Title - Shoes alter the spring-like function of the human foot during running

Author affiliation -
Dr Luke A Kelly [a]
Dr Glen A Lichtwark [a]
Dr Dominic J Farris [a]
Prof. Andrew Cresswell [a]

[a] - Centre for Sensorimotor Performance, School of Human Movement and Nutrition Sciences, The University of Queensland, Australia

Corresponding author

Dr Luke Kelly,

Centre for Sensorimotor Performance, School of Human Movement and Nutrition Sciences, The University of Queensland, Australia.

26B Blair Drive,
St Lucia
QLD 4072
Australia

Email l.kelly3@uq.edu.au
Phone - +61 7 33656825

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Abstract

The capacity to store and return energy in legs and feet that behave like springs is crucial to human running economy. Recent comparisons of shod and barefoot running have led to suggestions that modern running shoes may actually impede leg and foot spring function by reducing the contributions from the leg and foot musculature. Here we examined the effect of running shoes on foot longitudinal arch motion and activation of the intrinsic foot muscles. Participants ran on a force-instrumented treadmill with and without running shoes. We recorded foot kinematics and muscle activation of the intrinsic foot muscles using intramuscular electromyography. In contrast to previous assertions, we observed an increase in both the peak (flexor digitorum brevis +60%) and total stance muscle activation (flexor digitorum brevis +70%, abductor hallucis +53%) of the intrinsic foot muscles when running with shoes. Increased intrinsic muscle activation corresponded with a reduction in longitudinal arch compression (-25%). We confirm that running shoes do indeed influence the mechanical function of the foot. However, our findings suggest that these mechanical adjustments are likely to have occurred as a result of increased neuromuscular output, rather than impaired control as previously speculated. We propose a theoretical model for foot-shoe interaction to explain these novel findings.

Introduction

It has been suggested that humans may have evolved to run and have done so for millions of years [1,2]. Hard surfaces have been encountered by humans when running throughout evolution, however the modern running environment, characterised by stiff, invariant substrates such as roads and footpaths, has transformed at a far greater rate than evolution can progress [1-3]. The apparent lack of natural variability in surface terrain and compliance that is endemic in our modern running world is believed to have altered the biomechanical demands of running [4,5], possibly contributing to the high injury rate in those who habitually partake in this activity [6].

The human foot is the interface between the body and the ground. The unique structure of the foot allows force produced by muscles of the lower limb to be transmitted to the ground, to support body weight and also generate forward propulsion [7,8]. A pronounced structural feature of the human foot is the longitudinal arch (LA), which allows the foot to function in a spring-like manner [1,2,9,10] in series with the entire lower limb [11,12]. The LA compresses during early stance, absorbing mechanical energy as the ground reaction force increases. Presumably the energy absorbed is stored within elastic structures supporting the arch [9,13,14]. In late stance, when ground reaction force decreases, the LA recoils, returning elastic energy to deliver power for propulsion [9]. Stiffness of the LA is provided by passive ligamentous structures [9,14,15] acting in parallel with the intrinsic foot muscles whose relative contribution is continually adjusted by the central nervous system (CNS) in response to mechano-sensory stimuli [10,16]. This elegant arrangement allows the mechanical characteristics of the foot to be rapidly adapted to loading or task demands [10] and is thought to improve the efficiency of human running, returning between 8 and 17% of the mechanical energy required for one stride, via passive mechanisms alone [9,13].

Footwear has provided mechanical and thermal protection for human feet when running, for thousands of years [17]. The contemporary running shoe, however, was not invented until the 1970’s [18] and has evolved in parallel with the surge in popularity of running as a recreational pursuit. A defining characteristic of the modern running shoe is the thick visco-elastic midsole that is designed to compress and rebound when cyclically loaded and unloaded during running [19,20]. This design feature, generally referred to as cushioning, allows the shoe to function in a similar “spring-like” manner to the lower limb and foot, absorbing the potentially harmful impact transients that are encountered when the foot impacts with the ground [21-24], while also returning some of this energy to aid power generation for propulsion [25]. Another key feature of the modern running shoe is the contoured midsole, designed to provide external support and reduce excessive strain on the muscles and ligaments of the LA [21].

However, despite the huge financial investment in the development of running shoes, running injury rates remain relatively unchanged over the last 40 years [6,26,27], leading some to question the efficacy of modern running shoes in preventing injury [3,28-31]. Some scholars have gone as far to suggest that cushioned midsoles may actually hinder our running performance [3,28-30,32]. These scholars have speculated that a thick cushioned interface between the runner and the ground impairs mechano-sensory feedback and therefore, the inherent capacity of the CNS to contend with large impact force transients via adjustments in leg- and foot-spring stiffness [3,29,33]. Furthermore, it has been speculated that an apparent reliance on the shoe to attenuate impact and provide mechanical support for the LA may reduce the required contributions from the foot and ankle musculature, precipitating foot and ankle muscle weakness and predisposing a runner to injury [28,31,34]. While there is some evidence that runners tend to land differently when they run without shoes [28,35-38], there is no evidence that shoes have a detrimental influence on the spring-like function of the foot, or the contributions to this function from foot and ankle musculature.

