 plantarflexion and $< 5^\circ$ of knee flexion, which accounts for individual differences in resting
322 fascicle lengths. Despite personalizing the maximal force-generating capacity, activation,
323 fascicle length and velocity, and pennation angle, some model parameters remained generic.
324 For example, the shape of the force-length and force-velocity relationships were consistent
325 across models and individuals whereas the inter-individual variability in these relationships
326 has been suggested in human GM (Hager et al., 2020) and vastus lateralis muscles (Brennan
327 et al., 2018). However, the influence of these parameters on predicted forces is likely small
328 given the relatively low sensitivity of Hill-type models to, for example, the curvature of the
329 force-velocity relationship and the maximum unloaded shortening velocity (Dick et al., 2017).
330 On the other hand, previous studies have shown that the Hill-type model is also sensitive to
331 tendon slack length and optimal fiber length (Bujalski et al., 2018; Scovil & Ronsky, 2006).
332 Further work is needed to test the effect of personalising these parameters on muscle force
333 estimation, although directly measuring these parameters in humans *in vivo* is currently not
334 possible.

335 In conclusion, when predicting individual muscle force-sharing strategies, our results
336 highlight the importance for Hill-type models to be personalized with *in vivo* imaging data.
337 Future research is necessary to determine the sensitivity of Hill-type models to additional

338 subject-specific inputs, for example by using elastography to estimate the fascicle slack length
339 and the muscle's passive force-length properties (Hug et al., 2013) or by estimating subject-
340 specific force-length relationships (Maganaris, 2003).

341 **Acknowledgements:**

342 We thank Aiman Al-Najjar, Nicole Atcheson, and Donald Maillet from the UQ Centre for
343 Advanced Imaging (CAI) for their support and expertise in MR imaging. We further thank
344 Bart Bolsterlee (NeuRA & University of New-South Wales) for assistance in MRI and DTI
345 processing.

346 **Declaration of competing interest**

347 The authors in this paper have no financial or other relationships that might lead to a conflict
348 of interest.

349 **Funding**

350 This work was supported by a University of Queensland Early Career Research Grant to
351 Taylor JM Dick. François Hug is supported by a fellowship from the Institut Universitaire de
352 France (IUF) and a travel grant from the Société de Biomécanique. Support was received
353 from the French national research agency (ANR-19-CE17-002, COMMODE project; to FH).

354 **Data availability:**

355 The predicted force data are available from figshare: [10.6084/m9.figshare.17099864](https://doi.org/10.6084/m9.figshare.17099864)

356

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504 **TABLES AND FIGURES**

505 **Table 1: Force parameters estimated using the Hill-type model during level and incline walking.**

	Level walking				Incline walking			
	GM		GL		GM		GL	
	Scaling	Experimental	Scaling	Experimental	Scaling	Experimental	Scaling	Experimental
Peak force (N)	378 ± 127	346 ± 137	120 ± 41*	128 ± 55*	467 ± 152†	423 ± 155†	186 ± 64*†	195 ± 74*†
Force integral (N.s)	123 ± 36	114 ± 43	43 ± 15*	45 ± 17*	149 ± 48†	136 ± 52†	61 ± 21*†	65 ± 26*†

506 Values are presented for the gastrocnemius medialis and lateralis during both level and incline walking. The
 507 maximal force-generating capacity was estimated using either the scaling or experimental method. GM,
 508 gastrocnemius medialis, GL, gastrocnemius lateralis. Values are reported as mean ± standard deviation.
 509 *Indicates a significant difference with GM. †Indicates a significant difference with level walking. $n = 12$. No
 510 difference between methods was found for any muscle or condition.

511 **Table 2: Gastrocnemius medialis to gastrocnemius lateralis [GM/(GM+GL)] force ratio**
 512 **estimated using the Hill-type model during level and incline walking.**

	Level walking		Incline walking	
	Scaling method	Experimental method	Scaling method	Experimental method
Peak force ratio (%)	75.4 ± 6.2	72.4 ± 7.3	71.1 ± 7.8†	68.0 ± 7.9†
Force integral ratio (%)	74.1 ± 6.2	71.2 ± 7.3	70.5 ± 7.0	67.4 ± 7.5

513 Values are presented for both level and incline walking. The maximal force-generating capacity was estimated
 514 using either a scaling or experimental method. Values are reported as mean ± standard deviation. †Indicates
 515 significant difference with level walking. $n = 12$. No difference between methods was found for any muscle or
 516 condition.

