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The capacity of the human iliotibial band to store elastic energy during running

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22 **Abstract**

23 The human iliotibial band (ITB) is a poorly understood fascial structure that may
24 contribute to energy savings during locomotion. This study evaluated the capacity of the
25 ITB to store and release elastic energy during running, at speeds ranging from 2-5 m/s,
26 using a model that characterizes the three-dimensional musculoskeletal geometry of the
27 human lower limb and the force-length properties of the ITB, tensor fascia lata (TFL),
28 and gluteus maximus (GMax). The model was based on detailed analyses of muscle
29 architecture, dissections of 3-D anatomy, and measurements of the muscles' moment
30 arms about the hip and knee in five cadaveric specimens. The model was used, in
31 combination with measured joint kinematics and published EMG recordings, to estimate
32 the forces and corresponding strains in the ITB during running. We found that forces
33 generated by TFL and GMax during running stretch the ITB substantially, resulting in
34 energy storage. Anterior and posterior regions of the ITB muscle-tendon units (MTUs)
35 show distinct length change patterns, in part due to different moment arms at the hip
36 and knee. The posterior ITB MTU likely stores more energy than the anterior ITB MTU
37 because it transmits larger muscle forces. We estimate that the ITB stores about 1 J of
38 energy per stride during slow running and 7 J during fast running, which represents
39 approximately 14% of the energy stored in the Achilles tendon at a comparable speed.
40 This previously unrecognized mechanism for storing elastic energy may be an
41 adaptation to increase human locomotor economy.

42

43 **Introduction**

44 Because bipedalism is a fundamental derived feature of hominins (species more
45 closely related to humans than chimpanzees), many distinctive features of the human
46 spine and lower extremity are adaptations to improve bipedal locomotor performance.
47 Many adaptations for standing and walking, for example, appear early in hominin
48 evolution including a inferiorly-oriented foramen magnum, a lordotic lumbar spine, and a
49 sagittally-oriented ilium (see Aiello and Dean, 1990; Zollikofer et al., 2005). Additional
50 features that first appear later in the genus *Homo* may reflect selection for endurance
51 running, including a stabilized sacroiliac joint, an expanded attachment of gluteus
52 maximus, and shorter toes (Bramble and Lieberman, 2004; Lieberman et al., 2006;
53 Rolian et al., 2009). Although the selective factors underlying the evolution of both
54 walking and running are debated, it is likely that locomotor economy played a key role.
55 Hypothesized energy-saving features for walking include long legs and dorsally oriented
56 ischia (Crompton et al., 1998; Pontzer et al., 2009; Robinson, 1972; Sockol et al., 2007).
57 Energy saving features for running in the genus *Homo* include a long, compliant Achilles
58 tendon and a spring-like median longitudinal arch, which are known to store and recover
59 elastic energy during running in other vertebrates (Biewener, 2003; Ker et al., 1987;
60 Roberts, 2002). In addition, the human lower extremity has a number of fascial
61 structures with elastic properties that are not present in apes, but whether these
62 structures store energy or serve another function remains poorly understood.

63 One of the most interesting of these structures is the iliotibial band (ITB). The ITB
64 is a thickening of the lateral fascia of the thigh that originates on the pelvis and inserts
65 on the tibia; it receives muscle fibers from the tensor fascia lata (TFL) anteriorly and

66 from the gluteus maximus (GMax) posteriorly (Gottschalk et al., 1989; Gray et al., 1995;
67 Kaplan, 1958; Ober, 1936; Stern, 1972). The ITB is traditionally considered to function
68 as a “strut” during walking, stabilizing the hip in the frontal plane (Gottschalk et al.,
69 1989; Inman, 1947; Kaplan, 1958). However, the high compliance of the ITB (Butler et
70 al., 1984; Derwin et al., 2008; Gratz, 1931), the fact that it crosses both the hip and
71 knee, and the presence of in-series muscles suggest that the ITB may play other roles.
72 If the ITB stretches substantially while transmitting muscle forces, storing elastic energy,
73 then it may decrease the metabolic cost of locomotion. Prior studies have estimated that
74 energy recovered from the Achilles tendon during running reduces muscle work by as
75 much as 35% (Alexander and Bennet-Clark, 1977; Ker et al., 1987). Whether the ITB
76 also stores and recovers elastic energy, and how this compares to Achilles tendon
77 energy recovery, is unknown.

78 As a first step toward evaluating the ITB’s role in locomotor economy, this study
79 examined the capacity of the ITB to store elastic energy at running speeds ranging from
80 2 to 5 m/s. We hypothesized that forces generated by TFL and GMax stretch the ITB
81 during running, storing elastic energy that may be recovered later in the stride. We
82 tested this hypothesis by developing a musculoskeletal model of the ITB and inserting
83 muscles. Our model characterizes the 3-D skeletal geometry, the hip and knee
84 kinematics, and the attachments and force-length (F-L) properties of the ITB, TFL and
85 GMax for an average-sized adult male (femur length: 39.8 cm; tibia length: 36.2 cm).
86 Because existing representations of TFL and GMax were not sufficiently accurate for
87 this study, we performed detailed analyses of these muscles’ architecture and
88 measured their moment arms (MAs) about the hip and knee in cadaveric specimens.

89 The TFL has largely been neglected in previous studies of muscle architecture (e.g.,
90 Ward et al., 2009; Wickiewicz et al., 1983) and locomotor function (e.g., Dorn et al.,
91 2012; Sasaki and Neptune, 2006), despite being active during running (Andersson et
92 al., 1997; Mann et al., 1986; Montgomery et al., 1994; Paré et al., 1981). GMax is
93 routinely modeled as a uniarticular hip extensor that inserts on the femur (e.g., Arnold et
94 al., 2010; Delp et al., 1990), despite evidence that a substantial portion of GMax inserts
95 on the ITB (Gray et al., 1995; Stern, 1972). Our refined musculoskeletal model, which
96 addresses these limitations, is available on SimTK (simtk.org). Using this model, we
97 estimated the forces transmitted to anterior and posterior regions of the ITB at body
98 positions corresponding to running, predicted the length changes of each region, and
99 calculated the corresponding ITB strain energies over the course of a stride based on
100 published measurements of the tissue's elastic modulus (Butler et al., 1984; Derwin et
101 al., 2008).

102

103 **Materials and methods**

104 *Muscle architecture measurements*

105 We characterized the isometric force-generating capacity of TFL and GMax
106 based on measurements of muscle architecture in three formalin-fixed human cadavers
107 (Table 1). Specimens were dissected and the muscles isolated and removed. Total
108 mass (M) of each muscle was measured; in addition, the masses of four regions of the
109 GMax were measured separately. A muscle fascicle was carefully dissected from each
110 region of GMax and from two regions of TFL and the fascicle lengths (L_f) measured.
111 Surface pennation angles between the fascicles and ITB were also measured. Under

112 magnification, muscle fiber bundles were isolated from each fascicle and mounted on
113 slides. Following Lieber et al. (1990), bundle sarcomere length (L_s') was determined by
114 laser diffraction and used to calculate optimal fascicle length (L_f):

$$115 \quad L_f = L_f' \left(\frac{2.7 \mu m}{L_s'} \right) \quad (1)$$

116 where 2.7 μm is the optimal sarcomere length for human muscle (Lieber et al., 1994).
117 Physiological cross-sectional area (PCSA) was calculated from muscle mass and
118 optimal fascicle length (Powell et al., 1984):

$$119 \quad PCSA = \frac{M}{\rho \cdot L_f} \quad (2)$$

120 where ρ is muscle density (1.056 g/cm³; Mendez and Keyes, 1960). Our architecture
121 data for GMax are consistent with data reported by Ward et al. (2009).

122 *Muscle moment arm measurements*

123 We measured MAs of the muscle-ITB paths in five fresh frozen cadaveric hemi-
124 pelvises obtained from MedCure (Portland, OR). MAs were determined for hip
125 flex/extension, rotation, ab/adduction, and knee flex/extension using the tendon
126 excursion method (An et al., 1984; Brand et al., 1975). We approximated TFL with two
127 Kevlar thread paths (Figure 1A&B) and GMax with four paths (Figure 1A&C). The ITB
128 was left intact during these measurements. Each thread was anchored to a screw eye
129 at the path's insertion, routed over the ITB through plastic tubing to a screw eye at the
130 path's origin, and attached to one of two cable-extension position transducers (PTX101,
131 Celesco, Canoga Park, CA) that measured length changes with an accuracy of ± 0.32
132 mm while applying a tension of 1.4 or 2.8 N. The tubing ensured a repeatable path

133 along the surface of the ITB and decreased friction. Detailed procedures for defining
134 each path are described in supplementary materials.

135 Hip and knee angles were measured simultaneously with muscle-ITB length
136 changes using a motion tracking system (Polhemus Fastrak, Colchester, VT) and
137 custom software (LabView, National Instruments Corporation, Austin, TX). Receivers
138 were rigidly attached to the pelvis, femur, and tibia to track the segments' positions and
139 orientations. Segment coordinate systems were defined along anatomical axes by
140 digitizing bony landmarks and determining the hip center (Figure S1), as described in
141 the supplementary materials. For each muscle-ITB path, we digitized the origin,
142 insertion and key "via" points that constrained the path with hip or knee motion. We also
143 tracked the relative motions of nine marker pairs sutured along the ITB using high-
144 speed video. These data guided development of the model and were analyzed to
145 determine the hip and knee angles at which the anterior and posterior ITB began to
146 stretch.

