1   **Intrinsic foot muscles contribute to elastic energy storage and return in the human foot**

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Abstract

The human foot is uniquely stiff to enable forward propulsion, yet also possesses sufficient elasticity to act as an energy store, recycling mechanical energy during locomotion. Historically this dichotomous function has been attributed to the passive contribution of the plantar aponeurosis. However, recent evidence highlights the potential for muscles to actively modulate the energetic function of the foot. Here we test the hypothesis that the central nervous system can actively control the foot's energetic function, via activation of the muscles within the foot's longitudinal arch. We used a custom-built loading apparatus to deliver cyclical loads to human feet *in-vivo*, in order to deform the arch in a manner similar to that observed in locomotion. We recorded foot motion and forces, alongside muscle activation and ultrasound images from flexor digitorum brevis (FDB), an intrinsic foot muscle that spans the arch. When active, the FDB muscle fascicles contracted in an isometric manner, facilitating elastic energy storage in the tendon, in addition to the energy stored within the plantar aponeurosis. We propose that the human foot is akin to an active suspension system for the human body, with mechanical and energetic properties that can be actively controlled by the central nervous system.

New and Noteworthy

The human foot is renowned for its ability to recycle mechanical energy during locomotion, contributing up to 17% of the energy required to power a stride. This mechanism has long been considered passive in nature, facilitated by the elastic ligaments within the arch of the foot. In this paper, we present the first direct evidence that the intrinsic foot muscles also contribute to elastic energy storage and return within the human foot. Isometric contraction of the *flexor digitorum brevis* muscle tissue facilitates tendon stretch and recoil during controlled loading of the foot. The significance of these muscles has been greatly debated by evolutionary biologists seeking to understand the origins of upright posture and gait, as well as applied and clinical scientists. The data we present here shows a potential function for these muscles in contributing to the energetic function of the human foot.

Introduction

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59 The human foot is a mechanical paradox. Compared to other non-human primates, the foot is

60 uniquely stiff, enabling forward propulsion (2, 7). Yet, the foot is also renowned for

61 compliance, possessing spring-like qualities that allow mechanical energy to be stored and

62 returned during each step, substantially improving the economy of locomotion (22, 31). This

63 unique interplay of mechanical function is considered to have played an important role in the

64 evolution to habitual upright locomotion (4).

65 The plantar aponeurosis and plantar ligaments have been attributed much of the credit for

66 determining human foot function. These ligamentous structures provide a means to store and

67 return mechanical energy via elastic stretch and recoil (22), whilst also passively increasing

68 foot stiffness to facilitate forward propulsion, via the windlass mechanism (14). The spring-

69 like function of the foot is considered a vital element in economical human locomotion,

70 providing a means to recycle mechanical energy, without the added metabolic cost of

71 activating muscles (22). However, the model of the foot as a passive structure, does not

72 explain the capacity for the foot to adapt to the varied mechanical requirements of

73 locomotion, with constantly varying speeds and substrates, whilst still facilitating effective

74 foot-ground force transmission (2, 6, 21). If the foot spring mechanism were purely passive in

75 nature, the magnitude of energy stored and returned within the foot would be directly

76 dependent on the magnitude of strain produced in the plantar aponeurosis and ligaments. In

77 contrast to this assertion, it has recently been shown that the magnitude of negative and

78 positive work performed at the foot can vary considerably with locomotion requirements,

79 independently of the magnitude of plantar aponeurosis strain (16, 18, 29). This suggests that

80 structures other than the ligamentous tissues of the foot may also be contributing to the

81 energetic function of the foot, and importantly, the foot spring may not be an entirely passive

82 mechanism.

83 The plantar intrinsic foot muscles are a group of muscles located within the longitudinal arch

84 (LA). They have muscle tendon units (MTUs) that course a parallel anatomical pathway to

85 the plantar aponeurosis, spanning from the calcaneus to the toes (24, 27), and therefore

86 generate torques about the LA in the same direction as the plantar aponeurosis. The plantar

87 intrinsic muscles display similar activation patterns to that of the triceps surae (calf) muscles,

88 with recruitment occurring prior to foot-ground contact and de-activation occurring through

89 late stance, during propulsion (20). We have estimated in previous experiments that the

90 MTUs of the largest intrinsic foot muscles, *flexor digitorum brevis* (FDB) and *abductor*

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hallucis (AH) actively lengthen and shorten during stance phase of locomotion, highlighting the potential for these muscles to perform negative and positive work at the foot, in addition to that performed by the plantar aponeurosis (20).