Despite the on-going speculation as to the potential benefits and detrimental effects that modern running shoes may have on running mechanics, it is apparent that there is a dearth of information pertaining to how the CNS regulates the spring-like function of the foot during shod running. Therefore, the aim of this study was to test the hypothesis that running shoes impair the spring-like function of the foot, thereby altering the required force contribution from the intrinsic foot muscles to actively support the LA during running. In order to test this hypothesis, we had participants run on a force-instrumented treadmill barefoot and wearing running shoes. In addition to the ground reaction forces (GRF), electromyograms (EMG) were recorded from the intrinsic foot muscles and ankle plantar flexors, while motion capture data were recorded to assess foot and ankle kinematics during multiple consecutive strides.

Methods

Participants

Sixteen healthy participants (seven females mean ± standard deviation for age 19 ± 1 years; height: 165 ± 4 cm; mass: 59 ± 7 kg, nine males age 24 ± 5 years; height: 172 ± 4 cm; mass: 73 ± 10 kg) with no history of lower limb injury in the previous six months or known neurological impairment volunteered to participate in the study. All participants were habitually shod recreational runners. Foot-strike technique (ie. rear-foot or forefoot) was not applied as an inclusion or exclusion criteria, however none of the participants recruited for this study displayed a forefoot running technique when either shod or barefoot. Written informed consent was obtained from each subject. The study protocol was approved by the institutional human research ethics committee and conducted in accordance with the Declaration of Helsinki.

Experimental Protocol

Following a 3-min warm up period and familiarisation procedure, participants ran on a force-instrumented treadmill (AMTI, force-sensing tandem treadmill, Watertown, MA, USA) at 14 $km.h^{-1}$ while barefoot and shod. The running shoe chosen for this study is described by the manufacturer as a “cushioned stability” shoe, with a heel height of 30mm and forefoot height of 20mm (Asics GT2000, Asics Corp. Japan). The inner lining was made of soft, flexible foam.

In order to prevent rubbing against the intramuscular electrodes, the raised edges of the inner lining were trimmed flat and had no contact with the skin of the LA. Kinetic, kinematic and EMG data were collected simultaneously with approximately 15-20 strides (toe-off to ipsilateral toe-off) being recorded for each condition (barefoot and shod).

Data Acquisition

Kinematic and kinetic measurements

Three-dimensional (3D) motion of the foot and shank, and GRF data were collected during each running trial. Retro-reflective markers (9.0 mm diameter) were secured on the skin of the right foot, overlying the medial and lateral malleoli, posterior calcaneus, navicular tuberosity and head of the first and fifth metatarsals, in order to quantify motions of the foot segments and the LA (Figure 1). Additional markers were applied to the medial and lateral femoral condyles and a rigid cluster of four markers was placed on the antero-lateral aspect of the shank. During a standing calibration trial, markers located on the segment endpoints were used to generate a two-segment model of the shank and foot. Following the calibration trial, the medial and lateral knee markers were markers were removed and the motion of the shank was tracked with the rigid marker cluster. In order to allow foot marker positions to be captured during the shod condition, circular holes of 25 mm diameter were cut in the shoe upper in positions corresponding to the foot marker locations. This allowed visualisation of the markers, while still allowing markers to be adhered to the skin. Markers were adhered with double sided adhesive and further secured with cohesive bandage, allowing secure positioning for both the shod and barefoot conditions.

Kinematic data were captured at 200 Hz using an eight camera 3D optoelectronic motion capture system (Qualysis, Gothenburg, Sweden) while GRF and EMG data were synchronously captured at 4000 Hz via a 14-bit analogue to digital converter (Qualysis, Gothenburg, Sweden). Kinematic, force and EMG data were collected simultaneously and synchronized using the Qualysis Track Management software from the same company.

Electromyography

Identification of the abductor hallucis (AH) and flexor digitorum brevis (FDB) muscles was conducted using real-time B-mode ultrasound imaging (10 MHz linear array, Ultrasonix RP, USA) in the right foot of each subject. Subsequently, bi-polar fine-wire electrodes (0.051 mm stainless steel, Teflon coated, Chalgren, USA) with a detection length of 2 mm and inter-electrode distance of 2 mm were inserted using delivery needles (0.5 mm x 50 mm) into the muscle tissue of AH and FDB under ultrasound guidance, in accordance with previously described methods [39]. Sterile techniques were used for the insertion of all wires. Surface EMG data were collected from medial gastrocnemius (MG) and soleus (SOL) from the right leg of all participants using Ag-AgCl electrodes with a diameter of 10 mm and an inter-electrode distance of 20 mm (Tyco Healthcare Group, Neustadt, Germany). A surface reference electrode (10 mm diameter, Ag/AgCl, Tyco Healthcare Group, Neustadt, Germany) was placed over the right fibula head. Prior to electrode placement, the areas of the leg corresponding to the electrode placement sites were shaved, lightly abraded and cleaned with isopropyl alcohol.

All EMG signals were amplified 1000 times and recorded with a bandwidth of 30 -1000 Hz (MA300, Motion Labs, LA, USA). In order to minimise movement artefacts, the fine-wire electrodes, surface electrodes, connectors, cabling and pre-amplifiers were secured with cohesive bandage around the foot and shank.