147 Each specimen was mounted in a custom frame (Figure 2) that allowed
148 independent control of hip flex/extension, rotation, ab/adduction, and knee flexion
149 following Arnold et al. (2000). Alignment and mounting of the specimen comprised four
150 main steps, each performed with real-time feedback to ensure that the pelvis, femur,
151 and tibia were secured to within 5 mm and 2° of the desired alignment. First, the pelvis
152 was secured to a table and aligned with either its medial-lateral axis (for flex/extension
153 MAs) or anterior-posterior axis (for ab/adduction MAs) perpendicular to the table.
154 Second, the femur was mounted on a cart equipped with two concentric rings. The
155 femur was secured to the inner ring so that the femur's long axis (from hip center to the

156 midpoint between femoral epicondyles) was centered perpendicular to the plane of the
157 rings. Third, the base of the cart was adjusted so that its wheels rolled in an arc about
158 the specimen's hip center. Fourth, the tibia was secured to a locking hinge attached to
159 the inner ring. When measuring knee MAs, the hinge was removed and the tibia was
160 flexed and extended. When measuring hip rotation MAs, the inner ring was rotated
161 relative to the outer ring, which internally and externally rotated the hip. When
162 measuring hip flex/extension or ab/adduction MAs, the cart was rotated about the
163 specimen's hip center, thereby flex/extending or ab/adducting the hip. When measuring
164 MAs about one axis, the other axes were locked in a neutral position (hip flexion = 0°,
165 hip rotation = 5°, hip adduction = 0°, knee flexion = 0°). To verify alignment, we
166 monitored coupling of hip angles and ensured that hip adduction varied < 2° and hip
167 rotation < 4° over a 75° range of flexion. When the specimen was aligned for hip
168 ab/adduction, we ensured that hip flexion varied < 2° and hip rotation < 4° over a 50°
169 range of ab/adduction.

170 To measure muscle-ITB MAs, the excursion of each thread path was recorded
171 while slowly moving the specimen through its ranges of hip and knee motion. Excursion
172 and joint angle data were sampled at 10 Hz (National Instruments BNC-2090 A/D
173 converter). The lengthening excursion versus joint angle data were fit with a fourth order
174 polynomial, and the derivative of the polynomial was averaged across trials to estimate
175 the MA. A minimum of five trials was collected for each condition.

176 Following MA measurements, muscles were freed, cleaned of fat and connective
177 tissue, and weighed (Table 2). In two specimens, the regions of GMax were carefully

178 dissected to determine the relative masses of the portions that insert on the ITB versus
179 the femur.

180 *Model of TFL, Gmax, and ITB F-L properties*

181 We modified the paths of TFL and GMax muscle-tendon units (MTUs) in the
182 model reported by Arnold et al. (2010) to match our digitized attachments and MA data
183 (Figure 3). Using SIMM (*Software for Interactive Musculoskeletal Modeling*, v7.0,
184 MusculoGraphics, Santa Rosa, CA), we initially created two paths for TFL and eight for
185 GMax (four to the ITB and four to the femur). Via points and wrapping surfaces were
186 iteratively adjusted so that the model's paths reproduced the three-dimensional paths
187 digitized during the experiments and the model's MAs matched the experimentally
188 determined MAs. Because the model's MAs are extremely consistent with our
189 experimental data (Figures 4 & S2), we are confident that the model accurately predicts
190 length changes of these MTUs.

191 To estimate strain in regions of the ITB during running, we created three
192 additional MTUs, representative of the major paths of ITB force transmission
193 determined from our experiments (Figure 3B,C). One path accounts for force
194 transmitted by the anterior ITB when TFL is active (TFL-ITB_{ant}). The other paths account
195 for the cumulative force transmitted by the posterior ITB when superior (GMax1,2-
196 ITB_{post1}) or inferior (GMax3,4-ITB_{post2}) portions of GMax are active. Attachments and via
197 points of each path were iteratively adjusted to yield average MAs of the combined
198 MTUs (Figures 4). This model represents the muscles as independent, proximal-to-
199 distal MTUs, even though the ITB is multi-layered and loaded from different directions,
200 based on detailed dissections and on biaxial testing of goat fascia lata, which showed

201 that the fascia’s material properties are not strongly influenced by its biaxial strain
202 environment (Eng et al., 2014).

203 We used a Hill-type muscle model (Delp et al., 1990; Zajac, 1989) to estimate
204 isometric forces generated by TFL-ITB_{ant}, GMax1,2-ITB_{post1}, and GMax3,4-ITB_{post2} at
205 different activation levels. Two parameters, maximum isometric force (F_{max}) and optimal
206 fiber length (L_{opt}), scaled normalized active and passive F-L curves to each muscle
207 (Table S1). F_{max} and an additional parameter, tendon slack length (L_{TS}), scaled a
208 normalized “tendon” F-L curve to each MTU. We specified parameters for each MTU
209 based on our architecture measurements and data reported by Ward et al. (2009). We
210 adjusted L_{TS} such that ITB_{ant} and ITB_{post} began to stretch passively at hip and knee
211 angles consistent with our experimental data.

212 For each MTU, we created a normalized F-L curve for the ITB (Figure 5) based
213 on published material properties of the human ITB (Butler et al., 1984; Derwin et al.,
214 2008). We assumed a transition strain of 4% based on data from goat fascia lata (Eng
215 et al., 2014). Above 4% strain, we assumed a linear relationship between force and
216 strain with a normalized stiffness (\tilde{k}) determined using the ITB’s elastic modulus (E),
217 the muscle’s F_{max} , and the ITB’s effective cross-sectional area (a):

218
$$\tilde{k} = \frac{E \times a}{F_{max}}$$

219 The effective cross-sectional area of the ITB was calculated from measurements
220 of thickness and width in cadaveric specimens (see Table S2). The width of each ITB
221 region was measured while placing tension on the inserting muscle and visually
222 assessing ITB strain. We used an elastic modulus of 400 MPa, which is consistent with
223 values reported in the literature (Butler et al., 1984; Derwin et al., 2008; Hammer et al.,

224 2012; Steinke et al., 2012). Below 4% strain, in the toe region, we decreased stiffness
225 by a factor of 2/3. At F_{max} , the ITB strains 5-11% in our model, which seems plausible
226 given the range of yield strains reported in the literature (10-27%; (Butler et al., 1984;
227 Hammer et al., 2012; Hinton et al., 1992). The regional variation in strain at F_{max} is
228 consistent with our measurements of ITB thickness, which are relatively uniform in
229 anterior and posterior regions despite the fact that the inserting muscles differ
230 substantially in force-generating capacity.

231 *Assessment of ITB energy storage*

232 We used our model in combination with published joint kinematics and EMG
233 recordings to examine the capacity of the ITB to store elastic energy during running.
234 First, we calculated the lengths of the MTUs at hip and knee angles corresponding to
235 running using data from 10 experienced runners, at speeds of 2, 3, 4, and 5 m/s
236 (Hamner and Delp, 2013). Next, we divided MTU lengths into muscle fiber lengths and
237 ITB lengths by independently activating each MTU in the model and solving for the
238 lengths at which the muscle and ITB forces were equivalent, accounting for pennation
239 angle. Maximum activation levels for running were assumed to range between 20% and
240 65% of the EMG activation measured during a maximum voluntary contraction (MVC).
241 In particular, we set each muscle's maximum activation to 20%, 35%, 50%, or 65% to
242 estimate ITB strains during running at 2, 3, 4, and 5 m/s, respectively. These values are
243 based on reported maximum activations of 20% MVC in GMax and TFL during level
244 walking (Perry, 1992), 40% MVC in GMax and TFL during level running at 4.0 m/s
245 (Montgomery et al., 1994), and 65% MVC in GMax during level running at 4.5 m/s
246 (Swanson and Caldwell, 2000). Time-varying patterns of activity were derived from

247 EMG recordings reported for GMax and TFL (Jönhagen et al., 1996; Montgomery et al.,
248 1994; Paré et al., 1981; Swanson and Caldwell, 2000), which we scaled to the
249 maximum activation at each speed (Figure 7). Lastly, we estimated energy storage
250 capacity at each speed by integrating the ITB F-L curves from L_{TS} to peak ITB length
251 during running. Length changes of the ITB were determined relative to slack length.
252 Total elastic energy stored in the posterior ITB was calculated as the sum of the
253 energies stored in GMax1,2-ITB_{post1} and GMax3,4-ITB_{post2}. We assessed the sensitivity
254 of our analysis to the F-L properties by varying normalized stiffness by $\pm 20\%$ and
255 transition strain by $\pm 2\%$ (Figure 5) and re-calculating energy storage.

256

257 **Results**

258 The TFL and GMax MTUs in our model undergo substantial excursions during
259 running (Figure 6). Because of its hip flexion and knee extension MAs, TFL-ITB_{ant} is
260 maximally stretched during early swing, when the hip is extended and the knee flexed
261 (Figure 3C). EMG recordings show that TFL is highly activated during this time (Figures
262 6 & 7) (Montgomery et al., 1994; Paré et al., 1981). In contrast, because of their role in
263 hip extension and knee flexion MAs, GMax-ITB_{post1} and GMax-ITB_{post2} are maximally
264 stretched during late swing, when the hip flexes and the knee extends (Figure 3C).
265 EMG recordings show that GMax is highly activated during this time (Figures 6 & 7)
266 (Jönhagen et al., 1996; Swanson and Caldwell, 2000). Inferior portions of GMax
267 lengthen about 7% more than proximal portions, due to larger hip extension MAs when
268 the hip is flexed.