In a similar anatomical arrangement to the ankle plantar flexor muscles and Achilles tendon, the FDB and AH muscles have very short muscle fibres (<25 mm) attached to long tendons (~100mm) (24, 27, 35), making them candidates for significant storage and return of elastic energy during a stretch-shorten cycle (3, 36)(3, 36). The plantar flexors have been shown to operate near isometrically during the stance phase of walking and running (13, 25, 28), allowing energy to be recycled through stretch and shorten of the elastic tendon. Given the structure and function of the intrinsic foot muscles, it is certainly feasible that a quasi-isometric function of the contractile tissue may actually facilitate elastic energy storage within the tendons of these muscles. This function may act to modulate the foot's energy storage capacity, in addition to the contribution of the plantar aponeurosis.

Here we explored whether the foot-spring mechanism is actively modulated by the central nervous system (CNS), via the function of the intrinsic foot muscles. Specifically we tested the hypothesis that FDB muscle would produce force in a quasi-isometric manner, facilitating storage and return of elastic energy within the tendinous tissue during compression and recoil of the foot's arch, providing additional scope for recycling of energy within the foot.

Methods

Participants

Ten healthy participants (one female and nine males, age 27 ± 7 years; height: 179 ± 7 cm; mass: 76 ± 10 kg) with no diagnosed history of lower limb injury in the previous six months or known neurological impairment volunteered to participate in the study. Written informed consent was obtained from each subject. The study protocol was approved by the institutional human research ethics committee of The University of Queensland and conducted in accordance with the Declaration of Helsinki.

Experimental Set-up

Each participant was seated with their right forefoot placed on a rigid supporting platform that was secured to a force plate (AMTI OR6-7-1000, AMTI, MA, USA). The ankle was orientated in approximately 10° of dorsiflexion and the thigh was parallel to the floor. A magnetically driven, servo-controlled actuator, connected to a computer with real time

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122   control of force output (Linmot PS10-70x400U-BL-QJ, NTI AG Linmot, Switzerland) was

123   positioned such that loads of up to 150% of body weight could be delivered in a downwards

124   direction to the distal aspect of thigh at controlled speeds, using a custom-built loading

125   apparatus (Figure 1). The heel was positioned on a horizontal plane with the forefoot, when

126   unloaded, and could move freely during each loading cycle. The loading apparatus was

127   positioned over the thigh such that the resultant ground reaction force vector was located

128   anterior to the ankle joint axis, similar to where it is located during mid to late-stance in

129   locomotion. This experimental set-up was designed to best replicate the gravitational and

130   muscular forces acting on the lower limb during locomotion, in a tightly controlled manner.

131   <u>Experimental Protocol</u>

132   The actuator induced five compression cycles of the foot, delivered sequentially with

133   approximately 10 s between each cycle. The time between each foot compression cycle was

134   varied by $\pm$ 2 s, to prevent preparatory activation prior to loading. Foot compression cycles

135   were performed at three loads; Low (50% BW), Moderate (100% BW) and High (150%

136   BW), reflecting the vertical ground reactions forces in bipedal stance (Low), unipedal stance

137   (Medium) and walking (High). The rate of loading and unloading delivered by the actuator

138   was programmed to remain constant across all conditions, with total cycle duration of 2

139   seconds. During the foot compression cycles, participants were instructed to maintain their

140   heel at the same height as their forefoot through active plantar flexion of the ankle. This was

141   achieved by activating the ankle plantar flexors to generate an internal ankle plantar flexion

142   torque, countering the torque at the ankle created by the actuator. Verbal feedback was given

143   to participants during and after each trial regarding their capacity to keep the heel in a

144   relatively constant position. This experimental approach was chosen in order to produce

145   sufficient force in the Achilles tendon, which is required to induce compression of the LA in

146   a similar manner to that observed during locomotion (11) (Figure 1).

