1 Title: Neuromechanical adaptations of foot function when hopping on a damped surface

- 2
- 3 Authors:
- 4 Jonathon V. Birch<sup>1,2</sup>
- 5 Dominic J. Farris<sup>1</sup>
- 6 Ryan Riddick<sup>2</sup>
- 7 Andrew G. Cresswell<sup>2</sup>
- 8 Sharon J. Dixon<sup>2</sup>
- 9 Luke A. Kelly<sup>2</sup>
- 10

# 11 Affiliations:

- Sport & Health Sciences, College of Life & Environmental Sciences, University of
   Exeter, St. Luke's Campus, Exeter, EX1 2LU, United Kingdom
- 14 2) School of Human Movement & Nutrition Sciences, The University of Queensland,
- 15 Brisbane, Queensland, 4072, Australia
- 16

# 17 Corresponding Author:

- 18 Jonathon V. Birch
- 19 School of Human Movement & Nutrition Sciences,
- 20 The University of Queensland,
- 21 Brisbane,
- 22 Queensland,
- 23 4072,
- 24 Australia
- 25 jb1015@exeter.ac.uk
- 26
- 27 Submission Type: Original Article
- 28
- Key Words: intrinsic foot muscles, quasi-stiffness, longitudinal arch, foot biomechanics, multi-
- 31 segment foot models

32

33 New & Noteworthy

34 Adaptable foot mechanics play an important role in how we adjust to elastic surfaces.

- 35 However, natural substrates are rarely perfectly elastic and dissipate energy. Here, we
- 36 highlight the important role of the foot and intrinsic foot muscles in contributing to replace
- 37 dissipated work on damped surfaces and uncover an important energy-saving mechanism
- that may be exploited by the designers of footwear and other wearable devices.
- 39

#### 40 **Abstract:**

41 To preserve motion, humans must adopt actuator-like dynamics to replace energy that is 42 dissipated during contact with damped surfaces. Our ankle plantar flexors are credited as 43 the primary source of work generation. Our feet and their intrinsic foot muscles also appear 44 to be an important source of generative work, but their contributions to restoring energy to 45 the body remain unclear. Here, we test the hypothesis that our feet help to replace work 46 dissipated by a damped surface through controlled activation of the intrinsic foot muscles. 47 We used custom-built platforms to provide both elastic and damped surfaces and asked 48 participants to perform a bilateral hopping protocol on each. We recorded foot motion and 49 ground reaction forces, alongside muscle activation, using intramuscular electromyography 50 from flexor digitorum brevis, abductor hallucis, soleus and tibialis anterior. Hopping in the 51 Damped condition resulted in significantly greater positive work and contact-phase muscle 52 activation compared to the Elastic condition. The foot contributed 25% of the positive work 53 performed about the ankle, highlighting the importance of the foot when humans adapt to 54 different surfaces.

#### 55 Introduction:

56 In bouncing gaits, humans store and return elastic energy in their lower limbs to reduce the 57 muscular work that they must perform to drive their body's centre of mass (COM) forward 58 and upward (1–4). An elastic surface, such as a sprung floor, will also store and return 59 energy. Humans harness this energy by modifying their combined limb stiffness and 60 geometry at contact, reducing the requirement for muscles to perform work to sustain 61 running at a given speed or hopping to a given height (5–9). However, natural substrates are 62 rarely perfectly elastic, meaning that energy is always dissipated to some degree during foot-63 surface contact (10, 11).

64

65 To maintain steady-state motions when interacting with such substrates, humans must 66 replace energy that is dissipated with positive muscle work. Based on human hopping 67 studies on a damped surface, it appears that the ankle plantar flexors are the primary source 68 of this additional mechanical work (10, 11), accounting for twice the combined work that is 69 performed at the knee and hip. However, this research used passive rigid-foot models that 70 ignore the dynamic structures of the foot, and can lead to considerable inaccuracies in 71 measures of work and quasi-stiffness about the ankle joint (12, 13). We have previously 72 highlighted the significance of considering the foot as an active, multi-articular part of the 73 lower limb when humans adapt to different surfaces (14). It is therefore important to 74 understand the contribution of the human foot in tuning lower limb mechanics when 75 interacting with a damped surface.

