Title: Neuromechanical adaptations of foot function to changes in surface stiffness during hopping

Authors:

Jonathon V. Birch[1,2]

Luke A. Kelly[2]

Andrew G. Cresswell[2]

Sharon J. Dixon[2]

Dominic J. Farris[1]

Affiliations:

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

Corresponding Author:

Jonathon V. Birch

School of Human Movement & Nutrition Sciences,

The University of Queensland,

Brisbane,

Queensland,

4072,

Australia

jb1015@exeter.ac.uk

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New & Noteworthy

When seeking to understand how humans adapt their movement to changes in substrate, the role of the human foot has been neglected. Using multi-segment foot modelling, we highlight the importance of adaptable foot mechanics in adjusting to surfaces of different compliance. We also show, via electromyography, that the adaptations are under active muscular control.

Abstract:

Humans choose work-minimising movement strategies when interacting with compliant surfaces. Our ankles are credited with stiffening our lower limbs and maintaining the excursion of our body's centre of mass on a range of surface stiffnesses. We may also be able to stiffen our feet through an active contribution from our plantar intrinsic muscles (PIMs) on such surfaces. However, traditional modelling of the ankle joint has masked this contribution. We compared foot and ankle mechanics and muscle activation on Low, Medium and High stiffness surfaces during bilateral hopping using a traditional and anatomical ankle model. The traditional ankle model overestimated work and underestimated stiffness compared to the anatomical model. Hopping on a low stiffness surface resulted in less longitudinal arch compression with respect to the high stiffness surface. However, because midfoot torque was also reduced, midfoot stiffness remained unchanged. We observed lower activation of the PIMs, soleus and tibialis anterior on the low and medium stiffness conditions, which paralleled the pattern we saw in the work performed by the foot and ankle. Rather than performing unnecessary work, participants altered their landing posture to harness the energy stored by the sprung surface in the low and medium conditions. These findings highlight our preference to minimise mechanical work when transitioning to compliant surfaces and highlight the importance of considering the foot as an active, multi-articular, part of the human leg.

1. Introduction

Running and hopping can be described as 'bouncing' gaits and are characterised by spring-like centre of mass dynamics (1). These dynamics greatly benefit locomotion economy (1, 2) allowing energy recycling by tendons, that in-turn facilitates the decoupling of muscle from joint-level motion (28, 29). By regulating the biological stiffness contribution of our lower limbs, we are able to sustain this movement outcome and the elastic cycling of energy through perturbations that would otherwise incur significant mechanical work (4, 5). On compliant surfaces, we achieve this by altering, in real-time, the stiffness of our lower limbs to offset the effect of surface displacement on the trajectory of our body centre of mass (6, 7, 11, 12, 13, 24, 28, 29). We often choose spring-like gaits and tune them to the varied substrates that we encounter in our modern environment. Studying the neuromechanical requirements of spring-like motion is therefore paramount to understanding how and why humans make this choice.

Changes in our ankle mechanics are thought to have the greatest influence on the combined behaviour of our lower limbs on compliant surfaces (6, 7, 12, 13, 24, 31, 32). However, this understanding stems from an anatomically imprecise representation of our feet. Collating the actions of our feet into a single, rigid segment is known to skew, or even mask completely, their true contribution to whole-body movement (34, 37). It is therefore important to understand how a non-rigid representation of feet might have impacted existing understanding, and assess the contribution of feet in the adaptation of spring-mass mechanics to changing surface stiffness.

Our feet are not rigid. They bend, stretch and recoil in series with our legs (21, 23), passively storing and returning as much as 17% of the energy required to redirect our body centre of mass during running (23). However, this mechanical function is not fixed (8, 17, 19, 20, 22, 33). We can modify the energetic function of our feet through active contributions from our foot muscles (16, 18, 33, 35). This allows foot mechanics to be tuned on-demand by our central nervous system to meet task requirements (33). When our ability to use our plantar intrinsic foot muscles (PIMs) is removed, the versatility of our feet is greatly impaired (8). Prior work shows that through electrical stimulation our PIMs counter long arch compression in response to external load (21) and may act to stiffen the foot when we wear viscoelastic running shoes (22). Because the mechanical properties of the footwear were not tested we cannot be completely certain that the action of the PIMs was an effort to maintain system stiffness, or an effort to replace lost energy. More systematic work is required to show how the PIMs alter the function of our feet (and the leg spring) when we encounter changes in surface stiffness.

Given that changes in our ankle mechanics contribute greatly to tuning the spring-like function of our legs, our aims in this experiment were twofold. We first sought to test how a rigid representation of our feet as used in prior work has impacted our understanding of how humans adapt to spring-loaded surfaces, compared to a non-rigid foot. We hypothesised that rigid modelling of the foot would underestimate ankle quasi-stiffness compared to that determined using a multi-segment foot model, but would not change the understanding of how we adapt to a sprung surface. Because of the known contribution of the foot to movement, we then aimed to test the hypothesis that increased activation of the PIMs on spring-loaded surfaces acts to stiffen the foot in line with adjustments seen previously at more proximal structures. To do this we used motion capture of the foot and ankle, and fine-wire electromyography recording of the PIMs during a bilateral hopping protocol on Low, Medium and High stiffness surfaces.

2. Methods

2.1. *Participants*

Ten healthy participants (five females and five males; age, 27 ± 4 years; height, 170 ± 8 cm; mass, 73 ± 15 kg), with no history of diagnosed lower limb injury in the 6 months prior to data collection, provided written informed consent to participate in this study which was approved by the local ethics committee at the University of Exeter.

2.2. *Experimental protocol*

Participants completed a bilateral hopping task under three experimental conditions: a low stiffness, compression-sprung surface (Low), a medium stiffness, compression-sprung surface (Medium) and a high stiffness surface with no compression springs or vertical displacement (High). The compression-sprung surface used in the low and medium conditions is described below. The surface of an in-ground AMTI force plate (BP400600HF; AMTI, MA, United States) formed the high stiffness condition. Participants hopped in place for a duration of 30 s, timing the start of each hop with the beat of a metronome set to their preferred hopping frequency as recorded in the High condition (mean frequency, 2.4 Hz). The order of subsequent trials (Low and Medium) was randomised. Participants were unshod for all conditions and given a period of familiarisation to each surface condition to ensure that there was no learning effect between conditions. Data collection was started once it was deemed that participants were able to closely match their frequency on each surface to the metronome.

2.3. *Low and Medium condition platform characteristics*

Two, adjustable, compression-sprung platforms were used so we could record the ground reaction forces applied only to the right foot in the Low and Medium stiffness conditions. One, the primary platform as pictured in, was fixed to the surface of the force plate (Figure 1), with the second platform positioned adjacent to this on the laboratory floor. Each had identical mechanical properties with the same spring arrangement and only differed in placement within the capture volume. It was not possible for either platform to slip during experimental trials. The platforms comprised of carbon-fibre upper and lower surfaces stabilised with four linear bearings, and with a parallel compression-spring arrangement. The springs were secured using polylactide spring seats which also allowed ease of adjustment between Low and Medium conditions. The slope of the force-displacement relationship of the upper surface during a static load test was used to quantify the stiffness of the Low and Medium conditions; which were 55.26 and 77.02 $kN.m^{-1}$, respectively. The upper surface of the plate was tracked using motion capture and along with ground reaction forces recorded during each trial its position was used to quantify the energy stored during compression in the Low and Medium conditions; 15.1 ± 4.90 J and 11.5 ± 4.64 J, respectively. Both Low and Medium surface configurations dissipated less than 1 J, respectively.