269 The largest strains in ITB_{ant} occur in early swing (Figure 7A), with ITB_{ant} stretching
270 0.9 to 1.7 cm beyond slack length in our model. TFL muscle fiber length is longer than
271 optimal when it begins generating force in late stance, and near optimal when it is
272 maximally activated in early swing. Peak strains in ITB_{post} occur in late swing (Figure
273 7B), with ITB_{post} stretching 1.4 to 3.0 cm beyond slack length in our model. GMax3,4 is
274 shorter than optimal length when it begins generating force in mid swing; however, it is
275 stretched beyond optimal length as the hip flexes in swing. In late swing, when GMax3,4
276 is maximally activated, it operates near optimal length and generates forces that stretch
277 ITB_{post} in our model. A similar pattern occurs in GMax1,2-ITB_{post2}. Passive strains in the
278 ITB, without muscle activation, are relatively small in our model. ITB_{ant} strains 1.7% and
279 ITB_{post} strains 1.1% over the stride cycle when the muscles are not activated.

280 Because the TFL and GMax MTUs are stretched to relatively long lengths when
281 the muscles are active during running, both anterior and posterior regions of the ITB in
282 our model have the capacity to store elastic energy. We estimate that ITB_{ant} strains
283 about 4% during running at 5 m/s, which means that the ITB_{ant} may store nearly 1 J of
284 energy per stride during early swing (Figure 8A). ITB_{post1} and ITB_{post2} strain about 4%
285 during slow running and 7% during faster running in late swing when GMax is maximally
286 active in our model. These data suggest that the ITB_{post} may store as much as 6 J per
287 stride during late swing (Figure 8B).

288

289 **Discussion**

290 This is the first study to quantitatively characterize the 3-D musculoskeletal
291 geometry of the human ITB and its inserting muscles. Dissections confirmed that all

292 fibers of TFL insert into the anterior ITB and a large fraction of GMax (40-70% by mass)
293 inserts into the posterior ITB. Thus, the ITB likely transmits substantial force.
294 Additionally, our MA measurements confirmed that the inserting muscles have relatively
295 large MAs about the hip, and thus undergo large MTU excursions, with hip flexion and
296 extension. In combination, the ITB's high compliance and its potential to transmit force
297 while changing length, suggest a plausible, previously unrecognized mechanism for
298 storing elastic energy during running.

299 We created a model that characterizes the geometry and F-L properties of the
300 ITB, TFL, and GMax to test the hypothesis that forces generated by TFL and GMax
301 stretch the ITB during running, storing elastic energy. Analysis of the model revealed
302 that the ITB has the capacity to store 7 J per stride during running at 5 m/s. The
303 posterior ITB stores substantially more energy than the anterior ITB because it transmits
304 larger muscle forces.

305 How does the amount of energy stored in the ITB during running compare to
306 energy stored in the Achilles tendon? Using a 3-D model and static optimization, Lai et
307 al. (2014) estimated that the soleus and gastrocnemius store 40-50 J per stride in the
308 Achilles tendon at slow to fast running speeds (3.5 – 5 m/s), an estimate consistent with
309 previous experimental studies (Alexander and Bennet-Clark, 1977; Hof et al., 2002; Ker
310 et al., 1987). We therefore calculate that the combined anterior and posterior ITB stores
311 14% as much energy as the Achilles tendon at a 5 m/s pace.

312 To provide additional context, we compared energy stored in the ITB to hip
313 muscle work during running. Sasaki and Neptune (2006) used a muscle-driven dynamic
314 simulation to estimate the mechanical work performed by hip muscles and series elastic

315 elements during running at 2.4 m/s. They reported that the hip extensors do 40 J of
316 work per stride during stance, while the hip flexors do 6 J of work during swing.
317 Recovery of 2 J from ITB_{post} during slow running could account for 5% of the work done
318 by hip extensors in stance, while recovery of 0.3 J from ITB_{ant} could contribute 5% of the
319 work done by hip flexors in swing. Although the extent to which energy recovery would
320 drive selection for endurance running is unknown, these comparisons suggest that
321 energy storage in the ITB is not negligible.

322 This analysis has several limitations. First, although our data confirm that forces
323 generated by TFL and GMax stretch the ITB during running, storing useful energy, our
324 study did not test whether the human ITB reduces muscle work or enhances locomotor
325 economy. Second, uncertainty exists in the parameters used to derive the F-L curves.
326 For example, our measures of ITB width and thickness in cadaveric specimens may not
327 be representative of healthy young subjects, thus potentially underestimating ITB
328 stiffness. However, varying normalized stiffness by $\pm 20\%$ and transition strain by $\pm 2\%$
329 altered our estimates of energy storage by only 0.1 J in the anterior ITB and by 1.2 J in
330 the posterior ITB at the fastest running speed. At the slowest running speed, varying
331 stiffness and transition strain altered our estimates of energy storage by about 0.05 J.
332 Thus, we are reasonably confident in our model of the ITB's force-strain behavior and
333 that the ITB contributes to energy storage at all running speeds. Third, we estimated the
334 peak forces generated by TFL and GMax ignoring the muscles' force-velocity (F-V)
335 properties and assuming the muscles' activation patterns during running. If the muscles
336 shorten substantially during running, or if we overestimated activation, then we likely
337 overestimated ITB energy storage. It is plausible, however, that the ITB's length and

338 compliance allow GMax to operate nearly isometrically when generating maximum force
339 in late stance, mitigating the effects of F-V properties on muscle-ITB mechanics. In the
340 running simulations described by Lai et al. (2014), muscles inserting on the Achilles
341 tendon contracted nearly isometrically across a range of running speeds. Lastly, we
342 estimated the capacity of the ITB to store elastic energy during running but not walking.
343 It is likely that the ITB transmits smaller forces, and thus stores less energy, during
344 walking than reported here.

345 Our study has implications for understanding the evolution of human bipedalism.
346 While these data do not exclude the possibility that the ITB stores substantial energy
347 during walking, selection for the capacity to run long distances would have presented
348 unique demands on the anatomy and physiology of *Homo* (see Bramble and Lieberman
349 (2004) for review). Among these demands is the need to efficiently accelerate the swing
350 limb, which is long and massive in humans (14% body mass) compared to chimpanzees
351 (9% body mass; Zihlman and Bruner, 1979). The human ITB is stretched substantially
352 just before swing, when the TFL is active and the hip is extending (Figures 6 & 7).
353 Subsequent recoil of the ITB may help accelerate the swing limb. Although the
354 energetic cost of running is primarily determined by muscle forces that support the body
355 during stance (Kram and Taylor, 1990), the cost of accelerating the swing limb may be
356 as much as 27% of total metabolic cost (Marsh et al., 2004; Modica and Kram, 2005;
357 Myers and Steudel, 1985). Thus, selection for increased running economy may have
358 favored traits that increase swing phase energy recovery in *Homo*. The need to
359 decrease locomotor costs may also help explain the expansion of GMax evident in
360 *Homo*. This adaptation is thought to play a role in trunk stabilization during endurance

361 running (Lieberman et al., 2006), but it may also facilitate elastic energy storage by
362 increasing the forces transmitted to the ITB as it is stretched in late swing.

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377

378

379 **Figure legends**

380

381 **Figure 1.** A: Lateral view of the human ITB showing paths of the inserting muscles, TFL
382 and GMax, as characterized during the moment arm measurements. B: Lateral diagram
383 showing the anterior and posterior paths of TFL. C: Posterior diagram showing the
384 superior (Gmax1,2) and inferior (GMax3,4) regions of GMax. Muscle-ITB paths are
385 described in the supplementary materials.

386

387 **Figure 2.** Hardware and procedure for measuring hip ab/adduction and rotation moment
388 arms. The hardware consisted of a fixed table for aligning and securing the pelvis, an
389 adjustable cart for moving the femur through a range of hip ab/adduction angles, and a
390 set of concentric rings for rotating the femur about its mechanical axis, following Arnold
391 et al. (2000). Receivers (shown in gray) were rigidly attached to the pelvis, femur, and
392 tibia to track their motions in real time. 1: The pelvis was secured to a fixed table with its
393 anterior-posterior axis perpendicular to the table. 2: The femur was secured to the inner
394 of the two rings so that the femur's long axis was centered perpendicular to the plane of
395 the rings. 3: The bases of the cart were adjusted so that the cart's wheels rolled in an
396 arc about the specimen's hip joint center. 4: The tibia was secured to a locking hinge.
397 Hip flex/extension moment arms were measured by re-orienting the pelvis on the table
398 so that its medial-lateral axis was perpendicular to the table. More details are provided
399 in the supplementary materials.

400

401 **Figure 3.** Lower extremity model modified from Arnold et al. (2010). A: Lateral view
402 showing the two TFL-ITB paths that reproduce our experimental data. B: Posterior view
403 showing the four GMax-ITB paths originating on the ilium, sacrum, and coccyx and
404 inserting on the ITB. C: Lateral view of the combined MTU paths used to estimate
405 energy storage. TFL-ITB_{ant}, GMax1,2-ITB_{post1}, and GMax3,4-ITB_{post2} paths are shown at
406 touchdown, midstance, toeoff, and midswing during running at 5 m/s. The TFL-ITB_{ant}
407 MTU is maximally stretched in early swing, while the GMax-ITB_{post} MTUs are most
408 stretched during late swing.