76

77 Human feet appear to be an important source of dissipative and generative mechanical work 78 (15–17). During locomotion tasks that require net-positive work to be performed on our 79 COM, foot muscles are actively modulated by the central nervous system to contribute as 80 much as 16% of this work (17, 18). Less is known about how foot function is controlled when 81 moving across surfaces that remove energy from the body. However, we uncovered in prior 82 work that running in cushioned shoes with a visco-elastic midsole leads to an increase in 83 intrinsic foot muscle activation, compared to barefoot running (19). When considered with 84 our recent findings that foot work and muscle activation decrease when hopping on an 85 elastic surface (14), we propose that feet may also play an important role in how humans 86 adjust to operating on surfaces that dissipate energy.

87

Therefore, the aim of this study was to test the hypothesis that feet perform work to replace energy that is dissipated through collisions with a damped surface. Participants performed a bilateral hopping protocol on a platform that allowed us to alter the damping properties of the surface. When damping of the platform was increased, we expected participants to compensate by increasing the amount of positive work performed within the foot by
increasing the activation of the intrinsic foot muscles. We recorded the motion, forces and
muscle activation of the right lower limb and foot in order to test this hypothesis.

95

#### 96 Methods:

#### 97 **Participants**

Fourteen healthy participants (five females, nine males; age,  $27 \pm 4$  yrs; height,  $170 \pm 8$  cm; mass,  $73 \pm 15$  kg) volunteered to participate in this study. All participants were free from lower-limb injury in the sixth months prior to data collection. The experimental procedures were approved by the local ethics review board at The University of Queensland (IRB:2020/HE000456) and performed in accordance with the declaration of Helsinki.

103

# 104 Experimental protocol

105 Participants completed a bilateral hopping protocol on elastic and damped surfaces. To 106 manage any learning effect; prior to data collection, participants were instructed to familiarise 107 themselves with each surface condition. Trials on each surface condition 108 during the familiarisation and data collection periods were performed in a counter-balanced 109 order. A digital metronome was used to control hopping frequency at 2.2 Hz, which best 110 represented a preferred frequency for participants (20). Collection for each trial began once 111 it was deemed by the researcher that participants were successfully timing their hops to 112 the beat of the metronome. Participants hopped in place for 30 s and were unshod for 113 all conditions.

114

# 115 Platform characteristics

116 To produce the Elastic and Damped hopping conditions, a modifiable surface was used to 117 alter the mechanical properties of specially fabricated platforms. Three-dimensional ground 118 reaction forces were measured for the right leg using an AMTI force plate (OR6-7; AMTI, 119 Massachusetts). Each platform had identical mechanical properties, only differing in 120 placement within the capture volume; one mounted atop the force plate and one adjacent 121 and level to the first, on the laboratory floor. Each platform was secured in place such that 122 any force applied to the one platform would not interfere with the force readings from the 123 adjacent platform.

124

Each platform was fabricated using extruded aluminium to produce an upper and lower frame with four linear sliding bearings mounted in each corner to stabilise the upper surface. Fixed to the lower frame was a spring (ASI Springs, Vic., Australia) and damper (MC-75, Ace Controls Inc., Langelfeld, Germany) mounting system that allowed 129 the characteristics of the upper surface to be adjusted between conditions, with the 'damped' 130 configuration dissipating  $\sim 5$  J of energy per hop and the Elastic condition  $\sim 1$  J per hop. The 131 acrylonitrile-butadiene-styrene 3D-printed housing allowed for the parallel arrangement of 132 both spring and damper in the damped condition and disengagement of the damper for the 133 Elastic condition (Figure 1). To quantify the characteristics of the Elastic and Damped 134 configurations, the displacement of the top surface was tracked using a motion capture 135 system (see below). The energy dissipated in each platform configuration was determined 136 based on force-displacement curves. The area under the curve from maximum platform 137 compression to take off (TO) was subtracted from the area under the curve from foot contact 138 (FC) to maximum compression.

139

#### 140 Data acquisition

# 141 Kinematic and kinetic measurements

The position of retro-reflective markers located on the platform and over anatomical 142 143 landmarks on the right shank and foot of participants were tracked at 200 Hz using an 11-144 camera optical motion capture system (Qualisys AB, Gothenburg, Sweden). Foot markers 145 were positioned in accordance with the Istituto Ortopedico Rizzoli (IOR) foot model 146 (Leardini et al., 2007). To minimise unwanted artefact, markers were attached using 147 adhesive spray and double-sided tape, and where possible further secured with cohesive bandage. Motion data were synchronously recorded with ground reaction forces and muscle 148 149 activation data via the Qualisys A/D board.