2.4. *Data acquisition*

2.4.1. *Kinematic and kinetic measurements*

Three-dimensional motion data were captured at 200 Hz using a 12 array optoelectronic system (CX1; Codamotion, Charnwood Dynamics Ltd., Rothley, United Kingdom). Ground reaction forces and electromyography (EMG) were synchronously captured with the motion data at 4000 Hz. Infra-red markers were positioned over anatomical landmarks on the right shank (16) and foot of participants in accordance with the Istituto Ortopedico Rizzoli (IOR) foot model (26) as well as the upper surface of the primary platform. Markers were attached and cables managed using adhesive spray and double-sided tape, and where possible, further secured with cohesive bandage.

2.4.2. *Muscle activation measurements*

Bi-polar fine-wire intra-muscular electrodes (0.051 mm, stainless steel, Teflon coated; Chalgren Enterprises, CA, United States) were inserted into the right foot of each participant in accordance with previously described B-mode ultrasound-guided insertion techniques (20) to record the muscle activation (EMG) of two PIM’s spanning similar anatomical pathways to passive structures; abductor hallucis (AH) and flexor digitorum brevis (FDB). Sterile techniques were used for the insertion of all wires and voluntary contractions were performed to confirm correct placement (Kelly et al., 2018). Ag/AgCl surface electrodes (Covidien llc, MA, United States) were placed over the muscle belly of soleus (SOL) and tibialis anterior (TA) to record surface EMG (EMG) from the right leg of each participant. All EMG channels were sampled at 4000 Hz, pre-amplified with a 20-times gain, hardware filtered with a bandwidth of 20 to 2000 Hz (MA400; Motion Lab Systems, LA, United States) and grounded with a reference electrode placed over the tibial tuberosity. Motion artefacts were prevented by securing both pre-amplifiers and cabling with cohesive bandage.

2.5. *Data analysis*

2.5.1. *Kinematics and kinetics*

Marker trajectories and ground reaction force data were exported to Visual3D (C-motion Inc., MD, United States) for post processing. Marker position data were digitally filtered with a 10 Hz recursive second-order low-pass Butterworth filter and used to define and scale a rigid body model of the shank, calcaneus, midfoot, metatarsal and hallux segments for each participant. From this, six degree of freedom representations of the metatarsal-phalangeal joint (MTPj), midfoot, and ankle could be determined. Sagittal plane motion recorded using this approach shows good agreement with segment positions recorded using biplanar video radiography. The orientation of the hallux with relative to the metatarsal segment was used to calculate the angle of the MTPj. We computed the midfoot as the orientation of the metatarsal segment with respect to the calcaneus (Cal-Met angle) with a positive change in the angle representing dorsiflexion of the metatarsals relative to the calcaneus, resulting in compression of the long arch (Figure 1). The ankle angle was computed as the orientation of both a rigid foot segment relative to the shank (ShankFoot - traditional) and the calcaneus relative to the shank (ShankCal - anatomical) as per recent recommendations (37). Joint moments were calculated in Visual3D using an inverse dynamics solution. The moment about both MTPj and midfoot were represented as internal moments in the coordinate system of the proximal segment. Quasi-stiffness of the ankle, midfoot and MTPj was calculated as the ratio of the change in moment about each joint to its angular displacement. Ground reaction forces were digitally filtered with a 35 Hz recursive second-order low-pass Butterworth filter and using a vertical threshold of 50 N, used to locate the start and end of each hop cycle. The position of the body centre of mass (COM) during each hop was calculated by twice integrating the net force of each participant with respect to time during each hop (3). Leg stiffness was calculated as ratio of the peak vertical ground reaction force to the change in length of the leg spring during contact. The resting length of the leg spring was defined as the distance between markers located on the pelvis and metatarsal heads at the instance of each hop contact. Data were then exported to Matlab (The Mathworks Inc., MA, United States) for subsequent analyses.

2.5.2. *Muscle activation*

Following DC offset removal, all EMG signals were digitally band-pass filtered between 35 and 1000 Hz (intra-muscular) and 35-400 Hz (surface) to remove unwanted artefact. A digital notch filter (49-51 Hz) was then applied to remove AC-line noise (identified as a significant peak at 50 Hz in the fast-fourier transform power spectrum). EMG envelopes of the resultant signals were generated by calculating the root mean square (RMS) amplitude over a moving window of 50 ms and normalised to the maximum amplitude recorded for the respective muscle during the High condition. The normalised RMS envelopes were then integrated (iEMG) with respect to time for the contact and flight phases ($iEMG_{contact}$) and ($iEMG_{flight}$).

2.6. *Statistics*

Statistical analysis was performed in GraphPad Prism 8 software (GraphPad Software Inc., CA, United States). A two-way repeated measures ANOVA was used to test the influence of the ankle modelling approach and surface stiffness on estimates of ankle joint work and quasi-stiffness. A one-way, repeated measure ANOVA was used to determine the effect of surface on all outcome measures of foot mechanics and muscle activations. An alpha level of $p \leq 0.05$ was used to determine statistical significance. Results are presented as mean ± standard deviation (SD) unless otherwise stated.

3. Results

3.1. *Leg spring metrics*

Participants maintained the vertical excursion of their centre of mass with decreasing surface stiffness (High to Low) by increasing the combined stiffness of their legs (p = 0.005) (Table 1).

3.2. *Ankle joint mechanics*

Participants landed with their ankles in a more plantar flexed orientation on the High stiffness surface compared to the Low and Medium stiffness surfaces (p = 0.001). There was a main effect of ankle model type on both quasi-stiffness (p = 0.005) and net-work (p = 0.002). When modelled using only a shank and rigid foot segment the ankle was less stiff and performed greater net-work compared to the anatomical model, owing to greater angular displacement (Figure 2A & B). We also detected a main effect of surface on quasi-stiffness (p = 0.049) and net-work (p = 0.003). Post-hoc comparisons showed that ankle stiffness was greater on the Low with respect to the High stiffness condition when using the anatomical model (p = 0.003) but not the traditional model. Conversely, less net-work was performed on the Low (p = 0.01) and Medium (p = 0.01) conditions compared to the High stiffness condition (Figure 2 C & D).