517 **FIGURE LEGENDS**

518

519 **Fig. 1: Individual data for muscle volume (A), fascicle length (B) and maximal force-**
520 **generating capacity (F_{max} ; C) determined using the scaling and experimental methods.**

521 Data are depicted for both the gastrocnemius medialis (GM) and gastrocnemius lateralis (GL).
522 The ratio between these muscles [$GM/(GM+GL)$] is also depicted for each variable. Each
523 graph depicts individual data obtained with the scaling method (top) and experimental method
524 (bottom). Each color represents an individual participant and the mean group value is
525 presented as a black diamond. Because the scaling method uses the same underlying
526 equations to scale all individuals, we can observe that the inter-individual variability in ratios
527 between muscles is concealed.

528

529 **Fig. 2: Individual time-varying forces estimated by the Hill-type model during level**
530 **walking for each participant (P).** The GM (green) and GL (purple) forces are depicted by

531 solid lines (experimental method) and dashed lines (scaling method). Heel-strike occurred at
532 0% on the x-axis and the dashed vertical lines represent the timing of toe-off during the gait
533 cycle. Each plot represents an individual participant. Predicted forces for incline walking are
534 presented in Fig. S1.

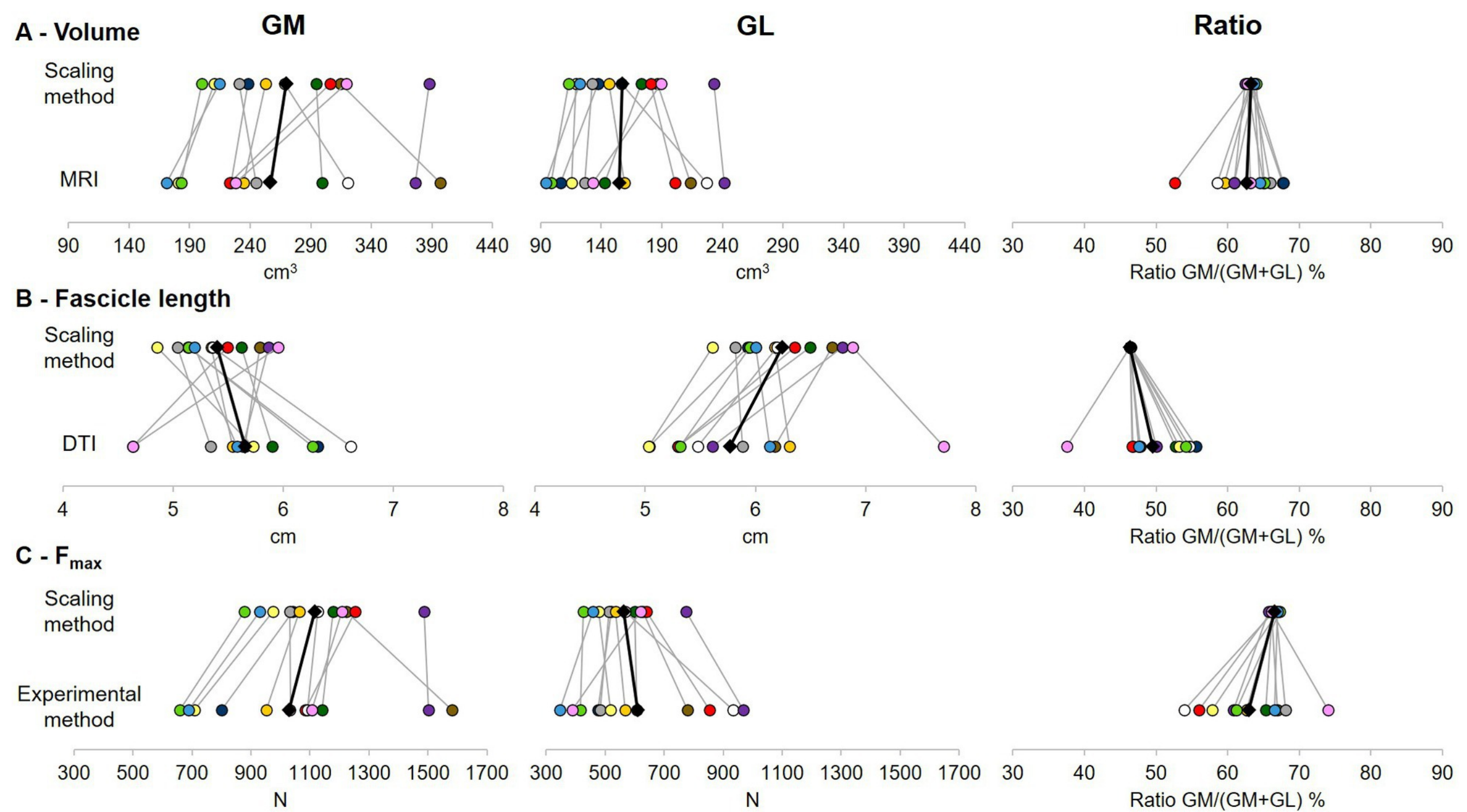
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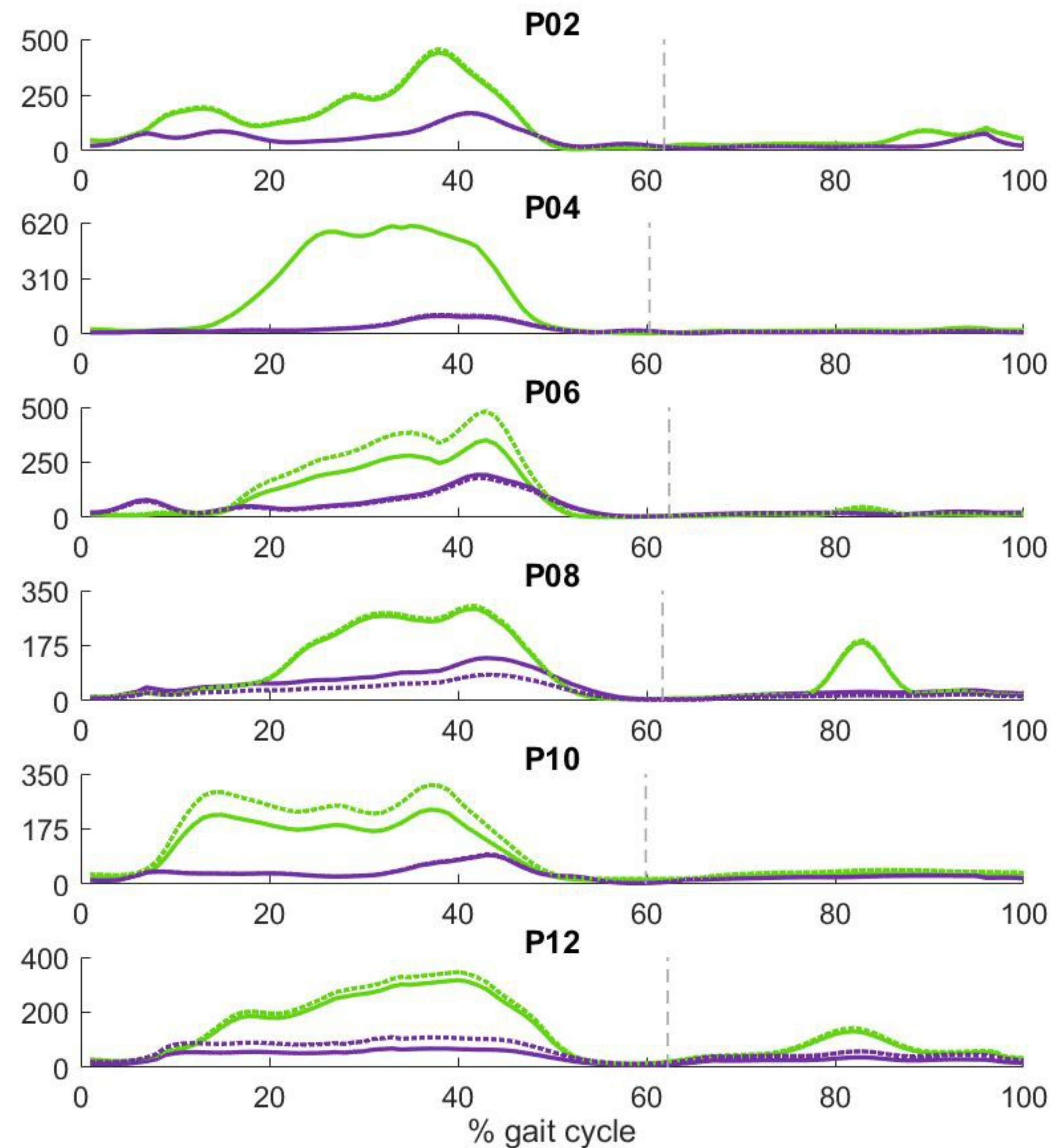
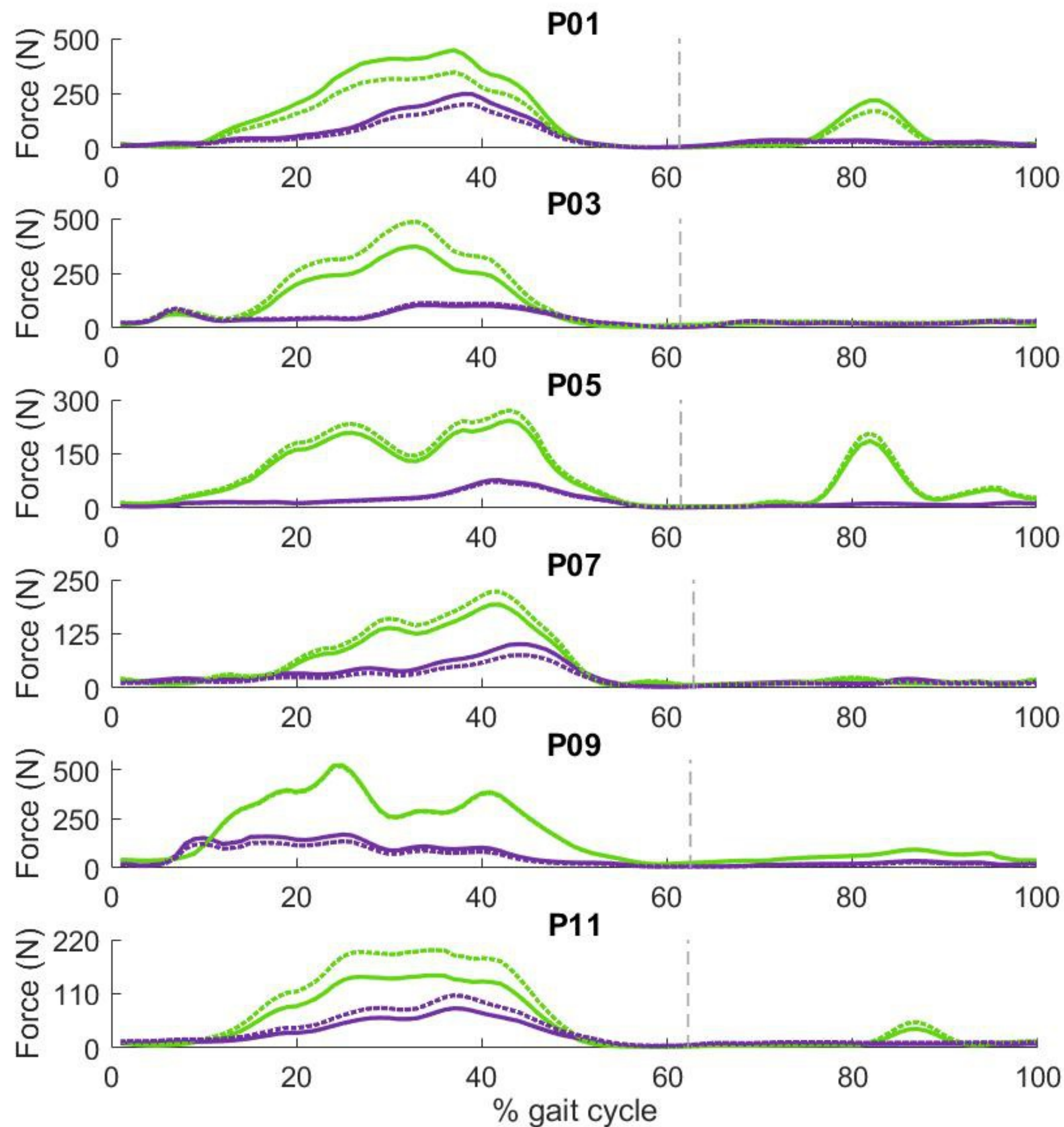
536 **Fig. 3: Individual data for peak force (A and B) and force integral (C and D) for level**
537 **walking (white area; A and C) and incline walking (grey area; B and D), determined**
538 **using the scaling and experimental methods.** Data are depicted for both the gastrocnemius