150

#### 151 Muscle activation measurements

152 Bipolar fine-wire intramuscular electrodes (0.051 mm, stainless steel, Teflon 153 coated; Chalgren Enterprises, California) were inserted under sterile conditions and in 154 accordance with previously described B-mode ultrasound-guided insertion techniques (21) 155 into the muscle tissue of abductor hallucis (AH) and flexor digitorum brevis (FDB) in the right 156 foot of each participant. Ag/AgCl surface electrodes (Covidien LLC., Massachusetts) were 157 placed in accordance with SENIAM guidelines over soleus (Sol) and tibialis anterior (TA) to 158 record surface electromyography (EMG) from the right leg of each participant. All EMG 159 channels were sampled at 4 kHz, amplified 1,000 times, hardware filtered with a bandwidth 160 of 20-2000 Hz and grounded with a reference electrode placed over the tibial tuberosity. 161 Preamplifiers and cabling were secured using cohesive bandage to prevent movement 162 artefacts in the EMG signals.

163

#### 164 Data analysis

#### 165 Kinematics and kinetics

166 Marker position data were digitally filtered using a 10 Hz recursive second-order low-pass 167 Butterworth filter and used to define and scale a rigid body model of the shank, calcaneus, 168 midfoot, metatarsal and hallux segments for each participant. From this, six degree of 169 freedom representations of the midfoot and ankle could be determined. Sagittal plane motion 170 recorded using this approach shows good agreement with segment positions recorded using 171 biplanar video radiography (22). A joint angle was defined at the midfoot, as the orientation 172 of the metatarsal segment with respect to the calcaneus (Cal-Met angle), with a positive 173 change in the angle representing dorsiflexion of the metatarsals relative to the calcaneus, 174 i.e., compression of the longitudinal arch (Figure 1). This functional joint represents the 175 combined angular rotation of all the small joints in the midfoot region of the foot (19, 23). The 176 ankle angle was computed as the orientation of the calcaneus relative to the shank as per 177 recent recommendations (12, 13). Joint moments were calculated in Visual3D using an 178 inverse dynamics solution. Mechanical work was calculated as the area under the moment-179 angle curve for each joint. Ground reaction forces were digitally filtered with a 35 Hz 180 recursive second-order low-pass Butterworth filter, and using a vertical threshold of 50 N, to 181 determine the start and end of each hop cycle. The excursion of the COM during each hop 182 was calculated by twice integrating the net force of each participant with respect to time 183 during each hop (24). Leg stiffness was calculated as the ratio of the peak vertical ground 184 reaction force to the change in length of the leg-spring during contact. The resting length of 185 the leg-spring was defined as the straight line distance between markers located on the 186 pelvis and metatarsal heads at the instance of each hop contact. Duty factor was calculated 187 as the ratio of contact time to hop duration. Data were then exported to Matlab 188 (The Mathworks Inc., MA, United States) for subsequent analyses.

189

#### 190 Muscle activation

191 Following direct current offset removal, all EMG signals were digitally filtered: intramuscular 192 channels high-pass at 35 Hz; surface channels, band-pass between 35-400 Hz. EMG 193 envelopes of the resultant signals were generated by calculating the root mean square 194 (RMS) amplitude over a moving window of 50 ms and normalised to the maximum amplitude 195 recorded for the respective muscle recorded during a control condition on an infinitely stiff 196 surface. The normalised RMS envelopes were then integrated with respect to time from foot 197 from take off (TO) to foot contact (FC) and from foot contact to take off to yield an integrated 198 EMG value during flight (iEMG<sub>flight</sub>) and contact (iEMG<sub>contact</sub>).

199

#### 200 Statistics

- 201 Statistical analyses were performed in GraphPad Prism 9 software (GraphPad Software Inc.,
- 202 CA, United States). Data were checked for normal distribution and paired-sample t-

tests were used to test the influence of surface damping on measures of foot and ankle work and muscle activations. An alpha level of  $p \le 0.05$  was used to determine statistical significance. Results are presented as mean ± standard deviation (SD) unless otherwise stated.

207

# 208 <u>Results:</u>

## 209 Global hopping parameters

Participants preserved the vertical excursion of their COM on both surface conditions (Table 1). In the Damped condition, participants spent significantly longer in contact with the platform surface than they did in the Elastic condition (P = 0.02). Since the participants matched the metronome beat on both surfaces, the increased contact time on the damped surface resulted in an increase in duty factor (P = 0.01; Table 1).

215

# 216 Ankle mechanics

Compared to the Elastic condition, participants plantar flexed and dorsiflexed their ankles more during platform contact with the damped surface condition. The ~15% increase in plantar flexion excursion resulted in a 51% greater net plantar flexion excursion at the ankle compared to the elastic surface (P = 0.03; Table 2, Figure 3A). This resulted in participants generating more positive work about their ankles in the damped surface condition (P = 0.02), which is evident in the ankle angle versus ankle moment plot, immediately prior to take-off (Figure 3C).