3.3. *Foot mechanics*

In a similar manner to the ankle, Cal-Met (midfoot) excursion was greater for the High stiffness condition (p = 0.03) (Table 1). As a consequence, participants performed significantly more work about their midfoot with respect to the Low stiffness surface (p = 0.03) (Figure 3C and Table 1). Work at the MTPj (forefoot) was also reduced for the Low (p = 0.01) and Medium (p = 0.03) surfaces compared to the High stiffness surface (Table 2). The lower peak torque about the midfoot on the compliant surface conditions (p = 0.01) meant that we detected no effect of surface stiffness on joint quasi-stiffness during loading (Table 2).

3.4. *Muscle activation*

Soleus, AH and FDB muscles displayed similar patterns of activity (increases in amplitude) for each stiffness condition. There was a period inactivity when participants were not in contact with the platforms, followed by a burst of activity during contact (Figure 4). Integrated EMG during contact revealed a lower activation of SOL (p = 0.001) , TA (p = 0.008), AH (p = 0.001) and FDB (p = 0.001) on the low compared to the high surface stiffness and medium compared to high stiffness surface (Table 3).

4. Discussion

When humans encounter compliant surfaces, we stiffen our legs by altering the mechanical function of our ankles to maintain an invariant system stiffness with our environment (6, 11). Prior work in this area has assumed that our feet and ankles are single, rigid non-adaptable structures. However, human feet are not rigid. Through active muscular contributions, we can alter the energetic and mechanical function of the foot and ankle to meet varied task demands (33). It has been shown that running in cushioned shoes appears to simultaneously increase our longitudinal arch quasi-stiffness and foot muscle activation (22). Here we expected that increased activation of the PIMs would act to stiffen the foot and compensate for the more compliant Low and Medium surface conditions. However, this was not the case, with activation of the PIMs reducing on the Low and Medium conditions.

Despite this, participants still altered their foot and ankle kinematics and kinetics to adjust to the different surface stiffnesses. The strategy used by participants on the compliant surfaces involved altering foot-ankle landing geometry to harness the energy stored and returned by the springs incorporated into the platforms; reducing the requirement for their foot and ankle muscles to be as active as when they hopped on a rigid surface.

Our participants adopted work-minimising movement strategies when adjusting to the compliant surface. The observed reduction in both PIMs and SOL peak activation and iEMG (Figure 4 and Table 3) on the compliant surfaces paralleled the changes we saw in the mechanical work performed at the foot and ankle. As surface compliance increased, so did the potential for the sprung platforms to store and return energy and assume some of the mechanical work (negative and positive) associated with hopping to a given height and frequency. With concurrent reductions in activation of foot and ankle muscles and work done at the foot and ankle, the sprung platforms appeared to assist our hoppers in maintaining a constant hopping motion, but with reduced muscular effort. That humans harness the energy stored and returned by the compliant surfaces to reduce the need to contract our PIMs and SOL to produce foot and ankle mechanical work matches the trends reported elsewhere for the lower limb (6, 24). Elastic surfaces operating in series with the leg can assist hoppers and runners by reducing the mechanical work and metabolic cost required to maintain spring-like centre of mass dynamics, since the compression and recoil of the surface is able to perform negative and positive work on the centre of mass (24). This is also similar to the reductions seen in muscle activation and force output for hopping with passive exoskeletal devices located in parallel with the lower limb (9, 10, 14). Despite the required increase in biological stiffness required to maintain an invariant system stiffness with a series spring, humans reduce the active contribution to work from their foot and ankle muscles. With this in mind, it is likely that the altered landing geometry and increased ground contact time that we observed in the compliant surface conditions was part of a strategy to reduce muscular contributions to work and harness the energy stored in the platforms. Our participants chose to adopt a more plantar flexed position at landing on the high stiffness surface, where energy was not being stored and then returned by springs to the hopper. This meant that on the high stiffness surface, joints of the foot and ankle went through larger ranges of motion and muscles were more active and joint torques greater, resulting in more work being observed. This is similar to the increase in PIM activation and midfoot work that was observed by our group in fore-foot strike running compared to rear-foot strike running (19). In that study, the fore-foot strike technique resulted in a more plantar flexed ankle position at ground contact, similar to reorienting the foot for the high stiffness surface seen in this study. Landing in a more plantar flexed posture seems to require considerably more muscle activity, and it seems that when an alternative source of that work is available (e.g. the sprung platforms) we are able to harness this to reduce muscular contributions. It should be noted that participants in our study were given a period of familiarisation to each surface stiffness and thus were familiar with each stiffness condition, so this may well be a conscious voluntary choice. That our participants altered their landing position is consistent with prior work on expected changes in surface stiffness (30). The findings reported here add to the notion that humans tune their movement strategy to one that is mechanically inexpensive when adapting to changes induced by spring-loaded surfaces or devices. We have extended prior work to show that the intrinsic muscles of the foot are actively involved in such tuning.

Contrary to our hypothesis, we observed no change in MLA and MTPj quasi-stiffness despite reductions in PIMs activation when our participants hopped on the Low and Medium surface conditions. These findings are at odds with prior work from our group where increases in intrinsic foot muscle activation occurred in parallel with a reduction in longitudinal arch compression when running in cushioned running shoes (22). While participants in the present study displayed significantly lower Cal-Met excursion for the Low and Medium conditions, lower torque was generated about their midfoot. In a prior study, kinematic measures were used as a surrogate for quasi-stiffness (22). Our findings here highlight the importance of not solely relying on the motion of the foot and activation of the PIMs when commenting on its stiffness. However, data processing cannot explain why activation of the PIMs decreased on compliant surfaces in the present study, but increased in compliant running shoes in previous work from our group (22). This is likely explained by the elastic nature of the surface used in the current study, compared to the viscoelastic nature of the running shoes used in the earlier study. In the current experiment, our sprung platforms performed very little net-negative work; storing energy when they were compressed and returning energy to the participant as the springs returned to their resting length. Materials with elastic properties in-series with the lower limb have been shown previously to reduce the metabolic cost of running by reducing the muscular effort required to cushion foot-ground impacts (36). A cushioned running shoe with a viscoelastic midsole, however, is likely to have dissipated up to 35% of the absorbed energy (15); increasing the cost of each foot contact (27). This loss of energy must be compensated for. It has been shown that additional work is performed by lower limb extensor muscles when humans hop in place on surfaces with high compliance but low resilience (high damping) (27, 31, 32). The PIMs also have potential to contribute to this compensatory muscle work. The foot's function can be modified by PIMs to contribute to changes in work performed by the lower limb (16, 33). Therefore we suggest that the increased activation of the PIMs recorded in response to cushioned shoes in the earlier cited studies occurred as a response to replace the energy dissipated by the shoe. The present study further supports the idea that our central nervous system alters our foot mechanics to meet the energetic demands of locomotion (22, 33). Combining our findings with other recent works (8, 22, 33) we suggest that activation of the PIMs is more tightly coupled to the mechanical work done by the foot rather than quasi-stiffness of the longitudinal arch.