409

410 **Figure 4.** Hip and knee moment arms of TFL-ITB_{ant} and GMax-ITB_{post} compared with
411 experimental data. A: TFL has a large hip flexion MA that increases as the hip flexes. B:
412 TFL has a large hip abduction MA that increases with hip abduction. C: The most
413 posterior part of TFL has a small knee extension MA that decreases with knee flexion.
414 D,G: All portions of GMax that insert on the ITB have large hip extension MAs. E: The
415 superior portions of GMax have hip abduction MAs. H: The inferior portions of GMax
416 have hip adduction MAs. F,I: The portions of GMax that insert on the ITB have small
417 knee flexion MAs. Solid lines and shaded regions indicate the means and standard
418 deviations of experimentally determined MAs from five cadaveric limbs. A-C: Dashed
419 lines show the MAs of TFL1-ITB (dark gray), TFL2-ITB (light gray), and the combined
420 TFL1,2-ITB_{ant} (black) predicted by our model. D-I: Dashed lines show the MAs (from
421 superior to inferior) of GMax1 (dark gray), GMax2 (light gray), GMax3 (dark gray),
422 GMax4 (light gray), and the combined paths for GMax1,2-ITB_{post1} (black, D-F) and
423 GMax3,4-ITB_{post2} (black, G-I) as predicted by our model. Note the y-axes have different
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Figure 5. Normalized force-length curves for anterior and posterior regions of the ITB derived from experimental data (Butler et al., 1984; Derwin et al., 2008; Eng et al., 2014). Curves are shown for TFL-ITB_{ant} (short dash), GMax1,2-ITB_{post1} (long dash), and GMax3,4-ITB_{post2} (dot-dash) with shaded regions indicating $\pm 20\%$ stiffness used in the sensitivity analysis. The ITB is more compliant than tendon (solid line), as shown by the typical tendon force-length curve generated by Millard et al. (2013) and by ultrasound-based measures of tendon force-length properties reported by Magnusson et al. (2001; light gray). This figure is adapted from figure 3 in Millard et al. (2013).

Figure 6. Length changes of TFL-ITB and GMax-ITB MTUs during fast running (5 m/s). TFL-ITB_{ant} (light gray) stretches during stance phase, while GMax1,2-ITB_{post1} (dark gray) and GMax3,4-ITB_{post2} (black) stretch during the swing phase. Regions of intermediate muscle activity (10-30% activation; intermediately thickened portion of each curve) and maximal muscle activity (31-65% activation; thickened portion of each curve) demonstrate that these muscles are maximally active when the MTU is near maximum length.

Figure 7. TFL-ITB_{ant} and GMax3,4-ITB_{post} activation patterns over the stride cycle. For each muscle, the time-varying pattern was scaled to an activation level of 20%, 35%, 50%, or 65% during running at 2, 3, 4, and 5 m/s, respectively (increasingly darker lines). Filled squares on each line indicate toe-off. Superimposed are plots of force versus normalized fiber length and force versus ITB strain at key points in the gait cycle during running at 5 m/s. Circles on the curves show where the muscle or ITB is acting at that point in the gait cycle. A: TFL is longer than optimal length (L_{opt}) prior to toe-off when the muscle begins to generate force. When TFL is maximally activated in early swing, it operates near optimal length and stretches ITB_{ant} to its longest length in our model. B: GMax3,4 is shorter than optimal length when it begins generating force in mid swing and is stretched beyond optimal length in swing. When GMax3,4 is maximally activated in late swing, it operates near optimal length and stretches ITB_{post} to its longest length in our model.

Figure 8. Elastic energy stored in the ITB during running at 2, 3, 4, and 5 m/s as predicted by the model. A: Peak energy stored in ITB_{ant} when TFL is activated 20, 35, 50, or 65%. B: Peak energy stored in ITB_{post} when GMax is activated 20, 35, 50, or 65%. The energy stored in GMax-ITB_{post} is calculated as the sum of energies stored in GMax1,2-ITB_{post1} (gray) and GMax3,4-ITB_{post2} (white).

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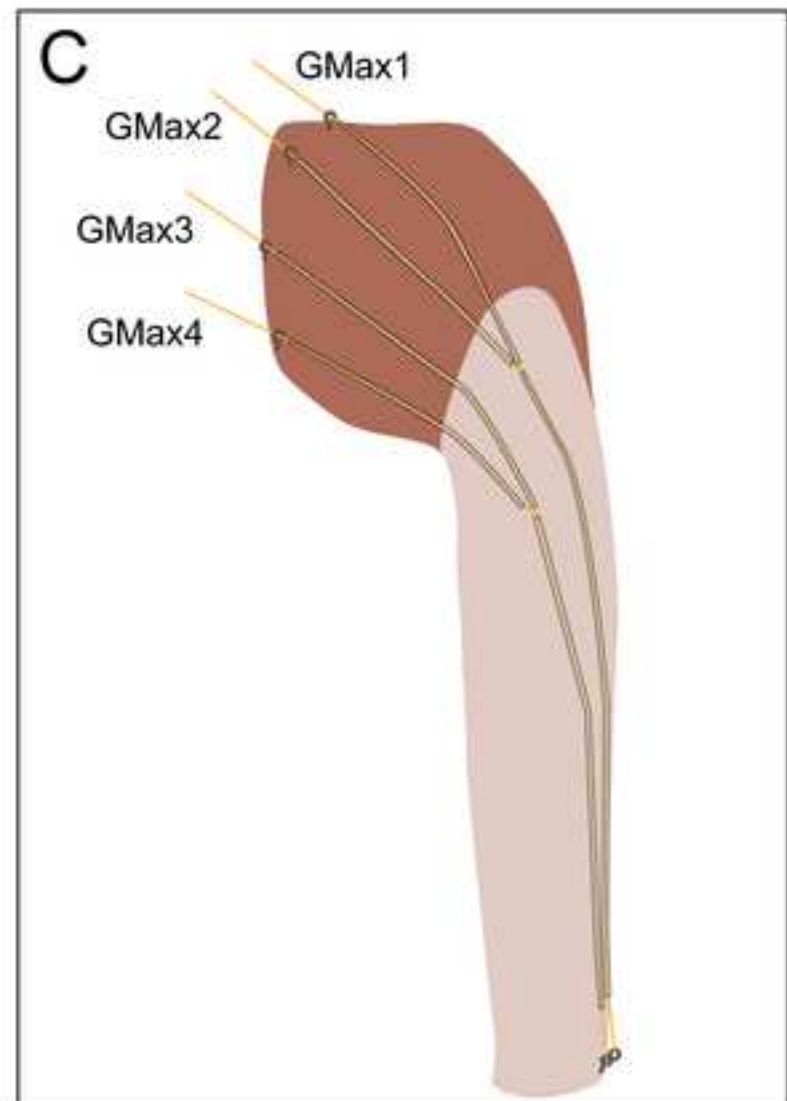
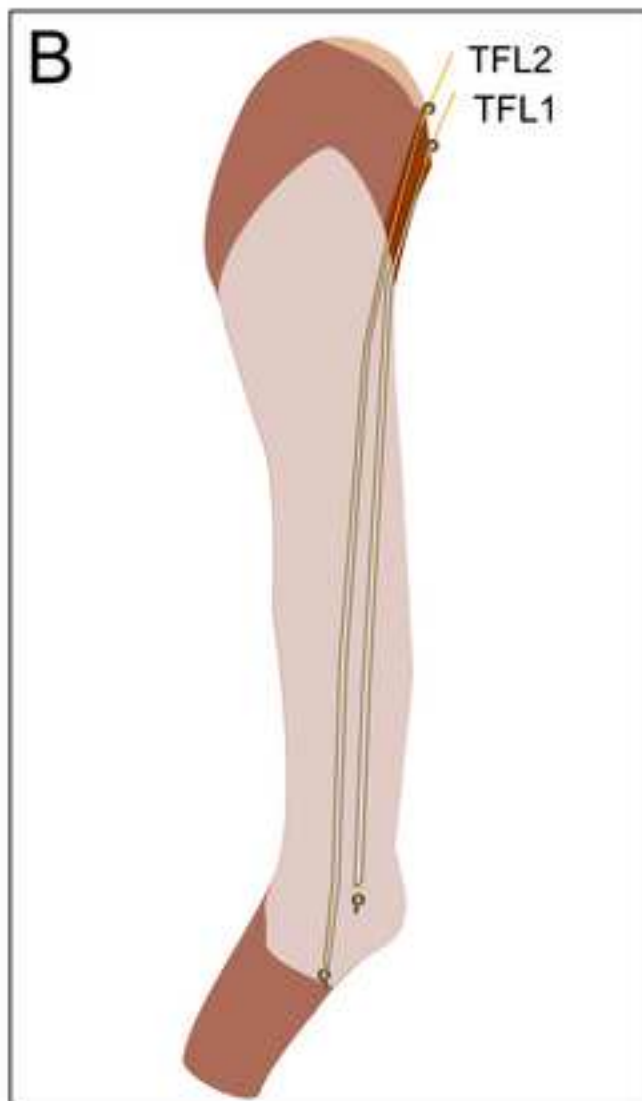