224

#### 225 Foot mechanics

In a similar manner to the ankle, participants compressed and recoiled their midfoot to a greater degree during contact with the damped surface. Notably, this resulted in net recoil of the midfoot being 115% greater for the damped condition (P = 0.03; Table 2, Figure 3B), allowing participants to generate significantly more positive work about their midfoot for the damped condition (P = 0.02; Table 2). This difference can be seen in the midfoot angle versus midfoot moment plot towards the end of the contact phase of the hop (Figure 3D).

232

#### 233 Muscle activation

Sol, AH and FDB muscles displayed similar overall patterns of activity (increase in integrated EMG) for the damped as compared to elastic condition. Increasing activity prior to contact was followed by a burst of activity during contact (Figure 4). Tibialis anterior also displayed a burst of activity on the damped condition immediately prior to TO. Integrated EMG during contact revealed greater activation of FDB (P = 0.02), AH (P = 0.02), SOL (P = 0.02), TA (P = 0.02) on the damped compared to the Elastic condition (Table 3). 240

#### 241 Discussion:

242 During terrestrial locomotion, energy is dissipated during contact with the ground. To 243 maintain constant COM dynamics, we must replace this dissipated energy by activating our 244 muscles to perform positive work. The contribution of our ankle plantar flexor muscles to this 245 function is well described, but the contribution from our feet is unknown, despite being the 246 interface between our body and the substrates we move across. Here we highlight the 247 structures contained within the foot, specifically the intrinsic muscles, contribute a substantial 248 proportion of the additional positive mechanical work required to help offset the energy 249 removed from a damped surface.

250

251 Our participants preserved the excursion of their COM when adjusting to the damped 252 surface by increasing the activation of their muscles to generate additional positive work. 253 This was not as necessary in the Elastic condition, since the platform surface had recoiled 254 closer to its resting height at take-off and assumed a greater portion of the work required to 255 hop to a given height and frequency. In prior work, we observed hopping humans alter their 256 landing geometry when transitioning from a stiff to an elastic surface to harness stored 257 energy, reducing the requirement for active contributions from muscle (14). However, in the 258 current study, we detected no change in landing geometry between surfaces, despite the 259 Elastic setting storing and returning more energy. Since the platform surface in both Damped 260 and Elastic conditions displaced similarly, participants were not able to alter their landing 261 geometry while preserving their COM. That our participants maintained their COM trajectory 262 is in agreement with findings reported previously for elastic and damped surfaces (6, 8, 10, 263 11).

264

265 To replace the energy dissipated in the Damped condition, participants altered their foot and 266 ankle mechanics and spent more time in contact with the surface of the platforms. The 267 strategy used by hoppers involved plantar flexing their ankles and recoiling their arch more 268 during the upward phase of the hop cycle. As hypothesised, this resulted in significantly 269 greater positive work being generated by the foot and ankle with respect to the Elastic 270 condition, which paralleled our observation of increased contact-phase intrinsic foot muscle 271 and soleus activation. This work-generating strategy has been observed previously at the 272 ankle (11) and matches trends reported elsewhere in the lower limb where hoppers choose 273 to activate their muscles to extend their joints more in the upward phase of the hop cycle 274 than they are flexed (10, 11). While the ankle contributed much of the increase in positive 275 work performed in the Damped condition, the intrinsic foot muscles were able to contribute 276 significant portion of this work (25% of that performed at the ankle). That the foot can contribute to replace energy dissipated by a damped surface is a novel finding and when
considered with the other recent work from our group (13, 14, 17, 18, 23, 25), further
highlights the versatility of our feet in the control of movement.

280

281 Qualitatively, the increase in muscle activation that we detected in the Damped condition 282 occurred earlier in the hop cycle than did the burst of positive work at the foot and ankle, 283 which was evident immediately prior to take-off. This pattern, coupled with the significant in-284 series compliance of the intrinsic foot muscles (26) and ankle plantar flexors (27), points 285 towards participants modulating their muscle-tendon interaction and utilising stored elastic energy to fulfil/assist with the positive work requirements of the Damped surface. This is 286 287 consistent with in-vivo (28, 29) and simulation (30) data of distal muscle-tendon unit 288 contractile mechanics during positive work generation, whereby the transfer of greater active 289 fascicle shortening to external work is delayed via elastic recoil. Noteworthy is the magnitude 290 of work performed by the foot, with the midfoot accounting for one third of that performed at 291 the ankle. Owing to simplified modelling techniques, prior studies have attributed this work in 292 its entirety to the ankle joint. As a consequence, its role in adapting leg mechanics to damped surfaces may have been overestimated (12-14). These findings underline the 293 294 importance of adopting multi-segment modelling approaches when considering surface 295 adaptations.