That our participants increased their leg stiffness when hopping on the Low and Medium compared to the High stiffness surface (Table 1) aligns with prior work documenting leg spring adaptations to springy surfaces (6, 11). To draw upon these findings and uncover how a non-rigid representation of our feet would impact our understanding of how we adapt to changes in surface stiffness, we contrasted estimates of ankle mechanics using two established modelling conventions, since it is our ankles that have been shown to have the greatest influence on our leg spring stiffness (6, 24). A traditional, two-segment ankle with a rigid foot segment was compared to an anatomical ankle where the kinematics of the rear foot, midfoot and MTPj were modelled. Compared to earlier work (6, 24), we did not detect a significant effect of surface on estimates of ankle stiffness calculated from the traditional model. However, a significant effect of surface was observed when quantifying stiffness with the anatomical model. This finding is likely explained by the minimum stiffness of our sprung surfaces being close to double that of those used by Farley and colleagues (6) who only observed a significant effect of surface on ankle stiffness from their most stiff to least stiff condition. Our results show that merging the actions of the foot increases estimates of ankle joint excursion, and as a consequence yields lower estimates of stiffness and higher estimates of ankle work. These insights into anatomical and traditional ankle joint modelling align well with prior work by Zelik & Honert (37) and Kessler and colleagues (25) that suggests a rigid representation of our feet introduces a systematic error into estimates of ankle joint mechanics. Our findings suggest that an anatomical model of the ankle may be more sensitive to detecting changes in quasi-stiffness.

4.1. *Strengths and limitations*

Hopping is not a natural gait employed by humans. However it shares many mechanical similarities with running and can be more readily manipulated for specific laboratory based experiments. We studied hopping due to its repetitive nature, allowing a rigorously controlled experimental protocol using a simple platform design. Furthermore, because the ankle joint is the primary power source during hopping, it provided an ideal task to test how traditional modelling techniques impact our understanding of adaptation to changes in surface stiffness. While we have linked activation of the PIMs to work and not stiffness, more complex platform designs that utilise a spring-damper to remove energy from the system would provide insight as to the neuromechanical function of the foot in this context. On the topic of platform design, though allowing ease of adjustment between conditions and minimising any inertial effects, the lightweight nature of our spring-loaded platforms resulted in slight flexing of the linear stabilising shafts when the upper surface was not loaded uniformly. As a consequence, uneven vertical displacement of the upper surface with respect to the lower surface was possible if participants landed with their centre of pressure away from the centre of the platform surface. Because we were interested in determining the effect of surface stiffness and not stability, we accounted for this by only including hops where the centre of pressure excursion from the platform centre fell within one standard deviation of the mean excursion of all hops recorded. We used similar criteria to exclude consecutive hops should their frequency fall outside one standard deviation of the mean frequency recorded for each trial. Because we imposed participants' preferred frequency on the high stiffness surface in each condition, it should also be noted that participants were faced with the high stiffness surface before experiencing the Low and Medium sprung surfaces. However, prior work (11) has shown that global aspects of hopping on a range of surface stiffnesses remain consistent irrespective of surface order.

5. Conclusion

In summary, we have presented novel evidence that human foot neuromechanics during hopping are tuned on-demand to changes in surface stiffness. We expected the foot to contribute to the stiffening of the lower limb through increased plantar intrinsic muscle activation on springy surfaces. Instead, hoppers in our experiment sought to reduce the muscular work that foot and ankle muscles performed by utilising the energy stored and returned by the sprung platforms. These findings further highlight our preference to minimise work for a given centre of mass trajectory when transitioning to surfaces with varied stiffness properties. They also show the importance of considering the foot as an active, multi-articular part of the human leg spring when exploring surface adaptations.

6. References

1. **Alexander RM**, **Bennet-Clark HC**. Storage of elastic strain energy in muscle and other tissues. *Nature* 265: 114–117, 1977.

2. **Cavagna G**. Storage & utilisation_elastic energy_skeletal muscle [Exerc Sport Sci Rev].pdf. 1977.

3. **Cavagna GA**. Force platforms as ergometers. *J Appl Physiol* 39: 174–179, 1975.

4. **Farley CT**, **Blickhan R**, **Saito J**, **Taylor CR**. Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits [Online]. *J. Appl. Physiol.*

https://www.physiology.org/doi/pdf/10.1152/jappl.1991.71.6.2127.

5. **Farley CT**, **González O**. Leg stiffness and stride frequency in human running [Online]. *J Biomech* 29: 181–186, 1996. http://www.sciencedirect.com/science/article/pii/0021929095000291.

6. **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.

7. **Farley CT**, **Morgenroth DC**. Leg stiffness primarily depends on ankle stiffness during human hopping [Online]. *J Biomech* 32: 267–273, 1999. http://www.sciencedirect.com/science/article/pii/S0021929098001705.

8. **Farris D**, **Kelly L**, **G. Cresswell A**, **A. Lichtwark G**. The functional importance of human foot muscles for bipedal locomotion. 2019.

9. **Farris DJ**, **Robertson BD**, **Sawicki GS**. Elastic ankle exoskeletons reduce soleus muscle force but not work in human hopping [Online]. *J Appl Physiol* 115: 579–585, 2013. http://www.physiology.org/doi/10.1152/japplphysiol.00253.2013.

10. **Ferris DP**, **Bohra ZA**, **Lukos JR**, **Kinnaird CR**. Neuromechanical adaptation to hopping with an elastic ankle-foot orthosis. [Online]. *J Appl Physiol* 100: 163–170, 2006. http://eutils.ncbi.nlm.nih.gov/entrez/eutils/elink.fcgi?dbfrom=pubmed&id=16179395&retmode=ref&cmd=prlinks.

11. **Ferris DP**, **Farley CT**. Interaction of leg stiffness and surface stiffness during human hopping [Online]. *J Appl Physiol* 82: 15–22, 1997. http://www.physiology.org/doi/10.1152/jappl.1997.82.1.15.

12. **Ferris DP**, **Liang K**, **Farley CT**. Runners adjust leg stiffness for their first step on a new running surface [Online]. *J Biomech* 32, 1999. https://doi.org/10.1016/S0021-9290(99)00078-0.

13. **Ferris DP**, **Louie M**, **Farley CT**. Running in the real world: adjusting leg stiffness for different surfaces [Online]. *Proc. R. Soc. B Biol. Sci.* http://rspb.royalsocietypublishing.org/content/royprsb/265/1400/989.full.pdf.

14. **Grabowski AM**, **Herr HM**. Leg exoskeleton reduces the metabolic cost of human hopping. *J Appl Physiol* 107: 670–678, 2009.

15. **Hoogkamer W**, **Kipp S**, **Frank JH**, **Farina EM**, **Luo G**, **Kram R**. A Comparison of the Energetic Cost of Running in Marathon Racing Shoes. *Sport Med* 48: 1009–1019, 2018.

16. **Kelly LA**, **Cresswell AG**, **Farris DJ**. The energetic behaviour of the human foot across a range of running speeds [Online]. *Sci Rep* 8: 1–6, 2018. http://dx.doi.org/10.1038/s41598-018-28946-1.