147   <u>Data Acquisition</u>

148   *Kinematic and kinetic measurements*

149   Motion data was captured at 200 Hz using a six-camera 3D optoelectronic motion capture

150   system (Oqus, Qualysis, Gothenburg, Sweden). Ground reaction force (GRF) and

151   electromyography (EMG) data were synchronously captured with the motion data at 4 kHz

152   using a 14-bit analogue to digital converter using and the Qualisys Track Management

153   software (Qualisys, Gothenburg, Sweden). Fourteen retro-reflective markers (diameter 9.0

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154   mm) were placed on the skin of the right foot and ankle according to a multi-segment foot

155   model developed to describe rear-, mid and forefoot motion (26). Two additional markers

156   were applied to the skin over the second and fourth toes, at the level of the middle phalanx, in

157   order to track the movement of the lesser toes. Three markers were placed on the shank and a

158   marker placed on the medial and lateral femoral condyles in order to track the position of the

159   shank segment (20).

160   *Muscle activation measurements*

161   Fine-wire intra-muscular electromyography (EMG) data was collected from the right foot of

162   each participant in accordance with previously described methods (20). All EMG signals

163   were amplified 1000 times and hardware filtered with a bandwidth of 30 to 1000 Hz

164   (MA300, Motion Labs, LA, USA). Surface EMG electrodes were also placed over the muscle

165   belly of soleus (SOL). In order to prevent movement artefacts, the fine-wire electrodes,

166   connectors, cabling and pre-amplifiers were secured with cohesive bandage around the distal

167   part of the shank. A surface ground electrode (Ag–AgCl electrode, 24 mm diameter; Tyco

168   Healthcare Group) was secured to the skin overlying the medial malleolus.

169   *Ultrasound measurements*

170   Muscle fascicle length for the FDB in the loaded foot was measured using B-mode ultrasound

171   imaging. A 128-element linear array ultrasound transducer (SonixTouch, Ultrasonix, BC,

172   Canada) was placed under the foot such that it imaged the muscle tissue of the FDB at an

173   orientation where the fascicles of the mid-belly could be visualised throughout the muscle.

174   The transducer was bandaged securely to the foot to hold it in place during the loading cycles

175   (Figure 1). Ultrasound images were sampled at 26 Hz.

176   <u>Data Analysis</u>

177   Kinetic, kinematic and EMG data files were exported to Visual3D (C-motion Inc.,

178   Germantown, MD, USA) for analysis. Analogue signals from the force plate were digitally

179   filtered with a 35 Hz recursive second order Butterworth filter. A force onset-offset threshold

180   was defined at 10% above the baseline vertical GRF (eg. 10% more than the mass of the leg

181   and foot). The start of the loading cycle was determined as the time-point when the rising

182   edge of the vertical GRF rose above the onset-offset threshold, while the end of the loading

183   cycle was determined as the time-point when the falling edge of the vertical GRF fell below

184   this threshold. Subsequently the peak vertical GRF was calculated during each loading cycle

185   and normalised to bodyweight (BW).

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Kinematic & Kinetic data

187   Marker trajectories were digitally filtered with a 10 Hz recursive second order low pass

188   Butterworth filter. Assumed rigid segments were created in accordance with a previously

189   described multi-segment foot model (26) including the shank, foot, calcaneus and

190   metatarsals. Ankle angle was defined as the rotation of the calcaneus segment relative the

191   shank segment, in the sagittal plane, with ankle dorsiflexion represented as positive rotations.

192   The mid-foot angle was defined as the sagittal plane rotation of the metatarsals relative to the

193   calcaneus, with mid-foot dorsiflexion being positive [15]. Under this definition, an increase

194   in mid-foot angle is indicative of a reduction in LA height. Ankle and mid-foot angles were

195   offset to a static unloaded trial, such that the unloaded angles are 0°. For each loading

196   condition, LA compression was calculated by subtracting the mid-foot angle at the start of the

197   loading cycle from the peak mid-foot angle recorded during the ensuing cycle. Mean LA

198   compression was calculated for each loading condition by averaging LA compression

199   occurring across all loading cycles for each loading condition.