296

297 In a previous paper, we observed that running in cushioned shoes with a visco-elastic 298 midsole induced an increase in intrinsic foot muscle activation compared to barefoot running. 299 In the absence of foot kinetics, we hypothesised that this finding was an effort by participants 300 to stiffen the longitudinal arch of their feet to maintain an invariant system stiffness (19). 301 However, in subsequent work, we found that participants actually reduce intrinsic foot 302 muscle activation when hopping on an elastic surface, utilising stored energy from the 303 surface to contribute to COM dynamics (14). Given that cushioned shoes with visco-elastic 304 midsoles are known to dissipate as much as 35% of the energy stored from midsole 305 compression (31), the results of the current study suggest that the increase in foot muscle 306 activity may have been an effort to replace energy dissipated during midsole compression. 307 The data presented here, highlight that the response from our central nervous system to 308 control foot and ankle mechanics is highly dependent on the properties of the material 309 beneath our feet. Our findings also provide a plausible explanation as to why shoes with 310 lightweight, thick and highly resilient (elastic) midsoles may provide an energetic advantage 311 during running (31).

312

313 While not a gait readily used by humans, we chose to study hopping for a number of reasons. It shares many mechanical similarities with running, relies primarily on the ankle as 314 315 its source of mechanical power and could be closely controlled across participants by 316 imposing a frequency constraint. Despite this, future work studying human foot function 317 when running across a damped surface are encouraged, and may help to explain 318 adaptations seen to shoes with varied mechanical properties. Our platforms allowed us to 319 carefully parse the difference between damping and stiffness on foot function and intrinsic 320 foot muscle activation. To detect only changes to surface damping, the stiffness of both 321 conditions was closely matched (see Table 2). This limited their capacity to remove energy 322 compared to those previously described (10, 11, 32) and as a result, the magnitude of work 323 generation that we observed at the ankle was far less than in prior work. Our platforms did, 324 however, remove a comparable amount of energy to a cushioned running shoe and as a 325 consequence, our findings may provide insight as to how we adjust to a real-world scenario. 326 We cannot discount the role of extrinsic foot muscles, such as flexor hallucis longus, in 327 generating some of this work. However, when considering the findings of studies that have 328 blocked the ability of the intrinsic foot muscles to contract (18, 23), the extra positive work 329 performed about the midfoot on the damped surface is well within the realms of what the 330 intrinsic muscles are capable of generating.

331

# 332 Conclusions

333 In summary, we have presented evidence that the human foot contributes substantial 334 positive work to replace that dissipated by a damped surface via active contributions from 335 the intrinsic foot muscles. These findings support recent work from our group highlighting the 336 foot as an important source of generative work when required and emphasises that the 337 energetic function of the foot is versatile and tuned based on our interaction with our 338 environment. Our results also offer insight as to an energy-saving mechanism that may be 339 exploited by designers of footwear and other wearable devices. Appreciating the important 340 contribution of our feet should be a fundamental consideration in understanding how 341 humans control movement across varied surface requirements.

342

#### 343 Grants:

This work was supported by Australian Research Council Discovery Early Career Research Award DE200100585 to L. A. Kelly, QUEX Institute Scholarship to J. V. Birch, and Australian Research Council Linkage Grant LP160101316 to L. A. Kelly, A. G. Cresswell, and D. J. Farris.