Prior to data collection, each participant was asked to perform foot manoeuvres known to activate each foot muscle separately [16,40]. When predicted EMG patterns could be detected, it was concluded that the fine-wire electrodes were in the correct location. If not, the electrodes were withdrawn by approximately 1mm until appropriate activation patterns could be detected and possible crosstalk excluded. In order to ensure quality of the intramuscular EMG signal throughout the experiment, signal quality was assessed following each experimental condition using the same technique described above. A Velcro strap was secured around the participant's waist, which enabled the EMG amplifier box to be secured to the subject without interfering with their gait. A lightweight optical cable connected the amplifier box to the analogue to digital converter.

Data analysis

Kinetic and kinematic data files were exported to Visual3D (C-motion Inc., Germantown, MD, USA) for analysis. Force plate data recorded during each experimental trial was digitally filtered with a recursive 35 Hz low pass, fourth order Butterworth filter. A vertical GRF threshold was set to define each toe-off as occurring when vertical GRF fell below 50 N, while foot contact was defined as occurring when vertical force rose above 50 N. Swing phase was defined as the period from right toe-off to right foot contact, while stance phase was defined as occurring between right foot contact and right toe-off. One stride cycle was defined as occurring from right toe-off to the subsequent right foot toe-off.

Subsequently the magnitude of the vertical and antero-posterior (A-P) components of the GRF were calculated and normalised to bodyweight for each participant. Peak loading rate was defined as the maximum value obtained from the first derivative of the vertical GRF in the first 50ms following foot contact, while peak propulsive force was defined as the peak positive value of the A-P component of the GRF.

Marker trajectories were digitally filtered with a recursive 20 Hz low pass, fourth order Butterworth filter. Assumed rigid segments were created for the shank and foot. Joint rotations were calculated in accordance with International Society of Biomechanics recommendations (+y up, +z medial, +x anterior) with rotation about the z-axis - sagittal plane motion, rotation about the x-axis – frontal plane motion and rotation about the y-axis – transverse plane motion [41]. Ankle angle was defined as the angle of the foot segment relative to the shank, with plantar flexion reported as a positive angular rotation. Ankle angle at contact was calculated as the sagittal plane ankle angle at foot contact and ankle excursion was calculated by subtracting the minimum ankle angle during stance phase from the ankle contact angle. The LA angle was defined as a sagittal planar angle created by the bisection of a vector projecting from the medial malleolus marker to the navicular marker and another vector projecting from the head of the first metatarsal to the navicular marker (Figure 2). Thus a decrease in LA angle is indicative of a reduction in LA height. In order to describe the spring-like behaviour of the LA during stance phase, measures of compression and recoil were calculated. Compression of the LA was defined as the reduction in LA angle (height) that occurs due to the application of load reduction and was calculated by subtracting the minimum LA angle during stance phase from the LA angle at foot contact. LA recoil was defined as the increase in LA angle (height) that occurs during unloading and was calculated by subtracting the minimal LA angle during stance phase from the LA angle at toe-off.

Due to technical difficulties associated with collecting intramuscular EMG data from the foot muscles within a running shoe, complete sets of muscle activation data from AH and FDB was only obtainable from 10 of the 16 participants, while surface EMG data from MG and SOL was collected from all participants. The EMG data were exported to Spike2 software (Cambridge Electronic Design, Cambridge, UK) prior to analysis. All signals were high-pass filtered using a recursive fourth order Butterworth filter at 35 Hz to remove any unwanted low-frequency movement artefact. The EMG signals were then visually inspected in order to identify any remaining artefact, which was defined as an abnormal spike in the signal, typically associated with foot contact. Any such remaining artefacts resulted in the EMG data for that particular stride being excluded from further analysis. Following DC-offset removal, root mean square (RMS) signal amplitude was calculated using a moving window of 50 ms to generate an EMG envelope. Subsequently, the EMG envelope for each muscle was normalised to its peak amplitude found across all conditions. Normalised peak EMG amplitude and total stance activity (based on the EMG envelope) was calculated during the stance phase for each stride cycle, allowing comparisons in magnitude of stance phase muscle activation between shod and unshod conditions. In order to provide insight into the magnitude of activation relative to the time that a muscle is generating force, total stance phase activity (%max.s) was calculated by multiplying the mean normalised RMS signal amplitude during stance (%max) by the mean stance phase duration (s) for each muscle and condition [42,43].

For each individual, the kinematic, kinetic and EMG data were averaged across a minimum of 10 stride cycles to form individual variable means for each condition.

Statistics

Paired t-tests were used to describe the influence of running shoes on stride temporal characteristics, peak vertical ground reaction force, peak loading rate, peak propulsive force, ankle contact angle, ankle excursion, LA compression and recoil and peak muscle activation. Statistical differences were established at $P \leq 0.05$. Results are presented as mean ± standard deviation (SD) unless otherwise stated.