200   Net joint moments generated about the mid-foot during each loading cycle were calculated by

201   applying an inverse dynamic analysis within Visual 3D software (C-Motion Inc,

202   Germantown, MD, USA) in accordance with previously described techniques (5, 18). Mid-

203   foot moments were represented as internal joint moments in the proximal segment's co-

204   ordinate system. Mean peak mid-foot plantar-flexion moment was calculated at each load by

205   averaging the peak values calculated during each foot compression cycle for a given

206   condition.

207   *Foot Power Analysis*

208   We applied a unified deformable (UD) foot model to quantify the instantaneous power of the

209   foot during the foot compression cycles (34). This approach (described in detailed elsewhere

210   (32-34)) represents the power due to the six degree of freedom movement between the

211   calcaneus and the ground, providing an estimate of combined power from all structures

212   within the foot distal to the calcaneus.

213   *Muscle-tendon unit length*

214   The length of the FDB MTU was calculated based on multi-segment foot motion, using a

215   previously described geometric model (20). Briefly, the MTU length was defined as the

216   straight-line distance from the muscle origin at the calcaneus, to the insertion at the toes, via a

217   tether point at the metatarso-phalangeal joint. Change in MTU length was calculated by

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218 subtracting the resting unloaded MTU length from the MTU length during each loading
219 cycle. The resting MTU length was calculated during a static unloaded trial, with the foot in
220 the experimental position. Subsequently, MTU strain was calculated by dividing the change
221 in MTU length by the resting MTU length. The shortening and lengthening velocity of the
222 FDB MTU was calculated as the first derivative of the MTU length with respect to time,
223 during each loading cycle.

224 *Muscle activation*
225 All EMG signals were high-pass filtered using a recursive second-order Butterworth filter at
226 35 Hz to remove any unwanted low-frequency movement artefact. Following DC-offset
227 removal, a root mean square (RMS) signal amplitude was calculated using a moving window
228 of 50 ms to generate an EMG envelope. The EMG envelope for the FDB and SOL muscles
229 was normalized to the peak RMS amplitude found across all conditions for the respective
230 muscle. Subsequently the magnitude of activation for each loading condition was determined
231 by calculating an average of the mean EMG RMS envelope amplitude during each
232 compression cycle, for each muscle.

233 *Muscle fascicle length*
234 Length changes of FDB muscle fascicles were assessed from the B-mode ultrasound images
235 recorded during each loading cycle. A previously described semi-automated tracking
236 algorithm was used track fascicle length throughout each trial (8, 12). Briefly, an area of
237 interest within the FDB muscle and a representative muscle fascicle was defined at the first
238 frame of the ultrasound data. Subsequently, the ultrasound image sequence was processed
239 using the Ultra-Track software (12), which tracks the end points of fascicles in a frame to
240 frame, iterative fashion. Once the image processing was complete, instantaneous muscle
241 fascicle length was produced as an output. Change in FDB fascicle length was calculated by
242 subtracting the resting unloaded fascicle length from the fascicle length during each foot
243 compression cycle. The resting fascicle length was calculated during a static, unloaded trial,
244 with the foot in the experimental position. Muscle fascicle strain was calculated by dividing
245 the change in fascicle length by the resting fascicle length. Shortening and lengthening
246 velocity of the FDB fascicles were calculated as the first derivative of their lengths with
247 respect to time, during each foot compression cycle.

248 <u>Statistics</u>

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249   A one-way repeated measures analysis of variance (ANOVA) was used to describe the
250   effects of loading condition (Low/Medium/High) on mid-foot angular displacement, peak
251   mid-foot moment, FDB muscle-tendon unit and fascicle length changes and average muscle
252   activation. Post-hoc multiple comparison tests including Bonferroni corrections were
253   performed between each loading condition. Statistical differences were established at P ≤
254   0.05. Results are presented as mean difference + standard deviation unless otherwise stated.
255   Effect sizes (ES) were calculated using partial ETA squared. Mid-foot motion and mid-foot
256   moment data was obtained from 9 participants, with one participant excluded due to issues
257   with marker reconstruction.