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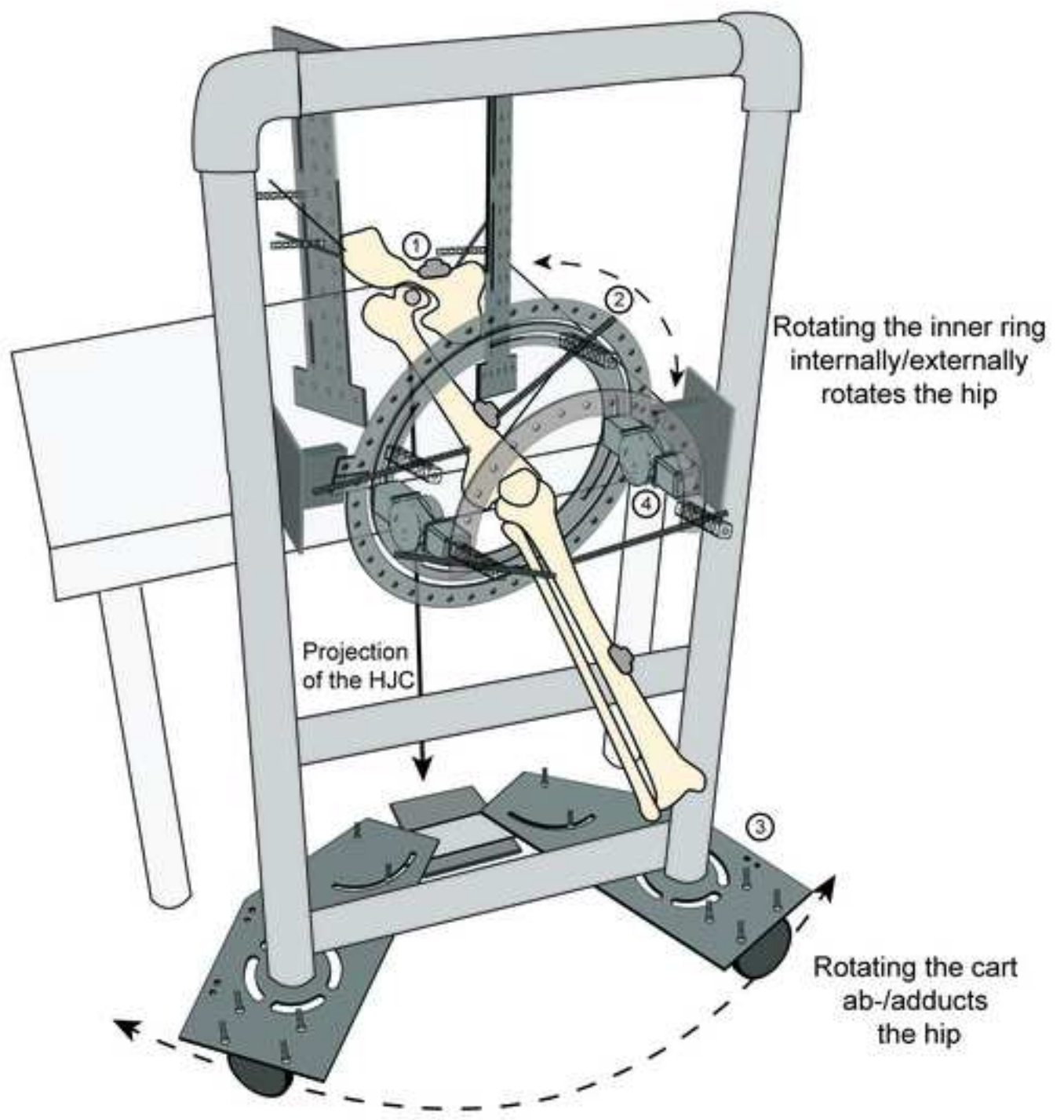


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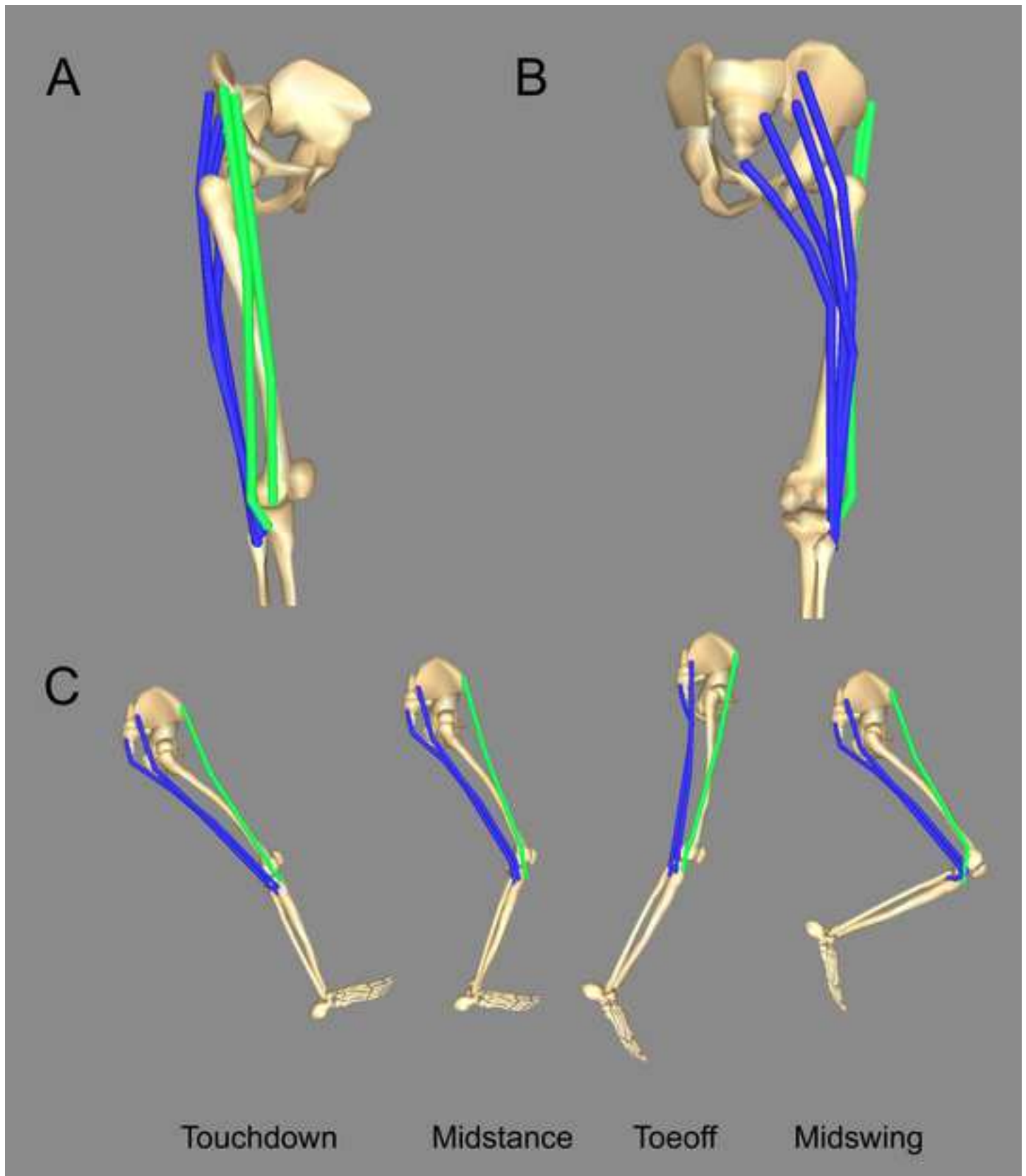


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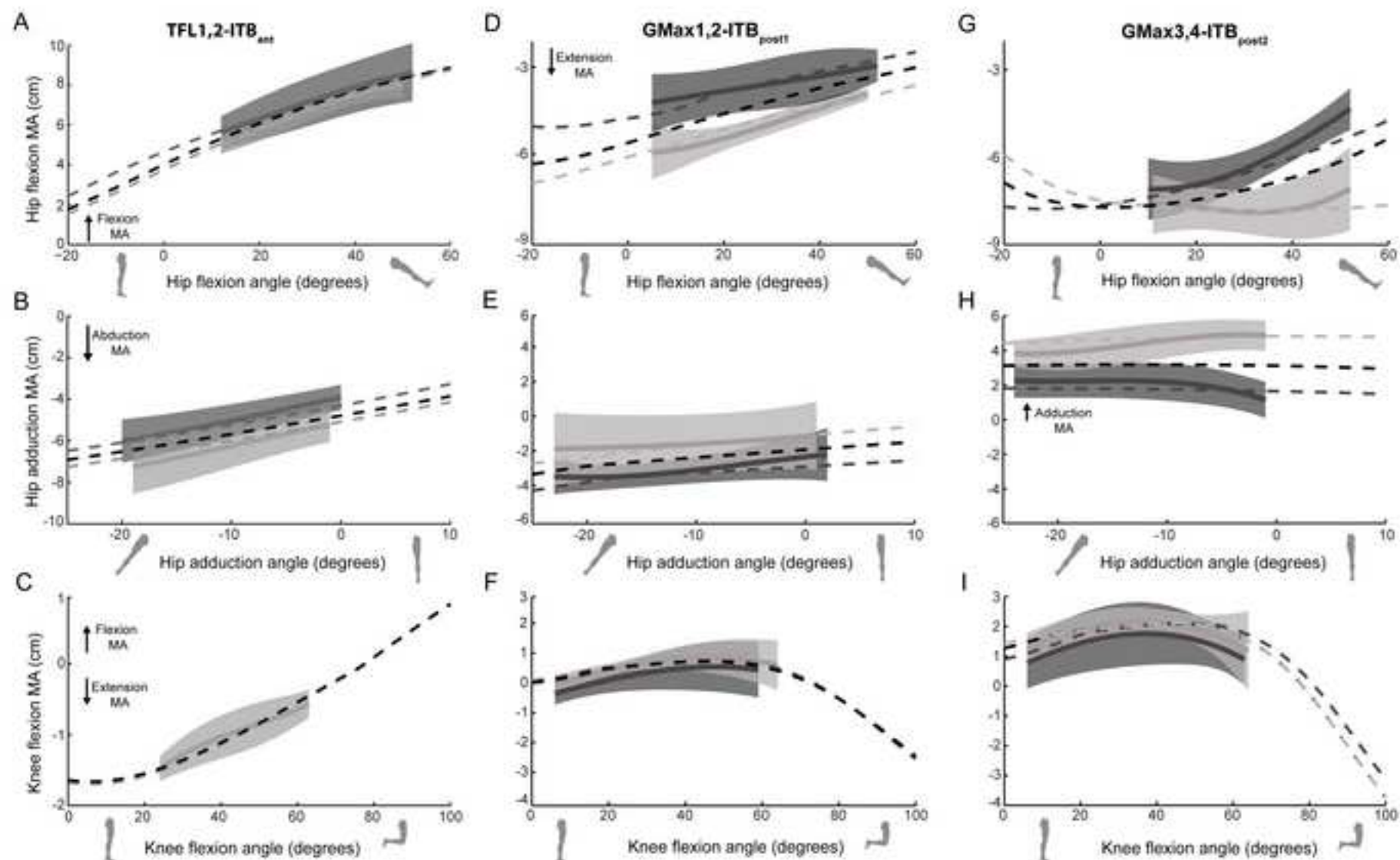