348

#### 349 **References**:

- Cavagna GA, Kaneko M. Mechanical work and efficiency in level walking and running. J
   *Physiol* 268: 467–481, 1977. doi: 10.1113/jphysiol.1977.sp011866.
- Alexander RM, Bennet-Clark HC. Storage of elastic strain energy in muscle and other tissues.
   *Nature* 265: 114–117, 1977. doi: 10.1038/265114a0.
- Cavagna GA, Saibene FP, Margaria R. Mechanical work in running. *J Appl Physiol* 19: 249–
   256, 1964. doi: 10.1152/jappl.1964.19.2.249.
- Sawicki GS, Lewis CL, Ferris DP. It Pays to Have a Spring in Your Step [Online]. *Exerc Sport Sci Rev* 37: 130–138, 2009. https://insights.ovid.com/crossref?an=00003677-200907000-00005.
- McMahon TA, Greene PR. The influence of track compliance on running. *J Biomech* 12: 893– 904, 1979. doi: https://doi.org/10.1016/0021-9290(79)90057-5.
- Ferris DP, Farley CT. Interaction of leg stiffness and surface stiffness during human hopping
   [Online]. J Appl Physiol 82: 15–22, 1997.
- 362 http://www.physiology.org/doi/10.1152/jappl.1997.82.1.15.
- Ferris DP, Louie M, Farley CT. Running in the real world: adjusting leg stiffness for different
   surfaces [Online].
- 365 http://rspb.royalsocietypublishing.org/content/royprsb/265/1400/989.full.pdf.
- Farley CT, Houdijk HHP, van Strien C, Louie M. Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses [Online]. *J Appl Physiol* 85: 1044–1055, 1998.
   http://www.physiology.org/doi/10.1152/jappl.1998.85.3.1044.
- 369 9. Kerdok AE, Biewener AA, McMahon TA, Weyand PG, Herr HM. Energetics and mechanics of
  370 human running on surfaces of different stiffnesses. J Appl Physiol 92: 469–478, 2002. doi:
  371 10.1152/japplphysiol.01164.2000.
- Moritz CT, Farley CT. Human hopping on damped surfaces: strategies for adjusting leg
   mechanics [Online]. *Proceedings of the Royal Society B: Biological Sciences* 270: 1741–1746,
   2003. http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2003.2435.
- Moritz CT, Greene SM, Farley CT. Neuromuscular changes for hopping on a range of damped
   surfaces [Online]. *J Appl Physiol* 96, 2004. https://doi.org/10.1152/japplphysiol.00983.2003.
- 377 12. Zelik K, Honert E. Ankle and foot power in gait analysis: Implications for science, technology
   378 and clinical assessment. 2018.
- Kessler SE, Lichtwark GA, Welte LKM, Rainbow MJ, Kelly LA. Regulation of foot and ankle
   quasi-stiffness during human hopping across a range of frequencies. *J Biomech* 108: 109853,
   2020. doi: https://doi.org/10.1016/j.jbiomech.2020.109853.
- Birch J v, Kelly LA, Cresswell AG, Dixon SJ, Farris DJ. Neuromechanical adaptations of foot
   function to changes in surface stiffness during hopping. *J Appl Physiol* 130: 1196–1204, 2021.
   doi: 10.1152/japplphysiol.00401.2020.
- 38515.Kelly LA, Cresswell AG, Farris DJ. The energetic behaviour of the human foot across a range386of running speeds [Online]. Sci Rep 8: 1–6, 2018. http://dx.doi.org/10.1038/s41598-018-38728946-1.

- Kelly LA, Farris DJ, Cresswell AG, Lichtwark GA. Intrinsic foot muscles contribute to elastic
   energy storage and return in the human foot. *J Appl Physiol* 126: 231–238, 2018. doi:
   10.1152/japplphysiol.00736.2018.
- Riddick R, Farris D, Kelly LA. The foot is more than a spring: Human foot muscles perform
   work to adapt to the energetic requirements of locomotion. 2019.
- Smith RE, Lichtwark GA, Kelly LA. The energetic function of the human foot and its muscles during accelerations and decelerations. *Journal of Experimental Biology* 224, 2021. doi: 10.1242/jeb.242263.
- Kelly LA, Lichtwark GA, Farris DJ, Cresswell A. Shoes alter the spring-like function of the human foot during running [Online]. *J R Soc Interface* 13: 20160174–20160179, 2016.
   http://rsif.royalsocietypublishing.org/lookup/doi/10.1098/rsif.2016.0174.
- 399 20. Farley CT, Blickhan R, Saito J, Taylor CR. Hopping frequency in humans: a test of how springs
  400 set stride frequency in bouncing gaits [Online].
  401 https://www.physiology.org/doi/pdf/10.1152/jappl.1991.71.6.2127.
- 402 21. Kelly LA, Kuitunen S, Racinais S, Cresswell AG. Recruitment of the plantar intrinsic foot
  403 muscles with increasing postural demand [Online]. *JCLB* 27: 46–51, 2012.
  404 http://dx.doi.org/10.1016/j.clinbiomech.2011.07.013.
- 405 22. Kessler SE, Rainbow MJ, Lichtwark GA, Cresswell AG, D'Andrea SE, Konow N, Kelly LA. A
  406 Direct Comparison of Biplanar Videoradiography and Optical Motion Capture for Foot and
  407 Ankle Kinematics. Front Bioeng Biotechnol 7: 199, 2019. doi: 10.3389/fbioe.2019.00199.
- Farris D, Kelly L, G. Cresswell A, A. Lichtwark G. The functional importance of human foot
   muscles for bipedal locomotion. 2019.
- 410 24. Cavagna GA. Force platforms as ergometers. *J Appl Physiol* 39: 174–179, 1975. doi:
  411 10.1152/jappl.1975.39.1.174.
- 412 25. Farris DJ, Birch J, Kelly L. Foot stiffening during the push-off phase of human walking is linked
  413 to active muscle contraction, and not the windlass mechanism. *J R Soc Interface* 17:
  414 20200208, 2020. doi: 10.1098/rsif.2020.0208.
- Kelly LA, Farris DJ, Cresswell AG, Lichtwark GA. Intrinsic foot muscles contribute to elastic
  energy storage and return in the human foot. *J Appl Physiol* 126: 231–238, 2018. doi:
  10.1152/japplphysiol.00736.2018.
- 418 27. Roberts TJ, Scales JA. Mechanical power output during running accelerations in wild turkeys
  419 [Online]. *Journal of Experimental Biology* 205: 1485 LP 1494, 2002.
  420 http://jeb.biologists.org/content/205/10/1485.abstract.
- 421 28. Farris DJ, Lichtwark GA, Brown NAT, Cresswell AG. The role of human ankle plantar flexor
  422 muscle-tendon interaction and architecture in maximal vertical jumping examined in vivo.
  423 Journal of Experimental Biology 219: 528–534, 2016. doi: 10.1242/jeb.126854.
- 424 29. Farris DJ, Raiteri BJ. Modulation of leg joint function to produce emulated acceleration
  425 during walking and running in humans. *R Soc Open Sci* 4: 160901, 2021. doi:
  426 10.1098/rsos.160901.