Results

Running mechanics

Shod running was typified by a longer stride duration (shod 0.68 ± 0.03s vs. barefoot 0.65 ± 0.03s, $P \leq 0.05$) and ground contact times (shod 0.21 ± 0.01s vs. barefoot 0.18 ± 0.01s, $P \leq 0.05$). When running shod and barefoot, participants produced comparable magnitudes of vertical ground reaction forces (shod 2.75 ± 0.24 body weights (BW) vs. barefoot 2.75 ± 0.22 BW, $P = 0.6$), however mean peak loading rate (shod 74.5 ± 10.0 BW s^{-1} vs. barefoot 86.4 ± 14.2 BW s^{-1}) and mean peak propulsive force (shod 0.41 ± 0.05 BW vs. barefoot 0.44 ± 0.05 BW) were both reduced when running with shoes (both $P \leq 0.05$, Figure 3). Participants adjusted the angular orientation of the ankle at foot contact depending on the running condition ($P \leq 0.05$), adopting a position of slight dorsiflexion when running in shoes (2.0 ± 2.8^{o}, range $-7.1 - 1.9^{o}$, Figure 4), while they landed in a position of slight plantar flexion when running barefoot (1.8 ± 2.3^{o}, range $-5.3 - 4.7^{o}$).

For shod and barefoot conditions, ankle dorsiflexion occurred following forefoot contact in early stance, until late stance when the ankle underwent rapid plantar flexion. Ankle dorsiflexion excursion was significantly less when running with shoes (shod 14.8 ± 4.6^{o} vs. barefoot 20.3 ± 6.8^{o}, $P \leq 0.05$), due to a more plantar flexed position of the ankle at initial foot contact and similar peak dorsiflexion angles during mid- to late-stance (Figure 4).

The LA compressed, during early to mid-stance as the vertical ground reaction force was rising and recoiled during late stance as the vertical ground reaction force subsided (Figure 4). The LA angle at foot contact was similar for both conditions (shod 150.4 ± 9.9^{o} vs. barefoot 151.0 ± 9.6^{o}, $P = 0.4$). However, when running with shoes, participants displayed reduced magnitudes of both LA compression (shod 8.6 ± 4.6^{o} vs. barefoot 11.5 ± 4.0^{o} $P \leq 0.05$) and recoil (shod 15.4 ± 5.7^{o} vs. barefoot 21.5 ± 5.5^{o}, $P \leq 0.05$) primarily due to a combination of a lower minimum LA angle at mid-stance and a higher LA angle at propulsion (Figure 4). When considered together, the reduction in LA compression and similar peak ground reaction forces, intimate that the LA is stiffer in the shod condition.

Muscle activation

The FDB and AH muscles recorded intramuscularly, displayed similar patterns of activation within each condition. Both showed periods of relative inactivity during swing and large bursts of activity during stance (Figure 4). Peak activation generally occurred during mid-stance for both muscles. Total stance activity was higher when running with shoes, for both FDB (shod 7.1 ± 2.7 %max.s vs. barefoot 4.2 ± 3.4 %max.s, $P \leq 0.05$) and AH (shod 6.3 ± 2.0 %max.s vs. barefoot 4.1 ± 1.8 %max.s, $P \leq 0.05$). Peak FDB activation was greater when running with shoes, compared to barefoot (shod 64.8 ± 25.9 % vs. barefoot 40.7 ± 19.0 %, $P \leq 0.05$, Figure 4), while no consistent differences were observed between the shod and unshod conditions for AH (shod 56.2 ± 19.3 % vs. barefoot 45.4 ± 19.3 %, $P = 0.17$, Figure 4).

Soleus and MG muscles were both relatively quiescent during early swing phase, with a large burst of activity that commenced during terminal swing and peaked prior to mid-stance (Figure

4). Total stance activity was higher when running with shoes, for both MG (shod 7.1 ± 2.4 %max.s vs. barefoot 5.9 ± 3.3 %max.s, $P \leq 0.05$) and SOL (shod 6.1 ± 1.2 %max.s vs. barefoot 5.0 ± 0.7 %max.s, $P \leq 0.05$). Peak MG activity was greater when running with shoes (shod 65.6 ± 15.4 % vs. barefoot 57.6 ± 16.2 %, $P \leq 0.05$, Figure 4) while no significant differences were observed in SOL activity between the shod and unshod conditions (shod 64.8 ± 15.4 % vs. barefoot 59.0 ± 14.6 %, $P = 0.09$).

Discussion

This study provides novel evidence of adjustments in the mechanical function of the foot when comparing running in shoes to barefoot. In line with our first hypothesis, running with shoes led to a reduction in the magnitude of LA compression and recoil, suggesting that running shoes influence foot-spring function. Of particular interest was the underlying mechanism for the observed alterations in LA motion when running in shoes, which we believe is at least partially driven by an increase in neuromuscular output, rather than a decrease, as we originally hypothesised.

Stance phase

During stance, the lower limbs of human runners behave in a spring-like manner, “compressing and recoiling” via concurrent ankle, knee and hip joint flexion then extension, in phase with the increasing and decreasing magnitude of the vertical ground reaction force [12,44,45]. This highly efficient mechanism allows recycling of elastic and kinetic energy during each foot contact [11,46], while also allowing a relatively stable centre of mass trajectory [45]. The central nervous system has the capacity to adjust the stiffness of the lower limb in order to minimise centre of mass vertical motion when running across terrains with varying undulations [47] and compliance [45,48,49]. The foot is considered a key contributor to leg-spring function [9,10,12,13] however to date, we believe, the influence of running shoes on the spring-like function of the foot has not been reported.