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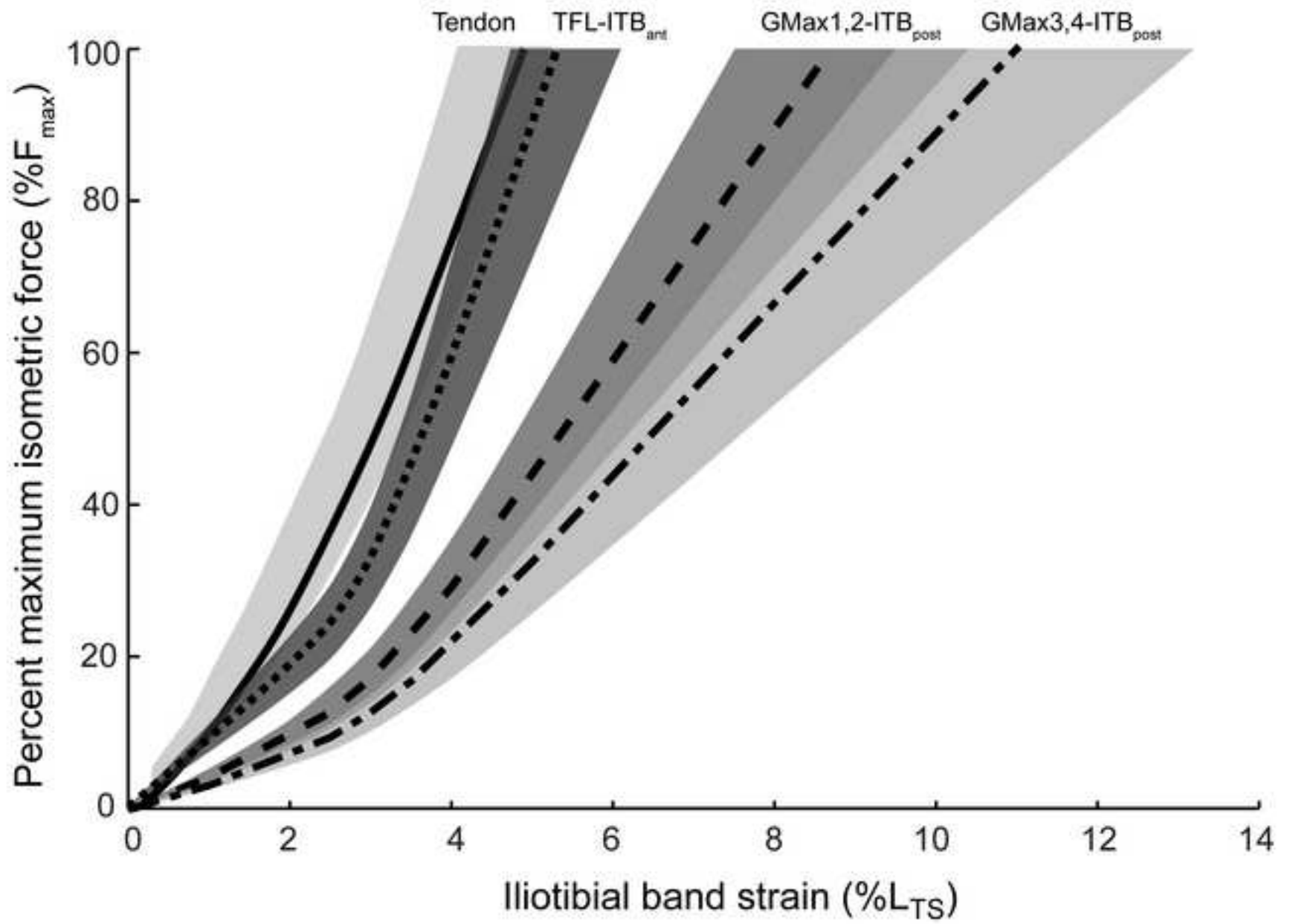


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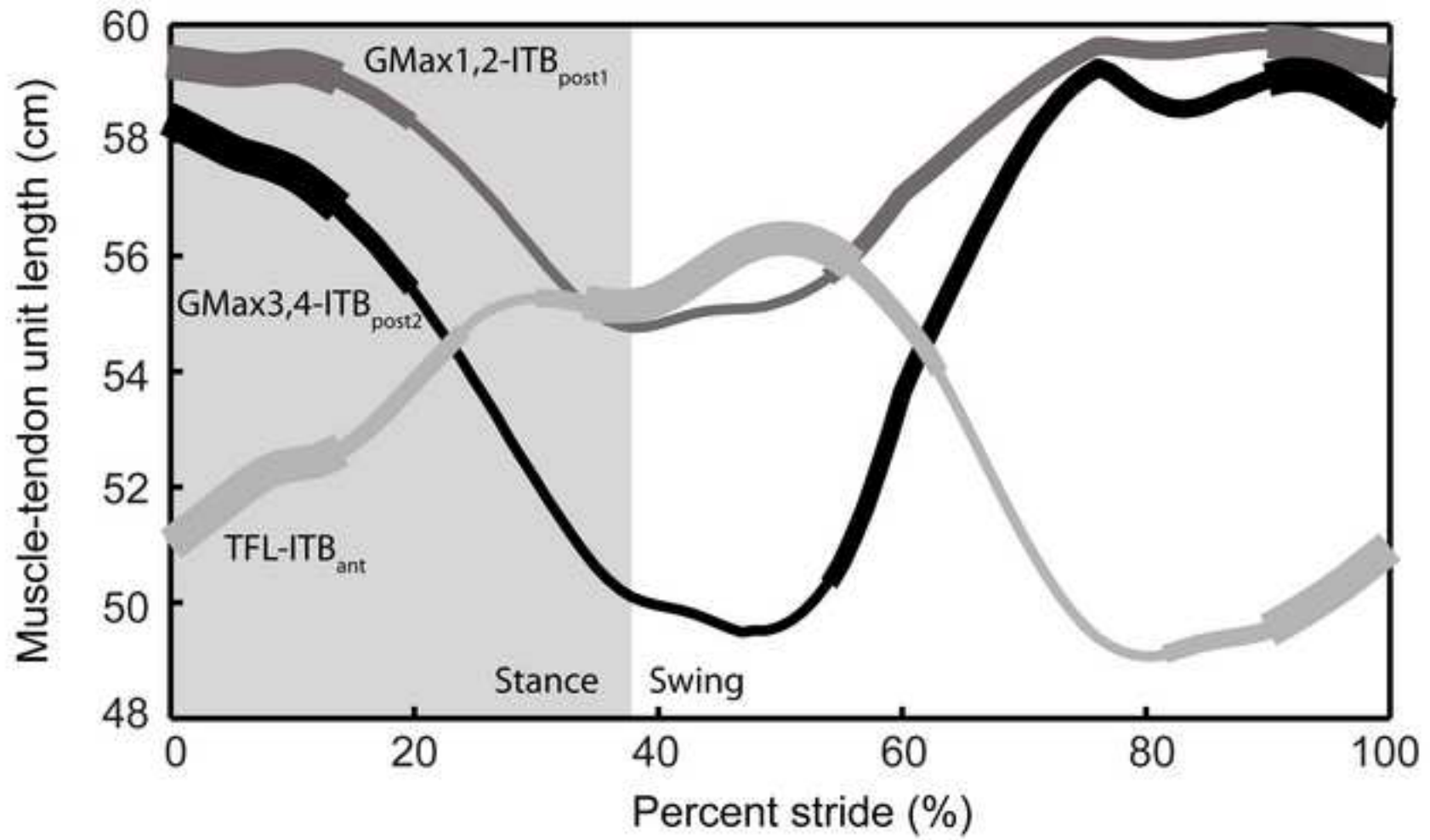