- 427 30. Lai A, Schache AG, Lin YC, Pandy MG. Tendon elastic strain energy in the human ankle 428 plantar-flexors and its role with increased running speed [Online]. Journal of Experimental 429 Biology 217: 3159–3168, 2014. http://jeb.biologists.org/cgi/doi/10.1242/jeb.100826. 430 31. Hoogkamer W, Kipp S, Frank JH, Farina EM, Luo G, Kram R. A Comparison of the Energetic 431 Cost of Running in Marathon Racing Shoes. Sports Medicine 48: 1009–1019, 2018. doi: 432 10.1007/s40279-017-0811-2. 433 32. Moritz CT, Farley CT. Human hoppers compensate for simultaneous changes in surface 434 compression and damping [Online]. J Biomech 39: 1030–1038, 2006. 435 http://linkinghub.elsevier.com/retrieve/pii/S002192900500103X. 436
- 437

# 438 Figure legends:

439

**Figure 1. Platform mounting configurations.** The right platform was placed atop a force plate for both conditions. Surface damping was altered by engaging and disengaging the shock-absorbers located in parallel with the compression springs. The lower panel shows the platform in its damped setting with the compression springs and shock absorbers engaged. For the Elastic condition, the damper was disengaged by winding the locking collar counter-clockwise and turning the damper clockwise into threaded base plate. The locking collar was retained in both conditions to seat the compression spring in place.

447

Figure 2. Medial view of experimental set-up on right foot. Medial view of right foot
showing IOR foot marker locations and definitions of Cal-Met and MTPj angles.

450

451 Figure 3. Group mean ± SD data (n=13) for the change in angle at the ankle and midfoot 452 (Cal-Met) A and B, respectively, from foot contact (FC) to toe-off (TO) for both the damped 453 (solid line) and elastic (dotted line) conditions. Black bars and asterisk indicate significantly 454 different net ankle plantar flexion and midfoot recoil, respectively. Group data for changes in ankle and midfoot angle versus joint moment for the ankle and midfoot, C and D, 455 456 respectively, for the same damped and elastic conditions. Boxes highlight the significantly 457 greater positive work performed in the Damped vs Elastic condition performed immediately 458 prior to take-off. Nb. Positive change in angle indicates ankle dorsiflexion and midfoot 459 compression, respectively.