Runners in our experiment displayed substantially less arch compression and recoil when running with shoes, as compared to barefoot. This finding is in line with the key design features of running shoes that aim to provide support for the LA and reduce strain on plantar soft-tissue structures [50,51]. However, this finding also highlights that running shoes may actually limit the capacity for the foot to store and return energy via elastic mechanisms, due to a reduction in the magnitude of arch compression and recoil [13]. A key argument of those who repudiate the efficacy of modern running footwear is the potential for the cushioning and support characteristics of the shoe to impair foot-spring function, with a likely consequence of reduced activation from muscles that support the arch, leading to their weakness and disuse atrophy [3,29,34]. Our findings partially support this notion. However, the observed concomitant increase in intrinsic foot muscle activation in shod running appears to indicate that the reduced arch compression observed when running with shoes is driven by an increase in muscle activation, rather than via the cushioning and external support features of the running shoes.

In a recent series of experiments we provided novel evidence that the intrinsic foot muscles function in parallel with the plantar aponeurosis, actively tuning the stiffness of the LA in response to load during stance and locomotion [10,16,39]. Employing intramuscular electrical stimulation to activate individual intrinsic foot muscles, it was observed that contraction of these muscles could produce a 5% increase in arch height, reversing the compression of the LA that occurred when the foot was loaded with forces equivalent to bodyweight [16]. Given that the intrinsic foot muscles are known to act in unison as a functional group [10,52], it is likely that their combined action and the action of the extrinsic muscles [53,54] may have a profound effect on LA function. Therefore when considering the findings of the current study with those of our earlier studies, it becomes apparent that the observed increase in intrinsic foot muscle activation when running with shoes, compared to barefoot, is likely to be partially responsible for the concomitant reduction in LA compression during stance.

Given that the LA acts as a spring with an actively adjustable stiffness [9] and running shoes with visco-elastic midsoles also behave in a spring-like manner [23,25], the foot and shoe can be modelled to behave as two springs acting either in parallel, or in series, during the stance phase (Figure 4). Modelling the interaction between running shoes and the LA, potentially allows us to reveal the underlying mechanism for the observed increase in muscle activity when running in shoes. Within this model, the LA behaves as a single spring of given stiffness (k_{foot}) that is continually adjusted via activation of the muscles that span the arch of the foot [16], in order to optimise forces acting between the body and the ground. For example, intrinsic foot muscle activation increases when running at faster velocities, stiffening the LA and thereby allowing greater forces to be transmitted between the body and ground during shorter ground contact periods [10]. When a runner wears shoes with a visco-elastic midsole, the shoe will behave as an additional spring, also with a given stiffness (k_{shoe}, Figure 5) and the two form a foot-shoe system that has a stiffness (k_{FS}) that is dependent on the configuration of the two springs.

If the arch and shoe springs are modelled to be in parallel, the net stiffness of the foot-shoe system (k_{FS}) is the summed stiffness of the longitudinal arch (k_{foot}) and shoe (k_{shoe}) springs acting together.

$$k_{FS} = k_{foot} + k_{shoe}$$

Alternatively, if we model the foot and shoe as springs acting in series, the net compliance (inverse of stiffness) of the foot-shoe system ($1/k_{FS}$) will be the common compliance of the longitudinal arch ($1/k_{foot}$) and shoe ($1/k_{shoe}$) springs acting together.

$$1/k_{FS} = 1/k_{foot} + 1/k_{shoe}$$

To interpret both of these models with our data, we will assume that the neuromuscular system seeks to maintain a constant overall lower limb stiffness, including a constant K_{FS}. This assumption is based on a wealth of prior studies showing that humans adjust muscle activations to maintain constant system stiffness on surfaces of varied compliance [45,48,55,56] and also when wearable devices are added to the limb that influence system stiffness [57-59].

For our model of springs in parallel ($k_{FS} = k_{foot} + k_{shoe}$) if a runner wears running shoes of a given stiffness, the addition of the shoe spring will lead to an overall increase in k_{FS}. Thus, under the assumption that constant system stiffness is beneficial during constant velocity running [45,48,60], a reduction in LA stiffness is required in order to offset the additional stiffness added by the shoe. Reduced longitudinal arch stiffness would be achieved by allowing greater arch compression, presumably through a reduction in force output from the arch musculature; neither of which were observed here.

If the model of springs in series is considered ($1/k_{FS} = 1/k_{foot} + 1/k_{shoe}$) running in shoes with a visco-elastic midsole will decrease k_{FS} due to the presence of an additional spring. Therefore, an increase in longitudinal arch stiffness is necessary to increase overall system stiffness, maintaining constant k_{FS}. An increase in longitudinal arch stiffness would require a reduction in longitudinal arch compression, which is achievable via an increase in force output from the intrinsic foot muscles (increased activation) [10]. This is in line with our observations that intrinsic foot muscle activation increased and longitudinal arch compression decreased, when running in shoes.