258   **Results**
259   During each foot compression cycle, vertical GRF increased (peak GRF 0.7 ± 0.1 BW at
260   Low, 1.1 ± 0.07 BW at Medium and 1.5 ± 0.2 BW at High, $P \leq 0.05$, ES = 0.94, Figure 2) as
261   downward force was applied by the actuator (loading phase), subsequently declining as the
262   force from the actuator was removed (unloading phase). Loading cycle duration remained
263   relatively constant across all conditions (1.85 ± 0.40 s at Low, 1.78 ± 0.35 s at Medium and
264   1.77 ± 0.35 s at High).

265   *Ankle Mechanics*
266   The ankle remained in a relatively constant orientation across all conditions, even though a
267   small increase in ankle joint dorsiflexion was observed between the 0.5 BW and 1.5 BW
268   conditions (Δ angle of 1.0 ± 0.5^{o} at Low, 2.2 ± 0.8^{o} at Medium and 2.5 ± 1.4^{o} at High, $P \leq$
269   0.05, ES = 0.53). Average SOL muscle activation increased substantially with increasing foot
270   compression force ($19.0 \pm 4.6\%$ at Low, $27.8 \pm 5.4\%$ at Medium and $35.0 \pm 7.4\%$ at High, $P \leq$
271   0.05, ES = 0.81, Figure 2).

272   *Foot Mechanics*
273   The LA compressed as force was applied to the leg by the actuator (loading phase) and
274   subsequently recoiled as the force was removed (unloading phase), in a similar manner to that
275   observed during locomotion (Figure 3). The magnitude of LA compression increased with
276   increasing foot compression force (3.0 ± 1.2^{o} at Low, 4.3 ± 1.2^{o} at Medium and 5.0 ± 1.6^{o} at
277   High, $P \leq 0.05$, ES = 0.85). Mid-foot plantar flexion moment increased substantially as
278   compression force increased (-0.27 ± 0.08 Nm.kg^{-1} at Low, -0.45 ± 0.17 Nm.kg^{-1} at Medium
279   and -0.59 ± 0.20 Nm.kg^{-1} at High, $P \leq 0.05$, ES = 0.81).

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280   The foot absorbed energy during the loading phase of the foot compression cycle, and

281   subsequently returned / generated mechanical energy during the unloading phase (Figure 3).

282   The magnitude of negative work (-0.03 ± 0.01 J.kg^{-1} at Low, -0.06 ± 0.02 J.kg^{-1} at Medium

283   and -0.10 ± 0.04 J.kg^{-1} at High, P ≤ 0.05, ES = 0.80) and positive work (0.03 ± 0.01 J.kg^{-1} at

284   Low, 0.07 ± 0.01 J.kg^{-1} at Medium and 0.10 ± 0.03 J.kg^{-1} at High, P ≤ 0.05, ES = 0.85)

285   increased with compression force. However, the net work performed by the foot remained

286   constant and was always close to zero (0.002 ± 0.005 J.kg^{-1} at Low, 0.004 ± 0.02 J.kg^{-1} at

287   Medium and 0.002 ± 0.02 J.kg^{-1} at High, P = 0.67, ES = 0.04).

288   *Flexor Digitorum Brevis Function*

289   The FDB MTU (unloaded length of 231 ± 11 mm) lengthened during the loading phase and

290   shortened during the unloading phase of the foot compression cycles . The magnitude of FDB

291   MTU stretch increased with load (4 ± 1 mm at Low, 5 ± 1 mm at Medium and 6 ± 1 mm at

292   High, P ≤ 0.05, ES = 0.82). For all loading conditions, the MTU displayed a positive

293   (lengthening) velocity during the loading phase and negative (shortening) velocity during the

294   unloading phase of the compression cycle (Figure 4). There was a significant group effect of

295   load on peak MTU lengthening velocity (17.1 ± 6.3 mm.s^{-1} at Low, 21.0 ± 4.8mms^{-1} at