460

461 **Figure 4.** Group mean ensembles ± SD (shaded area) for normalised root mean square

- 462 (RMS) EMG signal amplitude for (A) flexor digitorum brevis (FDB), (B) abductor hallucis
- 463 (AH), (C), soleus (Sol) and (D) tibialis anterior (TA) for the damped (solid line) and elastic

- 464 (dotted line) surface conditions. Ensembles are presented for a single hop cycle, i.e., from
- toe-off (TO) to toe-off. Contact with the surface (FC) is indicated by vertical dashed lines to
- 466 highlight changes in duty factor between conditions (Elastic = dotted line, Damped = solid
- line). For each muscle, data are normalised for each subject to the peak amplitude recorded
- 468 on a locked surface.
- 469

# **Neuromechanical adaptations of foot** function when hopping on a damped surface

Met excursion

Cal-

Midfoot moment

20-

15.

10.

FC

то

-45 -40 -35 -30 -25 -20

Cal-Met angle (·)

OUTCOME **METHODS** Increased contact-phase activation of foot muscles and soleus on damped surface Human feet are not rigid Activation paralleled greater positive work generated at foot and ankle - Active contributions on damped surface not yet fully understood AH EMG (%max) -05 10-FDB EMG (%max) Damped Ankle excursion (° 30-Elastic 20-10 -20--30 то 60 Damped EMG (%max) EMG (%max) Elastic 40-40 100 20. 20 Ankle r 0 4 50 TO FC то TO FC TO -10 0 10 Ankle angle (°) **CONCLUSION** Increased activation of foot muscles and greater work generated at the midfoot, previously attributed to the ankle, highlight

Foot motion, forces & EMG recorded while hopping on custom platforms

the important role of the foot in adapting movement to varied surfaces









	Surface configuration	
	Elastic	Damped
Actual frequency (Hz)	2.2 ± 0.1	$2.2 \pm 0.4$
Ground contact time (ms)	304 ± 44	316 ± 46*
Duty factor	0.67 ± 0.1	0.70 ± 0.1*
Net COM excursion (mm)	17 ± 1	17 ± 1

**Table 1.** Global hopping parameters (group mean  $\pm$  s.d., n = 13)

\*significant difference between surfaces P < 0.05.

	Surface configuration	
	Elastic	Damped
Platform		
Energy dissipated (J/kg)	$0.02 \pm 0.01$	$0.07 \pm 0.02$
Net displacement (mm)	-1.0 ± 1.0	-5.0 ± 1.0
Stiffness (kN/m)	108 ± 6.7	117 ± 9.1
Ankle		
Angle at contact (degrees)	-9.0 ± 3.9	-8.2 ± 4.2
Dorsiflexion excursion	17.6 ± 5.0	19.0 ± 3.6
(degrees)		
Plantar flexion excursion	21.5 ± 4.4	24.8 ± 4.3
(degrees)		
Net excursion (degrees)	3.9 ± 2.1	5.90 ± 2.2*
Positive work (J/kg)	0.36 ± 0.1	$0.42 \pm 0.1^*$
Midfoot		
Angle at contact (degrees)	-39.1 ± 6.0	-39.4 ± 5.2
Compression excursion	14.9 ± 4.1	15.4 ± 3.8
(degrees)		
Recoil excursion (degrees)	$16.2 \pm 4.5$	$18.0 \pm 4.3$
Net excursion (degrees)	1.2 ± 1.0	2.6 ± 1.2*
Positive work (J/kg)	0.11 ± 0.1	0.13 ± 0.1*

**Table 2.** Mean  $\pm$  SD, kinematics and kinetics per hop for the Elastic and Damped surface (n = 13, mass for normalisation, 73  $\pm$  15 kg)

\*significant difference between surfaces P < 0.05.

	Surface configuration	
	Elastic	Damped
Flexor digitorum brevis		
EMG <sub>contact</sub> (iEMG)	13.42 ± 3.78	14.29 ± 3.50*
EMG <sub>flight</sub> (iEMG)	$0.55 \pm 0.36$	0.71 ± 0.39
Abductor hallucis		
EMG <sub>contact</sub> (iEMG)	13.47 ± 3.78	14.29 ± 3.44*
EMG <sub>flight</sub> (iEMG)	$0.56 \pm 0.36$	$0.73 \pm 0.40$
Soleus		
EMG <sub>contact</sub> (iEMG)	13.55 ± 3.82	14.43 ± 3.52*
EMG <sub>flight</sub> (iEMG)	$0.55 \pm 0.35$	$0.72 \pm 0.40$
Tibialis anterior		
EMG <sub>contact</sub> (iEMG)	13.43 ± 3.79	14.29 ± 3.46*
EMG <sub>flight</sub> (iEMG)	$0.60 \pm 0.37$	$0.78 \pm 0.43$

**Table 3.** Mean  $\pm$  SD integrated EMG of normalised RMS signal amplitudes (n = 12)

\*significant difference between surfaces P < 0.05.