17. **Kelly LA**, **Cresswell AG**, **Racinais S**, **Whiteley R**, **Lichtwark GA**. Intrinsic foot muscles have the capacity to control deformation of the longitudinal arch [Online]. *J R Soc Interface* 11: 20131188, 2014. http://rsif.royalsocietypublishing.org/cgi/doi/10.1098/rsif.2013.1188.

18. **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.

19. **Kelly LA**, **Farris DJ**, **Lichtwark GA**, **Cresswell AG**. The Influence of Foot-Strike Technique on the Neuromechanical Function of the Foot [Online]. *Med Sci Sport Exerc* 50: 98–108, 2018. http://insights.ovid.com/crossref?an=00005768-201801000-00013.

20. **Kelly LA**, **Kuitunen S**, **Racinais S**, **Cresswell AG**. Recruitment of the plantar intrinsic foot muscles with increasing postural demand [Online]. *JCLB* 27: 46–51, 2012. http://dx.doi.org/10.1016/j.clinbiomech.2011.07.013.

21. **Kelly LA**, **Lichtwark G**, **Cresswell AG**. Active regulation of longitudinal arch compression and recoil during walking and running [Online]. *J R Soc Interface* 12: 20141076, 2014. http://rsif.royalsocietypublishing.org/cgi/doi/10.1098/rsif.2014.1076.

22. **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.

23. **Ker RF**, **Bennett MB**, **Bibby SR**, **Kester RC**, **Alexander RM**. The spring in the arch of the human foot [Online]. *Nature* 325: 147–149, 1987. http://www.nature.com/articles/325147a0.

24. **Kerdok AE**, **Biewener AA**, **McMahon TA**, **Weyand PG**, **Herr HM**. Energetics and mechanics of human running on surfaces of different stiffnesses [Online]. *J Appl Physiol* 92: 469–478, 2002. http://www.physiology.org/doi/10.1152/japplphysiol.01164.2000.

25. **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.

26. **Leardini A**, **Benedetti MG**, **Berti L**, **Bettinelli D**, **Nativo R**, **Giannini S**. Rear-foot, mid-foot and fore-foot motion during the stance phase of gait [Online]. *Gait Posture* 25: 453–462, 2007. http://linkinghub.elsevier.com/retrieve/pii/S0966636206001603.

27. **Lejeune TM**, **Willems PA**, **Heglund NC**. Mechanics and energetics of human locomotion on sand. [Online]. *J Exp Biol* 201: 2071 LP – 2080, 1998. http://jeb.biologists.org/content/201/13/2071.abstract.

28. **Lichtwark GA**, **Wilson AM**. Effects of series elasticity and activation conditions on muscle power output and efficiency. *J Exp Biol* 208: 2845 LP – 2853, 2005.

29. **Lichtwark GA**, **Wilson AM**. Is Achilles tendon compliance optimised for maximum muscle efficiency during locomotion? *J Biomech* 40: 1768–1775, 2007.

30. **Moritz CT**, **Farley C**. Passive dynamics change leg mechanics for an unexpected surface during human hopping [Online]. *J Appl Physiol* 97: 1313–1322, 2004. http://www.physiology.org/doi/10.1152/japplphysiol.00393.2004.

31. **Moritz CT**, **Farley CT**. Human hopping on damped surfaces: strategies for adjusting leg mechanics [Online]. *Proc R Soc B Biol Sci* 270: 1741–1746, 2003. http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2003.2435.

32. **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.

33. **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.

34. **Takahashi KZ**, **Kepple TM**, **Stanhope SJ**. A unified deformable (UD) segment model for quantifying total power of anatomical and prosthetic below-knee structures during stance in gait [Online]. *J Biomech* 45: 2662–2667, 2012. http://dx.doi.org/10.1016/j.jbiomech.2012.08.017.

35. **Takahashi KZ**, **Worster K**, **Bruening DA**. Energy neutral: the human foot and ankle subsections combine to produce near zero net mechanical work during walking [Online]. *Sci.*

Rep. http://dx.doi.org/10.1038/s41598-017-15218-7.

36. **Worobets J**, **Wannop JW**, **Tomaras E**, **Stefanyshyn D**. Softer and more resilient running shoe cushioning properties enhance running economy. *Footwear Sci* 6: 147–153, 2014.

37. **Zelik K**, **Honert E**. Ankle and foot power in gait analysis: Implications for science, technology and clinical assessment. 2018.