According to the above scenarios that describe the potential interactions between human feet and running shoes, it seems that running shoes act as an additional spring in-series with the foot. While we cannot discount that deformation of the shoes may act to provide supporting forces to LA, an in-series spring model provided a sound mechanical rationale for our finding that running in shoes induced an increase in muscle activation from two of the primary muscles within the LA. The incorporation of intrinsic foot muscle activation data has therefore provided a unique insight into the underlying mechanism for the observed changes in LA function when running in shoes. Most importantly, these findings highlight that the alterations in lower limb biomechanics observed when running in shoes are not a result of reduced or impaired neuromuscular function.

The increase in ankle plantar flexor activation and reduction in ankle dorsiflexion observed when our runners were shod indicates that our runners may have also exhibited an increase in ankle stiffness in response to the increased compliance provided by the running shoe. Increased knee and ankle stiffness has previously been observed when running in shoes with visco-elastic midsoles [20,23] indicating that the cushioning properties of shoes may induce similar mechanical adaptations across the entire lower limb. This finding provides further support for our model that describes running shoes as springs acting in-series with the foot and leg. Furthermore, these findings are in line with previous research describing the in-series interaction between the lower limb and running support surface [48] and the apparent increase in leg stiffness that is observed when running on compliant surfaces [45,61].

Impact phase

The initial impact phase can be described to occur over the first 50 ms of ground contact and involves the rapid deceleration of the lower limb that occurs when the foot and ground collide [62] with forces up to twice bodyweight being transmitted at rates of up to 200 bodyweights per second [28,63]. Impact loading rates are considerably higher on stiff surfaces such as concrete, which are endemic in our modern running environment [64] and possibly contribute to the high prevalence of repetitive stress injury in runners [65]. The modern running shoe been designed to reduce the rate of force increase during the impact phase, thereby reducing the risk of injury to the runner. However, a counter argument has been raised that suggests that the presence of a cushioned midsole lends to the adoption of a marked heel-first landing pattern and a reliance on the shoe to attenuate impact, rather than via the body's natural shock absorbers: muscle and tendon [28,29]. Within the current experiments, our runners adopted a heel-strike pattern when running in shoes, while they contacted the ground with their mid-foot when barefoot. This finding is consistent with a number of previous comparisons of shod and un-shod running in runners who habitually wear shoes, further confirming that runners generally impact the ground differently when running in shoes as compared to barefoot [4,5,28,63,66]. It has been reported that barefoot runners tend to strike the ground with a forefoot first contact, allowing the body to effectively damp the large impact transients [67-69] via controlled dorsiflexion of the ankle and the associated stretch of the Achilles tendon [68]. Interestingly, despite our runners adopting a more plantar flexed ankle position when running without shoes, peak-loading rates still remained considerably higher. Thus, despite the modification in landing mechanics, the magnitude of adaptation in our habitually shod runners was insufficient to damp impacts in a manner comparable to the cushioned running shoe. Further research may elucidate if these observations persist across habitually barefoot running populations.

Methodological considerations

There are some methodological considerations that should be taken into account when considering these data. Within the present study we have attributed the observed increase in LA stiffness when running with shoes to an increase in intrinsic foot muscle activation. It is likely that other muscles such as tibialis posterior and the long digital flexors may have also contributed to the observed alteration in LA mechanics, as these muscles are also known to provide active support for this structure [53,54,70,71].

Our measure of "total stance activation" was calculated by multiplying the average of the RMS signal envelope during stance, by the stance phase duration for each condition. This calculation was adopted to provide an indication of the cost of muscle activation per step, taking into account the differences in stance phase duration between conditions [42,43]. Participants ran with a reduced cadence (longer stride duration) when shod, and thus, it may be suggested that the observed increase in total stance phase activation when shod may be offset by fewer strides in a minute. However within the current study this is not the case, as the difference in cadence between the two conditions is considerably smaller in magnitude than the difference in total stance activation. Based on the data presented in the manuscript, the average strides per minute for the barefoot condition is 92.3, while for the shod condition it is 88.2. If the total strides in a minute are multiplied by the total stance activity for the muscle with the smallest difference (AH), the shod condition has approximately 46% more activation per minute than the barefoot condition (shod 555.1 total stance activity$\cdot$min^{-1} v barefoot 378.4 total stance activity$\cdot$min^{-1}).

In our discussion of the foot and shoe interaction, we have made the assumption that constant leg stiffness is ideal during steady state running. This assumption is based on a growing body of evidence that indicates the CNS will adjust knee and ankle stiffness in order to maintain constant COM trajectory [45,48,55,56]. Further research is now required to determine if the foot behaves in series with the ankle and knee to govern overall limb stiffness during running, while also examining if the observed changes in LA stiffness during running are primarily due to an alteration in surface compliance.

Conclusion

In summary, we have described a novel mechanism for how human feet interact with modern running shoes. An in-series, spring-like arrangement of the foot and shoe dictates that the reduction in system stiffness that occurs when wearing a running shoe will need to be offset by an increase in the stiffness of the longitudinal arch, in order to maintain constant foot-shoe system stiffness. The observed increase in longitudinal arch stiffness in response to mechano-sensory stimuli, is likely achieved via the observed increase in activation from the intrinsic muscles of the arch. These findings further highlight the highly adaptable nature of the human foot and it's importance in upright bipedal locomotion.