296   Medium and 22.3 ± 7.4 mm.s^{-1} at High, P ≤ 0.05, ES = 0.32). However, post-hoc analysis

297   indicated that only the Low and High conditions were significantly different (P ≤ 0.05), while

298   the Medium condition was no different to either the Low or High conditions (0.5 BW v 1.0

299   BW, P=0.21 and 1.0 BW v 1.5 BW, P = 0.90). Peak MTU shortening velocity significantly

300   increased between each loading condition (-10.3 ± 6.4 mm.s^{-1} at Low, -14.5 ± 6.9 mm.s^{-1} at

301   Medium and -18.0 ± 9.2 mm.s^{-1} at High, P ≤ 0.05, ES = 0.50).

302   The FDB muscle fascicles were approximately 10% of the unloaded MTU length (unloaded

303   fascicle length of 22.0 ± 0.4 mm). Generally, the fascicle length changes during the foot

304   compression cycles were small (< 1 mm). Across all conditions, the fascicles displayed an

305   initial stretch at the start of the compression cycle (0.2 - 0.4 mm, Figure 4). Subsequent to

306   this initial stretch, the muscle fascicles displayed a divergent behaviour between loading

307   conditions, depending on the magnitude of muscle activation, with activation increasing with

308   compression force (P ≤ 0.05, ES = 0.60). During the Low load condition, very little FDB

309   activation was observed (7.5 ± 4.0 % max). Accordingly, the muscle fascicles continued to

310   lengthen (net length change of 0.8 ± 0.3 mm) until peak vertical force, then shortening during

311   the unloading phase. In the Medium load condition, an increase in FDB activation was

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312 observed (16.3 ± 7.6 % max) and the fascicles shortened slightly, after the initial stretch, with
313 a net length change of -0.4 ± 0.4 mm from the unloaded fascicle length. In the High load
314 condition, a marked increase in FDB activation was observed (24.0 ± 10.5 %) and fascicles
315 shortened following the initial stretch with a net length change of -0.6 ± 0.4 mm from the
316 unloaded fascicle length. Subsequently the fascicles lengthened back to the unloaded length,
317 as the compression force declined.

318 Despite considerable differences in the temporal patterns of fascicle lengthening and
319 shortening during the foot compression cycles, the magnitude of fascicle shortening velocity
320 (-2.7 ± 1.8 mm.s^{-1} at Low, -3.2 ± 1.8 mm.s^{-1} at Medium and -3.6 ± 2.7 mm.s^{-1} at High, P =
321 0.35, ES = 0.11) and lengthening velocity (3.4 ± 1.4 mm.s^{-1} at Low, 3.6 ± 1.7 mm.s^{-1} at
322 Medium and 3.5 ± 1.4 mm.s^{-1} at High, P = 0.86, ES = 0.02) was similar between loading
323 conditions.

324 **Discussion**

325 This study provides novel evidence for active contributions to the foot-spring mechanism.
326 Compared to the overall length changes observed in the FDB MTU, the muscle fascicles
327 contracted in a relatively isometric nature, facilitating storage and return of strain energy in
328 the elastic tendon in conjunction with the plantar aponeurosis. The capacity to both increase
329 energy absorbed at the foot with muscle activation, and to increase power generated via recoil
330 of tendon, rather than muscle, provides the foot with an adaptive mechanism to deal with
331 changes in locomotion requirements. This may be of considerable importance during tasks
332 that require acceleration, deceleration or change of direction.

333 The parallel anatomical arrangement of the FDB muscle and the plantar aponeurosis provides
334 a unique mechanism for the CNS to utilise both passive and active structures to modulate the
335 energetic function of the foot. During tasks such as bipedal standing and slow walking, when
336 loading forces are low, the intrinsic foot muscles remain relatively inactive, unless there is a
337 significant perturbation to the centre of mass (19, 20). Presumably, under these loading
338 scenarios, the foot can effectively operate as a passive spring-like structure. However, during
339 tasks that require larger magnitudes of energy to be absorbed or generated, the intrinsic foot
340 muscles can provide additional energetic capacity for the foot. Our data shows that when
341 active, the contractile element of the FDB MTU remained at a relatively constant length, with
342 the tendon (in parallel with the plantar aponeurosis) undergoing all of the stretch imposed on
343 the MTU. The force produced by the muscle increased the mechanical energy stored within

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344 the in-series (tendon), adding to that stored in parallel (plantar aponeurosis) elastic

345 components. This interaction between passive and active elastic elements within the foot

346 helps to explain how large magnitudes of mechanical energy (12 - 24 J when running (16))

347 can be stored within a structure with such marked stiffness.