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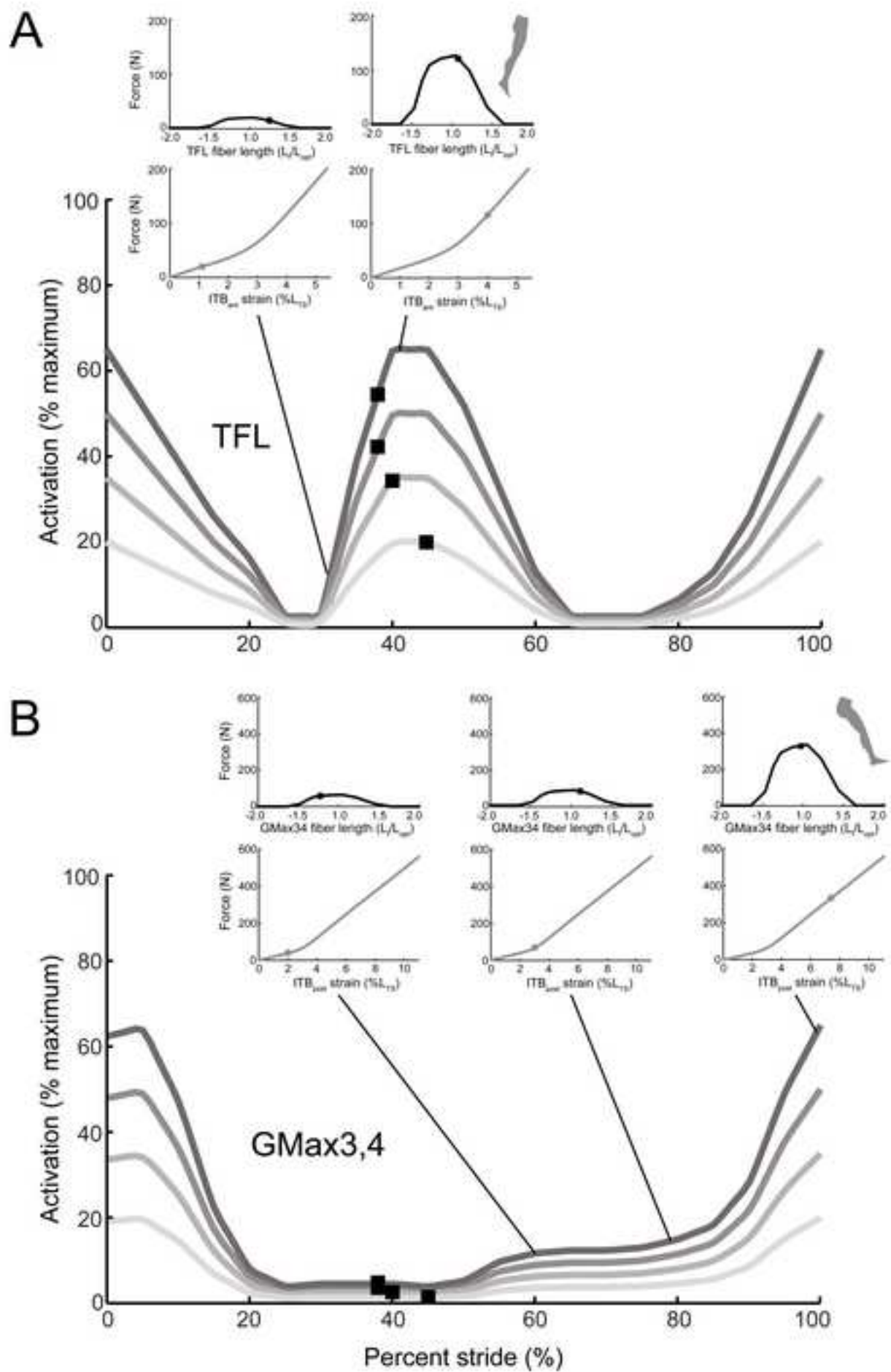
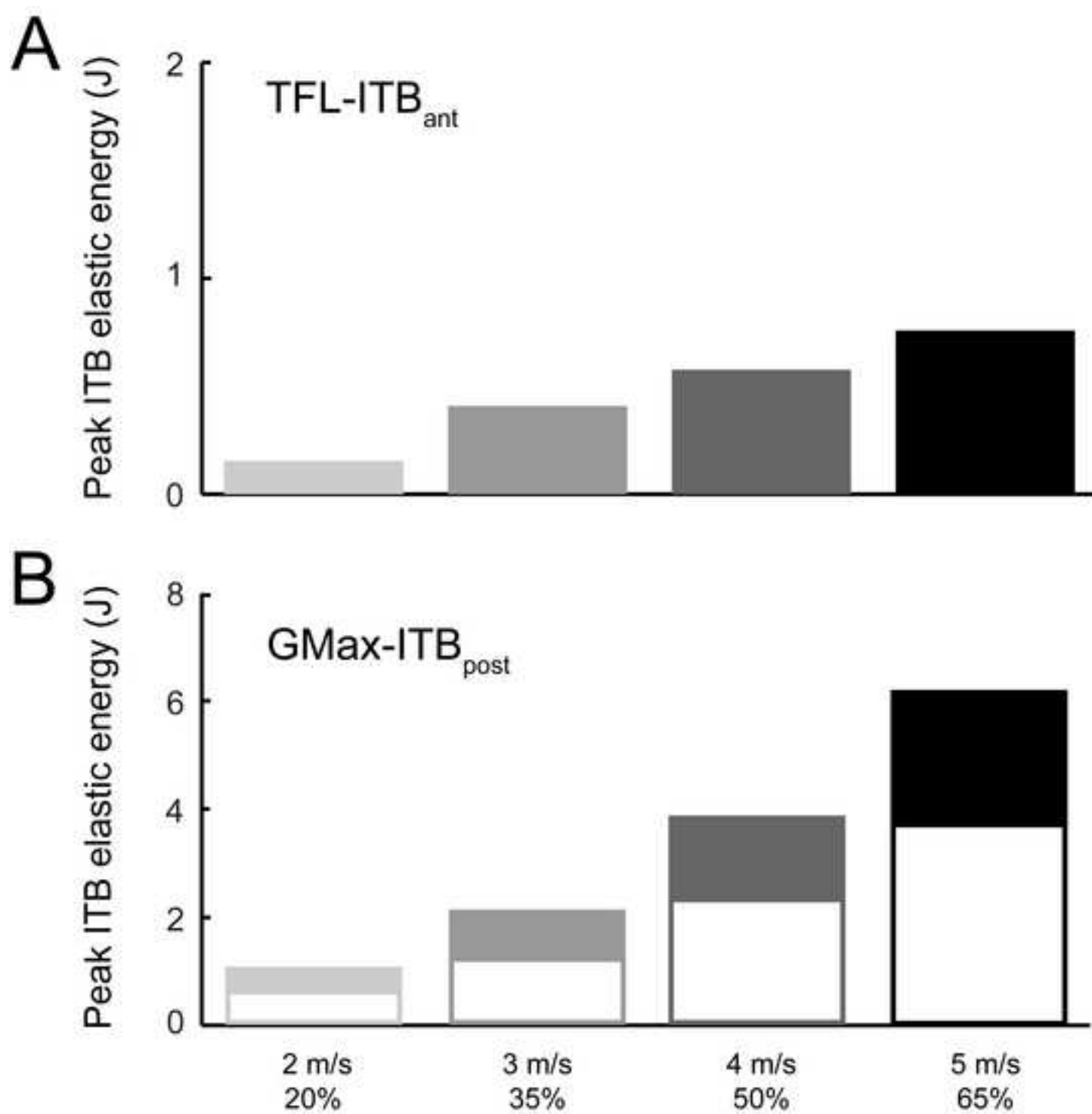
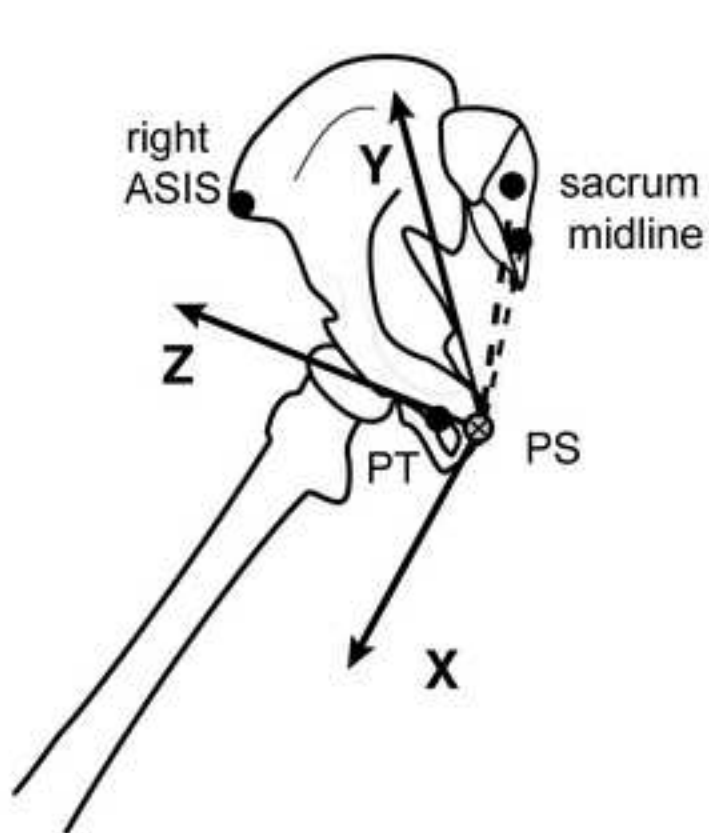
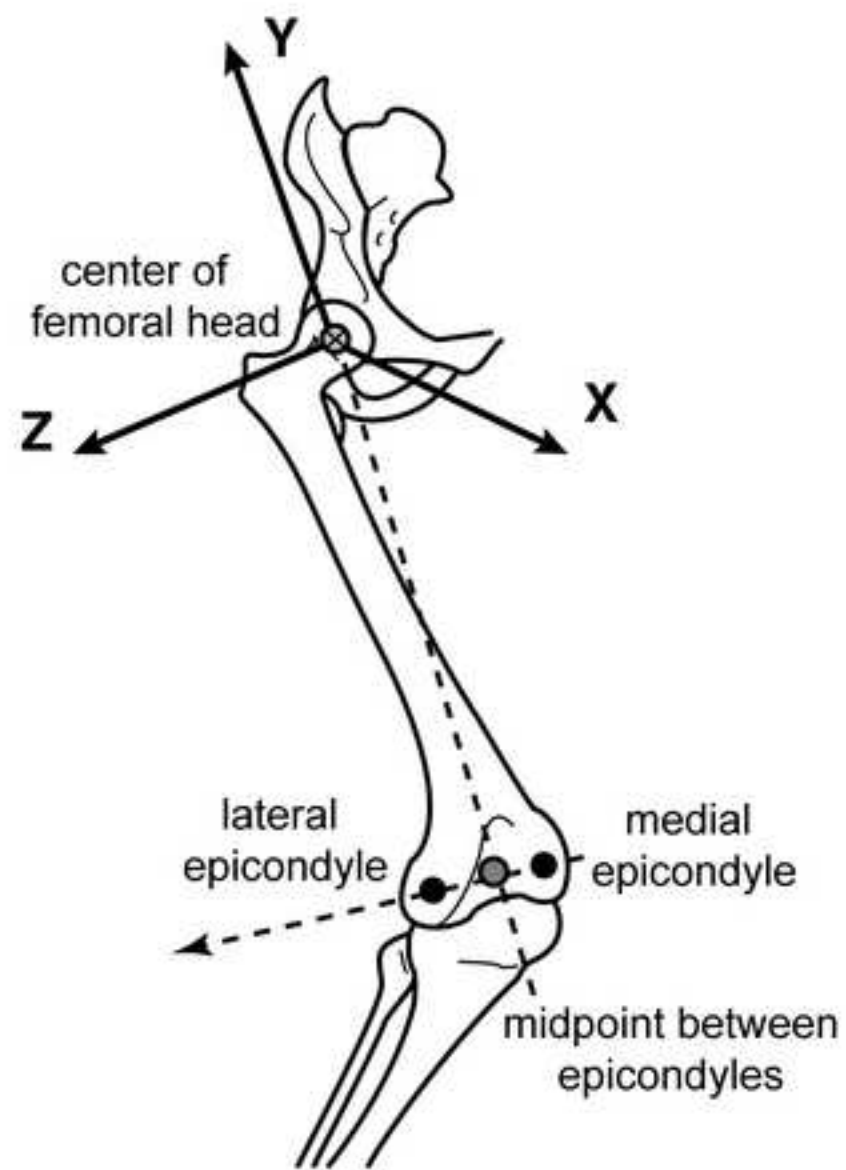