Author Contributions

LK – study design, data collection and analysis, manuscript preparation

GL - study design, data analysis and manuscript preparation

DF - data analysis and manuscript preparation

GL - study design, data analysis and manuscript preparation

Competing interests

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Figure Legends

Figure 1. Depiction of the Lower limb marker set employed for collection of kinematic data. White markers are removed following a static calibration trial, with the cluster of four markers on a rigid plastic shell used to track the motion of the shank.

Figure 2. Longitudinal arch angle is defined as the angle created by the bisection of a vector projecting from a marker located on the medial malleolus (A) to a marker located on the navicular tuberosity (B), with a vector projecting from a marker located on the head of the first metatarsal (C) to a marker on the navicular tuberosity (B). A reduction in longitudinal arch angle indicates arch compression, while an increase in arch angle indicates arch recoil.

Figure 3. Group mean $\pm$ standard deviation (shaded area) for vertical force (top), vertical force loading rate (middle) and antero-posterior force (bottom). Data is recorded from each participant running barefoot (red) and shod (blue) at 3.89 ms^{-1} and presented from from foot

contact to toe off from the right foot. Loading rate is defined as the first derivative of the vertical ground reaction force signal. All data is normalised to body weight.

Figure 4. Group mean ensembles ± standard deviation (shaded area) for changes (Δ) in longitudinal arch (LA) and ankle angle (degrees, º, top), electromyography (EMG) normalised root mean square signal amplitude for flexor digitorum brevis (FDB) and abductor hallucis (AH), gastrocnemius medilais (MG) and soleus (Sol). Group mean ensembles are defined from toe off (TO) to ipsilateral toe off for the right foot. Data recorded during running at 3.89 ms^{-1}. For each muscle EMG data is normalised to the maximal amplitude recorded for all trials. Change in LA and ankle angle was calculated by subtracting the angle at foot contact in the barefoot condition from the angle-time data from both shod and barefoot conditions. FC, foot contact. The barefoot condition is the red dashed lines and shod the solid blue lines

Figure 5. Depiction of a parallel (top) and in-series (bottom) spring arrangement between the longitudinal arch and running shoe. Both the longitudinal arch and running shoe will behave in a spring-like manner during running, compressing and recoiling as force is increased and decreased. If the longitudinal arch and running shoe act in-parallel, wearing a running shoe will increase the overall stiffness of the foot-shoe system. If the longitudinal arch and running shoe act in-series, wearing a running shoe will increase the overall compliance of the foot-shoe system. Based on the assumption that constant foot-shoe system stiffness is favoured during steady state running, the response of the intrinsic foot muscles in regulating the stiffness of the arch will vary depending on whether the longitudinal arch and running shoe behave in-parallel or in-series.