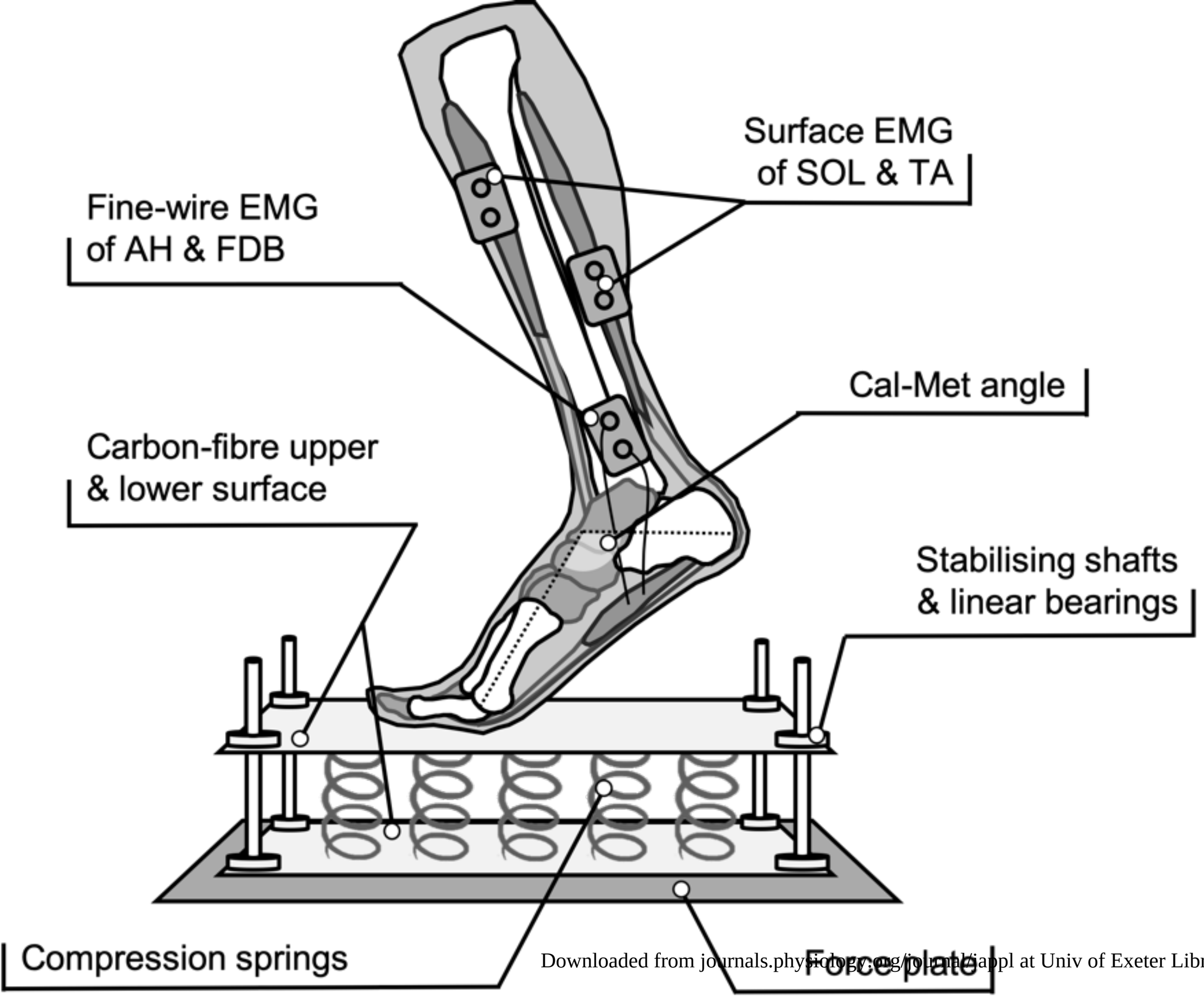
7. Figure legends

Figure 1. Experimental setup of the right leg and primary platform for the Low and Medium stiffness conditions. Surface stiffness was altered by changing the number of springs in parallel arrangement between the upper and lower surfaces. For the High stiffness condition the platform was removed from the force plate and participants hopped directly on the force plate. White segments are those used to define anatomical joint angles used in analysis.

Figure 2. A and B plot the ankle angle against its moment for the traditional and anatomical models, respectively. C and D plot the mean ± SD net, positive (no shading) and negative (grey shading) work per kilogram (normalised to body mass) of the traditional and anatomical ankle on the Low, Medium and High stiffness surface. Significant effects of surface on net work are represented by *.

Figure 3. A and B plot the Cal-Met angle against its moment and the MTPj angle against the MTPj moment, respectively. C and D plot the mean ± SD net, positive (no shading) and negative (grey shading) work per kilogram (normalised to body mass) of the midfoot and MTPj on the Low, Medium and High stiffness surface. Significant effects of surface on net work are represented by *.

Figure 4. Group mean ensembles ± SD (shaded area) for normalised RMS EMG signal amplitude for soleus (SOL, A), tibialis anterior (TA, B), abductor hallucis (AH, C) and flexor digitorum brevis (FDB, D) for the Low (black line), Medium (grey line) and High (dashed line) stiffness conditions. Ensembles are presented for a single hop cycle (i.e. from toe off (TO) to toe off). Foot contact (FC) is indicated by the vertical dashed line. For each muscle, data are normalised for each subject to the peak amplitude recorded during the High stiffness condition.



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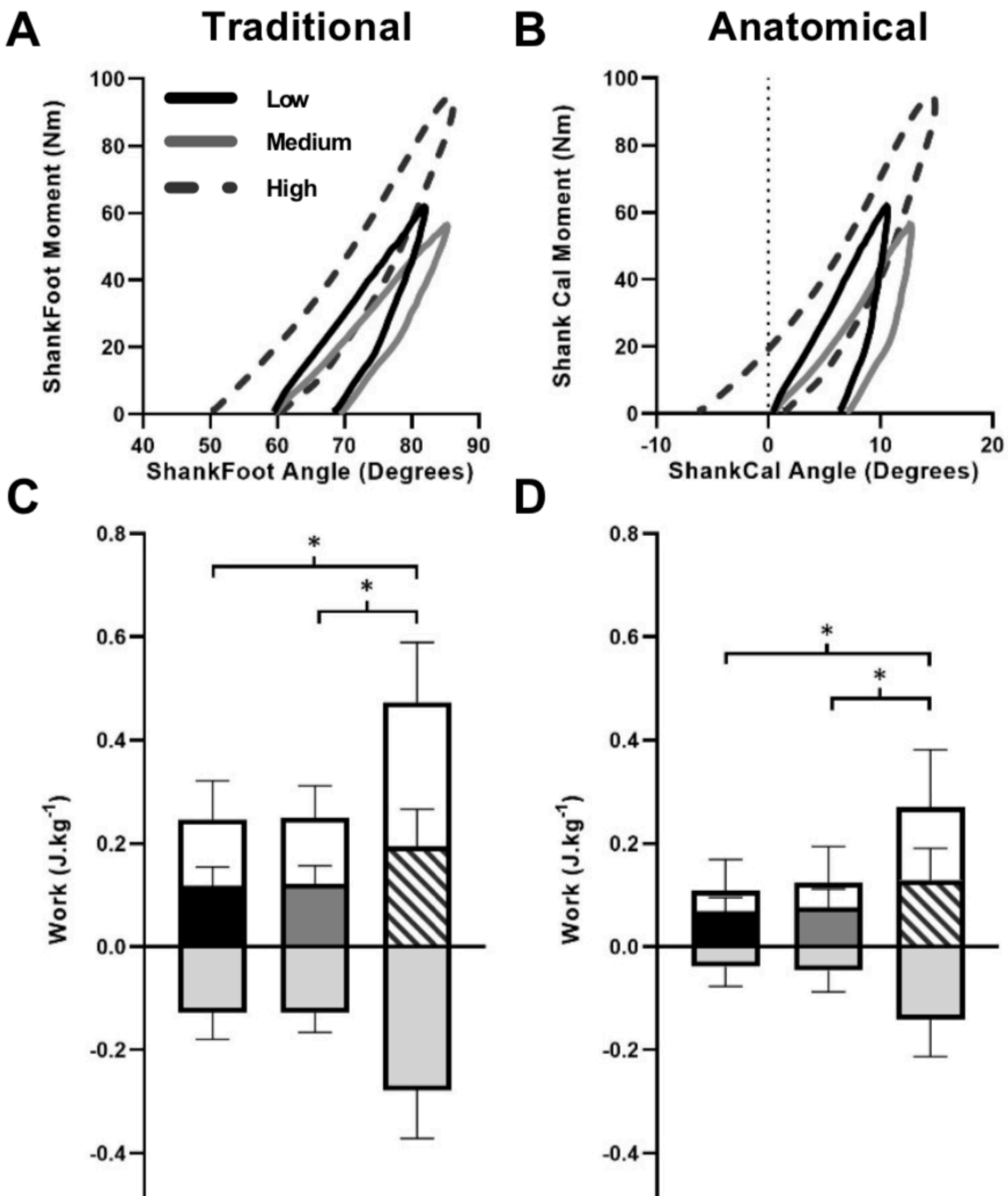