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Pelvis Coordinate System



Femur Coordinate System

Figure S2

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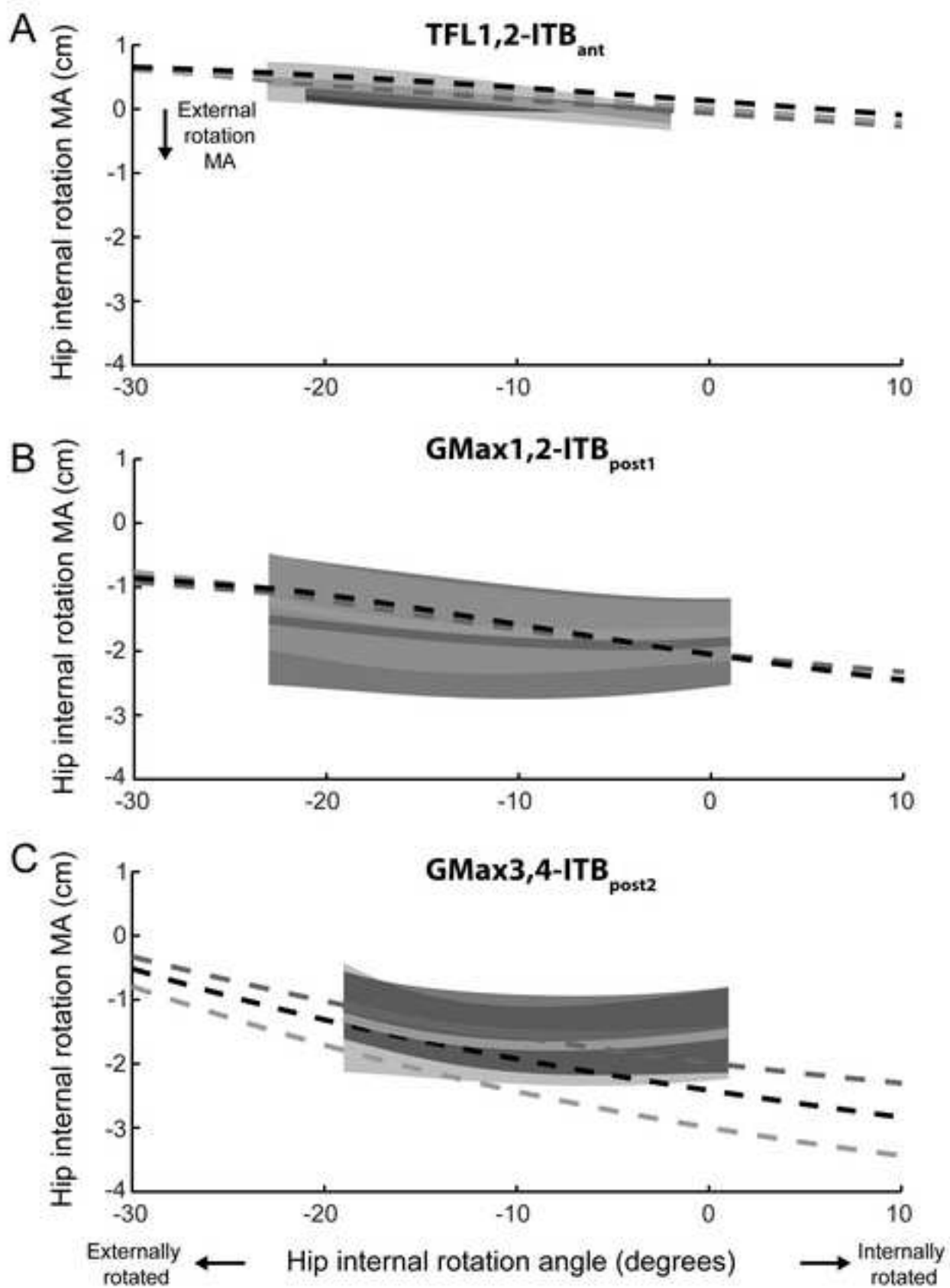


Table 1. Muscle architecture of tensor fascia lata (TFL) and gluteus maximus (GMax*)

Muscle	Mass (g)	Optimal fascicle length (cm)	Pennation angle (deg.)	PCSA* (cm²)
TFL	35.5 ± 9.6	9.8 ± 0.7	1.1 ± 1.1	3.2 ± 1.0
GMax	412.1 ± 69.7	14.4 ± 0.7	26.3 ± 5.0	30.6 ± 5.1

Data from 3 elderly cadaveric specimens (2 male, 1 female; mean age: 78 ± 6 years) are expressed as mean ± s.e.m.

*Pennation angle is not included in the PCSA calculation since our SIMM model multiplies PCSA, specific tension, and pennation angle to determine a muscle's maximum isometric force.

Table 2. Muscle regional masses of tensor fascia lata (TFL) and gluteus maximus (GMax)

Muscle	Total mass of region (g) (n=5)	Percentage of mass inserting on ITB (%) (n=2)
TFL1 [∞]	26.4 ± 7.2	100%
TFL2	21.4 ± 5.5	100%
GMax1 [‡]	110.6 ± 26.2	44.6 ± 4.9%
GMax2	109.4 ± 24.8	52.7 ± 7.8%
GMax3	121.9 ± 19.8	47.7 ± 11.3%
GMax4	104.7 ± 29.7	71.7 ± 28.3%

Data from 5 adult males (mean age: 62 ± 10 years) are expressed as mean ± s.e.m.

[∞]TFL was divided into two anterior-posterior regions based on origin and fascicle orientation.

[‡]GMax was separated into four superior-inferior regions.

Table S1. Parameters used to scale a generic Hill-type muscle model to TFL- and GMax-ITB muscle-tendon units

Muscle-tendon unit	Maximum isometric force (N; F_{max})[‡]	Optimal fiber length (cm; L_{opt})	Pennation angle (deg; θ)	Tendon slack length (cm; L_{TS})
TFL1,2-ITB _{ant} [§]	195.2	9.8	2.5	42.6
GMax1,2-ITB _{post1} [*]	455.9	15.2	26.3	42.3
GMax3,4-ITB _{post2} [*]	558.6	16.7	26.3	41.0

[§]TFL $PCSA$, L_{opt} , and θ and GMax $PCSA$ and θ from our measurements.

^{*}GMax L_{opt} from Ward et al. (2009).

[‡] F_{max} calculated as the product of $PCSA$ and muscle specific tension of 61 N/cm² used by Arnold et al. (2010).

Table S2. ITB thickness and width measurements used to calculate effective cross-sectional area and stiffness of each region

ITB Region	Thickness (mm)[*]	Width (mm)
ITB _{ant}	0.87 ± 0.34	16.35 ± 2.03
ITB _{post1}	0.97 ± 0.12	16.85 ± 1.85
ITB _{post2}		15.33 ± 1.86

Data from 3 elderly cadaveric specimens (2 male, 1 female; mean age: 78 ± 6 years) are expressed as mean ± s.e.m.

^{*}Thicknesses of anterior and posterior regions were measured at proximal, middle, and distal sites and averaged across sites.