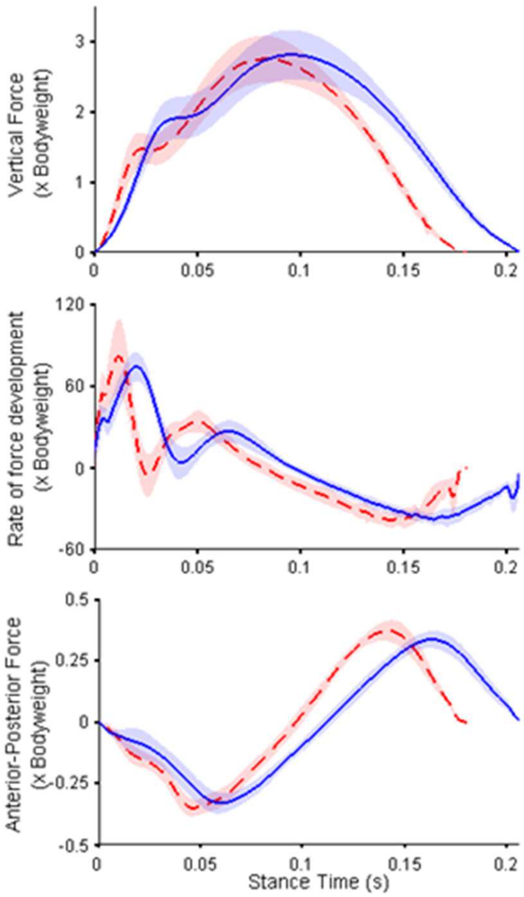
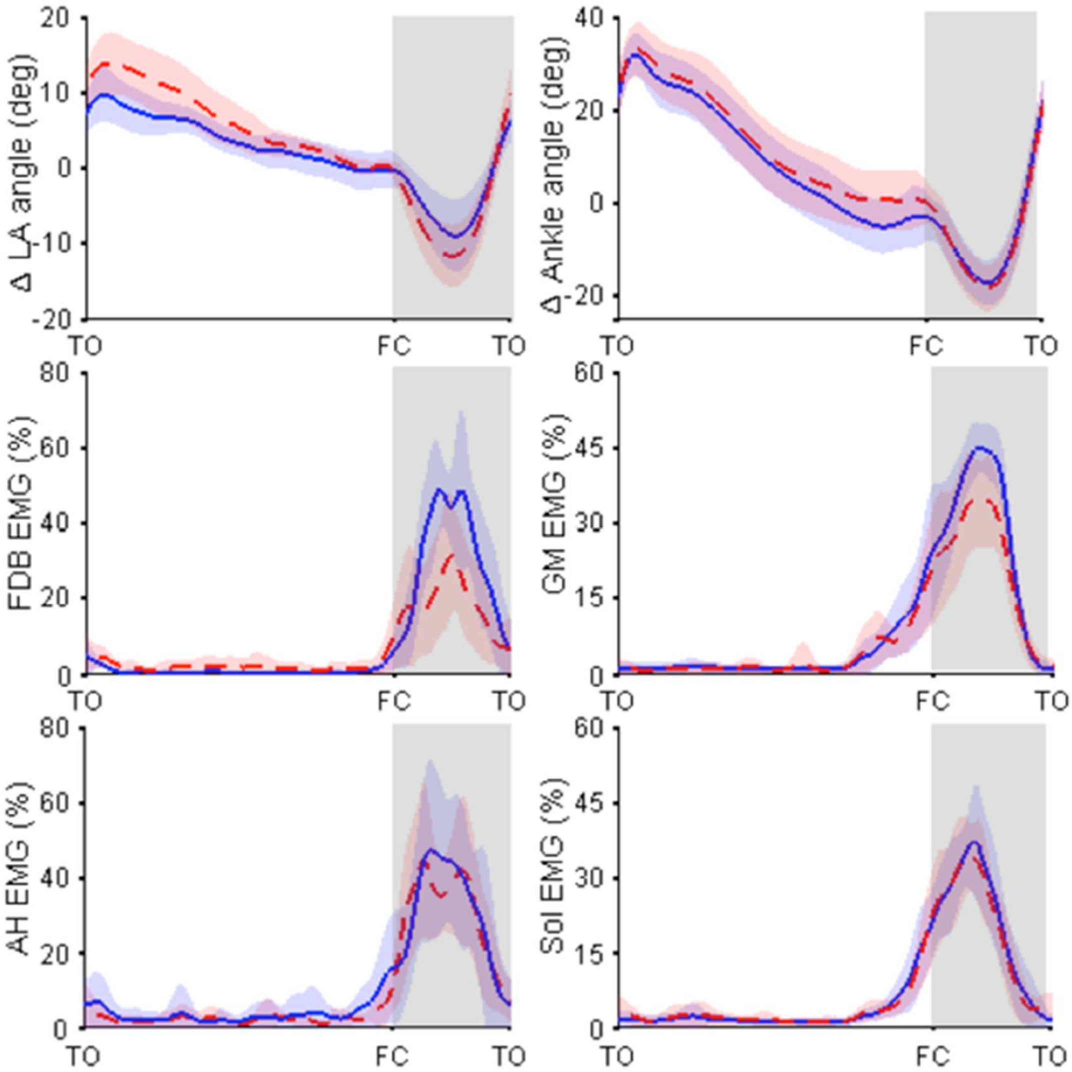


Figure 1. Group mean ± standard deviation for vertical force (top), vertical force loading rate (middle) and antero-posterior force (bottom). Data is recorded from each participant running barefoot (red) and shod (blue) at 3.89 ms^{-1} and presented from from foot contact to toe off from the right foot. Loading rate is defined as the first derivative of the vertical ground reaction force signal. All data is normalised to body weight.



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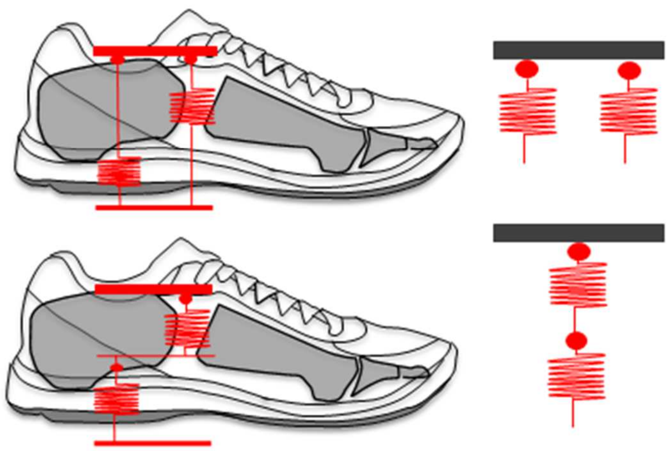
1



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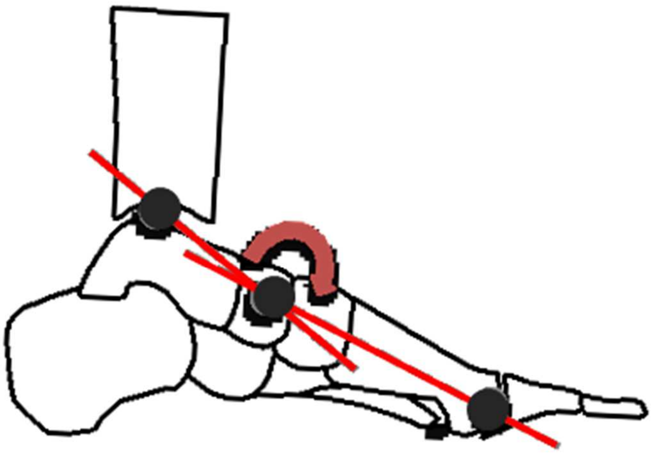

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