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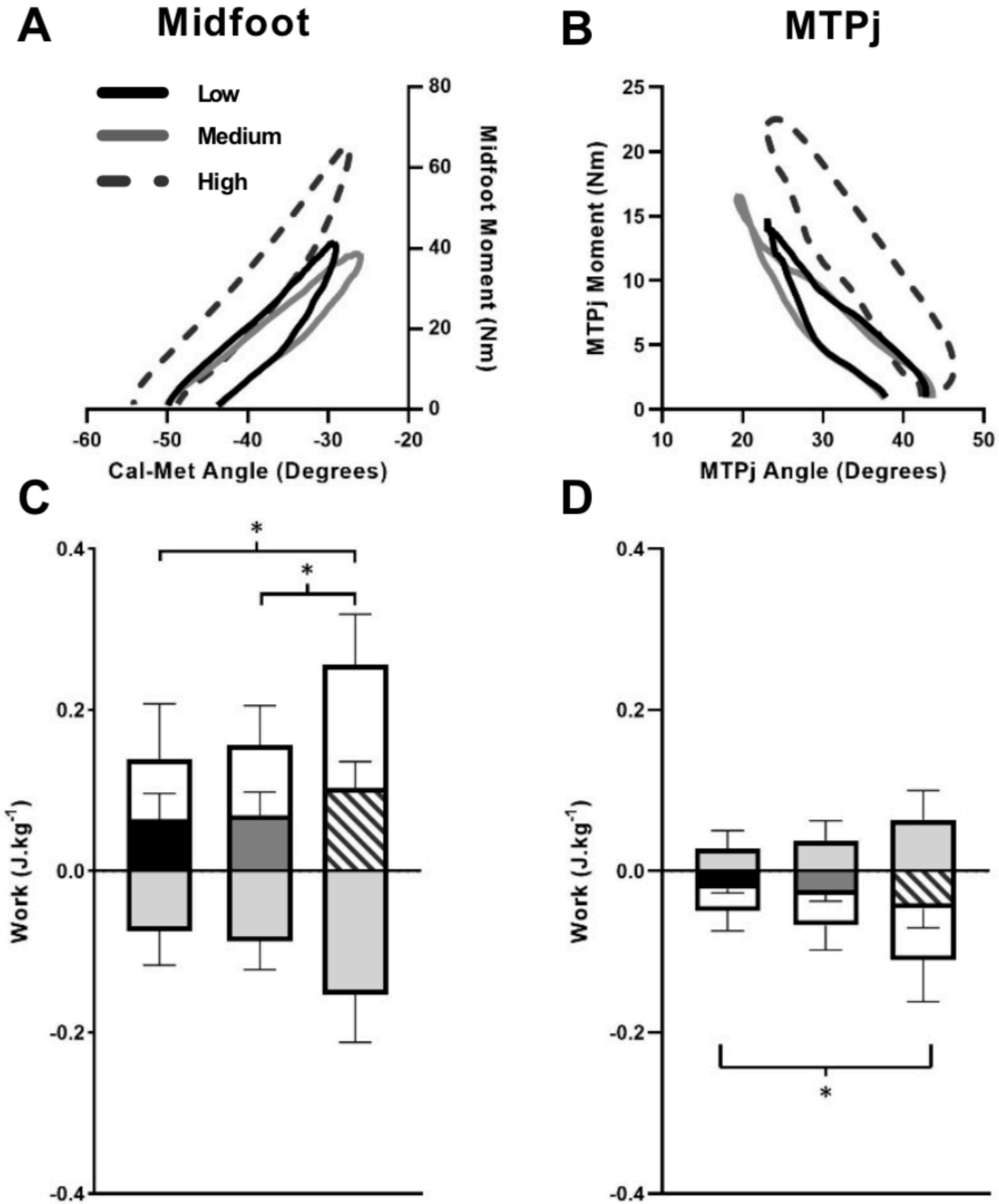

Figure 3. A and B plot the Cal-Met angle against the midfoot moment and the MTPj angle against the MTPj moment for the traditional and anatomical models, respectively. C and D plot the mean ± SD net, positive (no shading) and negative (grey shading) work per kilogram (normalised to body mass) of the traditional and anatomical ankle on the Low, Medium and High Stiffness surface. Significant effects of surface on net work are represented by *.