539 medialis (GM) and gastrocnemius lateralis (GL). The ratio [$GM/(GM+GL)$] is also depicted
540 for each variable. Each graph depicts individual data obtained with the scaling method and
541 experimental method. Each color represents an individual participant and the mean group
542 value is presented as a black diamond. The scaling method and the experimental method seem
543 to predict similar muscle force and force-sharing strategy during walking at the group level
544 but substantial differences between methods was apparent for some participants.

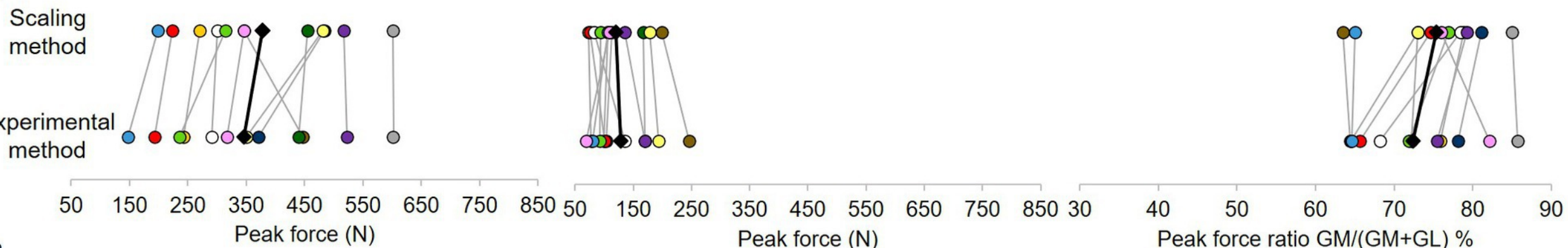
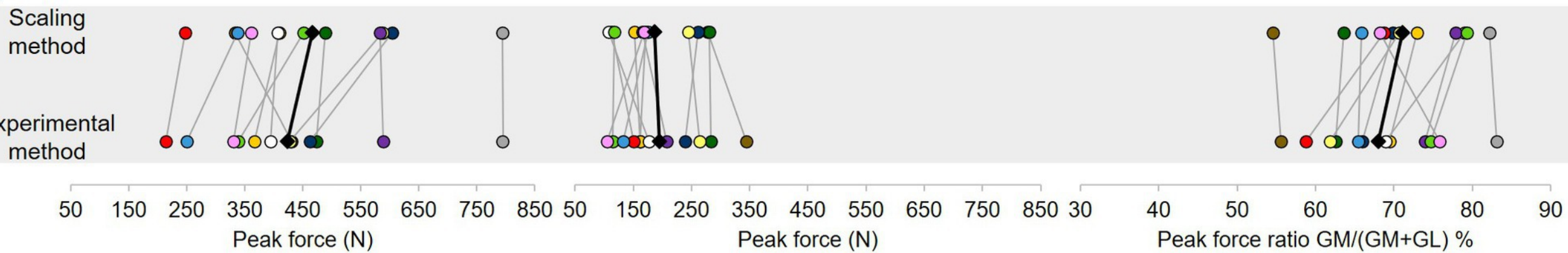
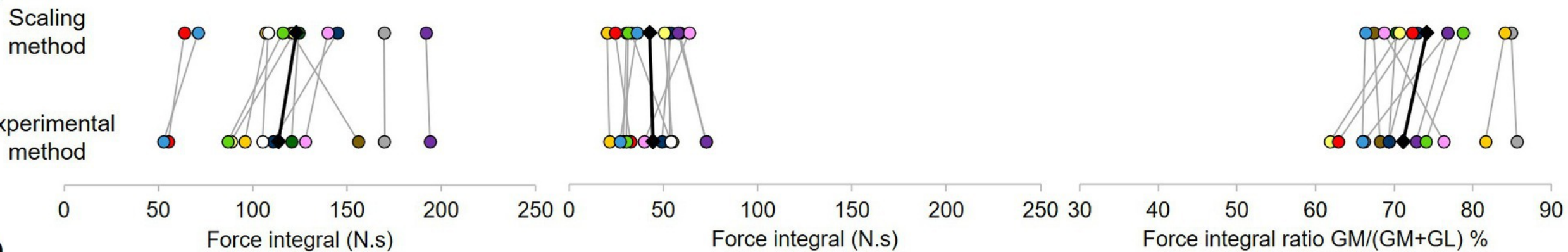
545 **SUPPLEMENTARY FIGURE**

546 *Fig. S1: Individual time-varying forces estimated by the Hill-type model during incline*
547 *walking for each participant (P). The GM (green) and GL (purple) forces are depicted by*
548 *solid lines (experimental method) and dashed lines (scaling method). Heel-strike occurred at*
549 *0% on the x-axis and the dashed vertical lines represent the timing of toe-off during the gait*
550 *cycle. Each plot represents an individual participant.*





— GM experimental method — GL experimental method GM scaling method GL scaling method

GM**GL****Ratio****A****B****C****D**