348 The FDB muscle has relatively short fibres and therefore the contractile element of the MTU

349 is limited in its capacity to generate mechanical power (3, 36). Based on FDB MTU length

350 changes and ground contact times reported in a previous experiment (20), we estimate that

351 the shortening velocity of this muscle approaches 8-10 fascicle lengths per second during

352 running. This is approaching the maximum shortening velocity predicted from the muscle

353 fibres (15). Thus, the power generating capacity of FDB would be almost completely

354 diminished if muscle fibres were required to add power alone. However, the attachment of an

355 elastic tendon allows the muscle to operate near isometrically, which is more favourable for

356 force production and facilitates energy storage in the tendon as the LA compresses. This

357 stored energy can be returned to the body as a burst of positive power as the LA recoils in

358 late stance, to aid forward propulsion. The tendon may also act as a buffer to attenuate some

359 of the energy associated with foot-ground collision, protecting the muscle fibres from

360 excessive stretch (23, 30) and potentially vibration (37).

361 An additional benefit of actively controlling the energetic function of the human foot is the

362 potential to transform the foot from an energy conserving structure to that of an energy

363 damper or motor, when locomotion requirements change. For example, active lengthening of

364 the FDB muscle fascicles during a rapid deceleration may help to dampen oscillations

365 associated with foot-ground contact (1), aiding in deceleration of the body's centre of mass.

366 Recent *in-vivo* data suggests that the foot functions more like a spring-damper during

367 locomotion, with a significant proportion of absorbed mechanical energy not being returned

368 to the body (34). It has been hypothesised that muscles within the foot may act to dissipate

369 some of this energy (34). Within the current experiment, the foot performed close to zero

370 mechanical work. This is probably due to the mechanical constraints of our experimental set-

371 up, with the mechanical actuator programed to perform external work on the foot in a

372 sinusoidal manner, with net zero mechanical work. Despite the foot performing zero

373 mechanical work and a predominantly isometric function of the FDB, periods of active

374 fascicle shortening and lengthening were observed. This suggests a potential for these

375 muscles to generate or dissipate mechanical energy, in order to adapt the foot energetic

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376 function during locomotion. Although, it must be highlighted that any length change and the

377 associated lengthening (or shortening) velocity in the FDB fascicles is very small (see Figure

378 4) compared to that of the entire MTU. Therefore, the magnitude of energy that can be

379 dissipated or generated by the contractile element of these muscles may be limited.

380 The underlying neurophysiology governing the control of this active tuning mechanism is of

381 considerable interest, but remains largely unknown. We have previously observed that the

382 intrinsic foot muscles remain relatively inactive until loads exceeding body mass are

383 encumbered on the foot, despite considerable deformation of the LA and MTU stretch (17).

384 Within the current experiment, we observed similar behaviour in the low-load condition, with

385 the FDB muscle remaining inactive, despite considerable MTU and fascicle stretch during the

386 loading phase of the foot compression cycle. This finding suggests the presence of inhibitory

387 inputs on the motoneurone pool of the FDB muscle. Indeed this notion is supported by a

388 relatively small range of modulation in H-reflex amplitude in the FDB muscle, compared to

389 other lower limb muscles (10). Increased inhibitory drive on the FDB motoneurone pool may

390 be an important element in the control of foot mechanics. For example, overly responsive

391 foot muscles may lead to unnecessary activation, which could potentially increase the

392 metabolic cost of locomotion. The close relationship between SOL muscle activation and

393 FDB activation observed in this study highlights the potential for heteronymous facilitation

394 between these muscles. Functionally, shared excitatory drive would make sense, as tasks that

395 require a large power output from the ankle plantar flexors, appear to also require a

396 concurrent increase in power output from the foot (18, 38). Further research is required to

397 explore the underlying control of the foot's mechanical and energetic function.