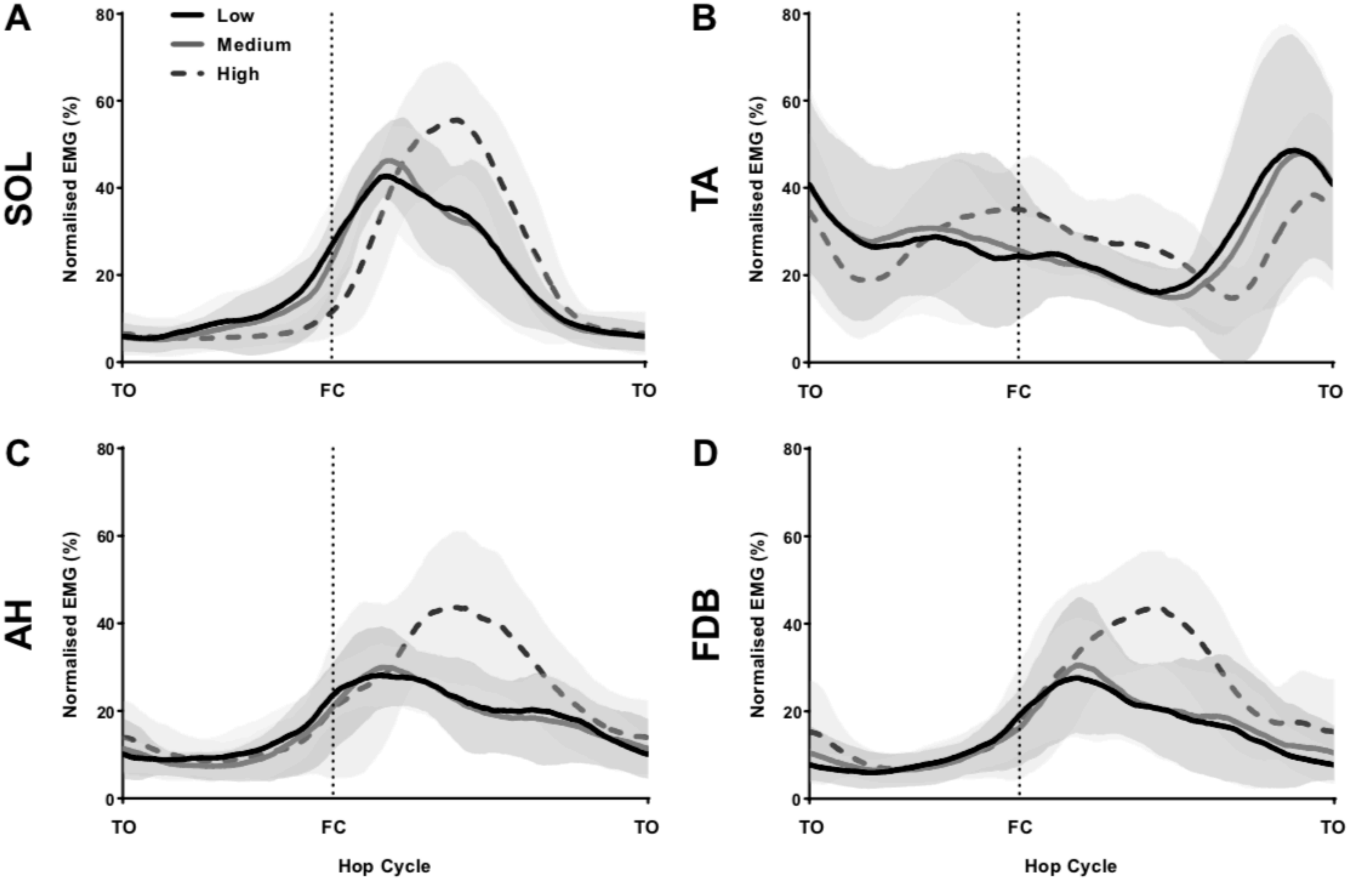

Figure 4. Group mean ensembles ± SD (shaded area) for normalised RMS EMG signal amplitude for soleus (SOL, *A*), tibialis anterior (TA, *B*), abductor hallucis (AH, *C*) and flexor digitorum brevis (FDB, *D)* for the Low (*black line*), Medium (*grey line*) and High (*dashed line*) stiffness conditions. Ensembles are presented for a single hop cycle, i.e. from toe off (*TO*) to toe off. Foot contact (*FC*) is indicated by the vertical dashed line. For each muscle, data are normalised for each subject to the peak amplitude recorded during the High stiffness condition.

Table 1. Global hopping metrics

	Low	Medium	High
Hop height (m)	0.04 ± 0.01	0.04 ± 0.02	0.05 ± 0.02
Hop time (s)	0.43 ± 0.05	0.43 ± 0.06	0.43 ± 0.06
Ground contact time (s)	0.25 ± 0.03*	0.24 ± 0.03*	0.22 ± 0.04
Impulse ($N.s^{-1}$)	157.0 ± 47.7	155.0 ± 47.1	151.0 ± 49.4
Leg stiffness ($kN.m^{-1}$)	22.5 ± 5.25*,**	17.1 ± 2.33*	14.0 ± 2.61

* Significant effect of surface compared to High stiffness surface condition, $p < 0.05$, ** significant effect of surface compared to Medium stiffness surface condition, $p < 0.05$

Table 2. Mean ± SD excursion, angle at contact, peak torque, quasi-stiffness and net-work for each surface condition and each defined joint.

		Surface stiffness condition		
		Low	Medium	High
Platform				
	Displacement during loading (m)	0.03 ± 0.01	0.02 ± 0.01	-
Centre of mass				
	Vertical excursion during contact (m)	0.09 ± 0.04	0.10 ± 0.03	0.10 ± 0.06
Traditional ankle				
	Excursion during loading (deg)	13.3 ± 7.44**	17.3 ± 5.74**	27.0 ± 7.29
	Angle at contact (deg)	69.6 ± 9.50**	71.4 ± 9.62**	60.9 ± 9.82
	Peak torque ($Nm.kg^{-1}$)	0.99 ± 0.40**	1.07 ± 0.23**	1.64 ± 0.25
	Quasi-stiffness ($Nm.kg^{-1}.deg^{-1}$)	0.07 ± 0.02	0.06 ± 0.03	0.06 ± 0.01
	Net-work ($J.kg^{-1}$)	0.12 ± 0.04	0.12 ± 0.03	0.19 ± 0.07
Anatomical ankle				
	Excursion during loading (deg)	5.04 ± 5.53**	6.44 ± 4.75**	14.0 ± 6.19
	Angle at contact (deg)	8.99 ± 9.44**	10.6 ± 8.36**	3.52 ± 7.19
	Peak torque ($Nm.kg^{-1}$)	0.99 ± 0.40**	1.07 ± 0.23**	1.64 ± 0.25
	Quasi-stiffness ($Nm.kg^{-1}.deg^{-1}$)	0.54 ± 0.47*,**	0.32 ± 0.14*	0.20 ± 0.09*
	Net-work ($J.kg^{-1}$)	0.07 ± 0.03*	0.08 ± 0.04*	0.13 ± 0.06
Midfoot				
	Excursion during loading (deg)	13.6 ± 5.71**	17.9 ± 4.62	21.5 ± 4.80
	Angle at contact (deg)	-45.3 ± 11.0**	-44.9 ± 9.59**	-50.3 ± 9.49
	Peak torque ($Nm.kg^{-1}$)	0.65 ± 0.28**	0.73 ± 0.18**	1.15 ± 0.24
	Quasi-stiffness ($Nm.kg^{-1}.deg^{-1}$	0.06 ± 0.02	0.05 ± 0.02	0.05 ± 0.02
	Net-work ($J.kg^{-1}$)	0.06 ± 0.03**	0.07 ± 0.03	0.12 ± 0.03
Metatarsal-phalangeal joint				
	Excursion during loading (deg)	6.14 ± 3.75	6.56 ± 4.78	6.60 ± 4.90
	Angle at contact (deg)	34.0 ± 11.5	33.0 ± 7.47	39.3 ± 6.56
	Peak torque ($Nm.kg^{-1}$)	0.28 ± 0.18	0.34 ± 0.15	0.43 ± 0.14
	Quasi-stiffness ($Nm.kg^{-1}.deg^{-1}$)	0.02 ± 0.02	0.02 ± 0.02	0.02 ± 0.01
	Net-work ($J.kg^{-1}$)	-0.02 ± 0.01**	-0.03 ± 0.01**	-0.05 ± 0.02

*Significant effect of model type, $p < 0.05$

** Significant effect of Low and Medium, compared to the High condition, $p < 0.05$

Table 3. Mean ± SD integrated EMG (iEMG). For each muscle, data are normalised for each subject to the peak amplitude recorded during the High stiffness condition.

	Surface stiffness condition		
	Low	**Med**	**High**
Soleus			
$iEMG_{contact}$	5.30 ± 1.68*	6.35 ± 1.24*	7.29 ± 1.00
$iEMG_{pre}$	1.76 ± 0.54*,**	1.62 ± 0.60	1.34 ± 0.36
Tibialis anterior			
$iEMG_{contact}$	6.28 ± 1.20*	6.35 ± 1.20*	7.28 ± 0.97
$iEMG_{pre}$	1.83 ± 0.60*,**	1.69 ± 0.63	1.40 ± 0.37
Abductor hallucis			
$iEMG_{contact}$	5.29 ± 1.68*	6.34 ± 1.25*	7.30 ± 1.00
$iEMG_{pre}$	1.77 ± 0.54*,**	1.63 ± 0.61	1.36 ± 0.38
Flexor digitorum brevis			
$iEMG_{contact}$	5.37 ± 1.60*	6.36 ± 1.20*	7.30 ± 1.00
$iEMG_{pre}$	1.80 ± 0.53*,**	1.66 ± 0.59	1.35 ± 0.35

* Significant effect of surface compared to High stiffness surface condition, $p < 0.05$, ** significant effect of surface compared to Medium stiffness surface condition, $p < 0.05$