398 The findings of this study need to be acknowledged in the context of a number of

399 experimental limitations. The primary limitation of this study is that it was performed using

400 an external actuator to apply compressive loading cycles on the foot. This experimental

401 paradigm was designed to consistently replicate the loading about the LA in locomotion,

402 whilst allowing evaluation of the mechanical behaviour of muscles deep within the arch of

403 the foot. We believe that the data presented here is an adequate representation of the

404 mechanical function of the intrinsic foot muscles during locomotion. However, it is possible

405 that this function may differ slightly due to differences the magnitude of torques produced

406 about the mid-foot and also the lack of a true foot-ground collision or need to generate

407 propulsive impulses. The observed torque production and LA deformation within the current

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408   experiment (0.6 Nm.kg^{-1}, 5° deformation) are lower than that produced during walking (1

409   Nm.kg^{-1}, 7° deformation) (5, 9, 20) and running (1.5 Nm.kg^{-1}, 10 ^{o} deformation) (18).

410   Therefore, it is likely that the observed FDB activation may actually be greater during

411   locomotion than those reported within this study. We have shown that the FDB MTU

412   contributes to elastic energy storage within the foot. Because of its similar anatomical

413   pathway, it is likely that the plantar aponeurosis was also stretched more as loading increased,

414   and shared some of the increased energy storage and return with the FDB tendons. However,

415   within the current experiment, we were unable to parse out the relative contribution to energy

416   storage of the plantar aponeurosis and FDB MTU, or indeed other tissues within the foot.

417   Further research is required to explore the capacity of the intrinsic foot muscles to modulate

418   the energetic function of the human foot.

419   This study provides novel evidence that the CNS utilises the parallel anatomical arrangement

420   of the intrinsic foot muscles and plantar aponeurosis to actively control the spring-like

421   behaviour of the human foot. It appears that considerable excitatory neural drive is required

422   in order to activate the intrinsic foot muscles, allowing the foot to function as a relatively

423   passive structure during tasks that require low forces to be generated. When active, the

424   isometric function of the FDB muscle fascicles facilitates energy storage and return from the

425   FDB tendon, in parallel to the energy stored within the plantar aponeurosis. This mechanism

426   may enhance the versatility of the human foot during locomotion.

Conflict of Interest

432   The authors have no conflict of interest to declare, financial or otherwise.

Data Availability

434   Data from this study is available at

435   https://www.dropbox.com/sh/okbsab120jsc2az/AAD05Q1dtaY6MLdi_dkaqUjsa?dl=0

Author Contributions

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LK devised study protocol, collected and analysed data, prepared and revised manuscript. DF devised study protocol, analysed data, prepared and revised manuscript. AC prepared and revised manuscript. GL devised study protocol, prepared and revised manuscript

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Figure Legends

Figure 1. Experimental set-up to apply cyclic compression of the longitudinal arch (LA). An actuator delivers and downward force over the knee and anterior to the ankle joint (left). The ankle plantar flexors are activated to counter the downward force applied by the actuator, with this force couple producing deformation of the LA. B-mode ultrasound images (top right) were collected from the flexor digitorum brevis muscle during the foot compression cycles (right).

Figure 2. Group mean ensemble data for vertical ground reaction force (top) and soleus electromyography (EMG) data (bottom) recorded during foot compression cycles at low (orange dash), medium (real dots) and high (purple full line) loading conditions. * Denotes significant difference between all conditions.

Figure 3. Group mean ensemble data for mid-foot angle (top), mid-foot moment (middle) and foot power (bottom) recorded during foot compression cycles at low (orange dash), medium (real dots) and high (purple full line) loading conditions. * Denotes significant difference between all conditions.

Figure 4. Group mean ensemble data for flexor digitorum brevis (FDB) muscle tendon unit (full lines) and fascicle (dots) strain (top), velocity (middle) and muscle activation (bottom) during foot compression cycles at low (left, orange), medium (middle, teal) and high (right, purple) loading conditions.

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actuator

ultrasound probe

force plate

actuator

ultrasound probe

force plate