

Northumbria Research Link

Citation: Wilkinson, Mick, Stoneham, Richard and Saxby, Lee (2018) Feet and Footwear: Applying Biological Design and Mismatch Theory to Running Injuries. *International Journal of Sports and Exercise Medicine*, 4 (2). ISSN 2469-5718

Published by: ClinMed International Library

URL: <http://dx.doi.org/10.23937/2469-5718/1510090> <<http://dx.doi.org/10.23937/2469-5718/1510090>>

This version was downloaded from Northumbria Research Link: <http://nrl.northumbria.ac.uk/34401/>

Northumbria University has developed Northumbria Research Link (NRL) to enable users to access the University's research output. Copyright © and moral rights for items on NRL are retained by the individual author(s) and/or other copyright owners. Single copies of full items can be reproduced, displayed or performed, and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided the authors, title and full bibliographic details are given, as well as a hyperlink and/or URL to the original metadata page. The content must not be changed in any way. Full items must not be sold commercially in any format or medium without formal permission of the copyright holder. The full policy is available online: <http://nrl.northumbria.ac.uk/policies.html>

This document may differ from the final, published version of the research and has been made available online in accordance with publisher policies. To read and/or cite from the published version of the research, please visit the publisher's website (a subscription may be required.)



**Northumbria
University**
NEWCASTLE



UniversityLibrary



OPINION ARTICLE

Feet and Footwear: Applying Biological Design and Mismatch Theory to Running Injuries

Michael Wilkinson*, Richard Stoneham and Lee Saxby

Faculty of Health and Life Sciences, Northumbria University, United Kingdom



*Corresponding author: Dr. Michael Wilkinson, Sport, Exercise and Rehabilitation, Northumbria University, Northumberland Building, Newcastle-upon-Tyne, NE1 8ST, United Kingdom, Tel: 44(0)-191-243-7097, E-mail: mic.wilkinson@northumbria.ac.uk

Abstract

The Endurance-Running hypothesis proposes that natural selection has shaped humans into endurance-running specialists. Running-related-injury rates between 20-79% suggests modern humans are prone to injury in this species-specific movement pattern. This opinion piece offers a novel perspective on high-injury prevalence in human endurance running, focussing on evolutionary mismatch between modern athletic footwear and evolved foot structure and function. We propose that non-anatomically shaped, structured, cushioned footwear can lead to maladapted foot structure and loss of biologically-normal function including stability, elasticity, sensory feedback and subsequent movement control. The structure and function of the human foot and its possible impairment by modern footwear has received little attention in running-related literature, but could provide a new area of enquiry and potential solutions for many running-related injuries.

Keywords

Running, Injury, Biomechanics, Foot structure, Foot function, Footwear

Key Points

Humans are adapted for endurance running, but injury rates are high. A mismatch between evolved structure and function of the foot, and design features of modern footwear could explain the high injury rate in the derived movement pattern of endurance running. Evidence suggests that the design features of modern footwear can deform foot structure and impair foot function. The loss of structure and function could explain many common running injuries.

Introduction

The Endurance-Running hypothesis proposes that natural selection has shaped humans into endur-

ance-running specialists [1-3]. However, injury rates ranging from 20-79% [4-6] suggest modern humans are prone to injury in running which the Endurance-Running hypothesis contends is a species-specific movement pattern for which we are well adapted.

Explanations and solutions focus largely on shoe design and gait mechanics. Foot structure and function, in contrast, have received little attention in running-related research [7]. Moreover, and despite continued interest in running-shoe design, there has been little attention on how footwear might influence foot structure and function and therefore the rest of the kinetic chain above it. This opinion piece addresses these issues and proposes a novel perspective that could add to factors explaining injury risk in endurance running.

Endurance-Running Hypothesis

The fossil record of the genus homo shows evidence of musculoskeletal adaptations that reduce the mechanical and energetic demands of bipedal-endurance running. Adaptations differentiating homo sapiens from early homo and from primate ancestors include the nuchal ligament for head stabilisation, a mobile thoracic spine permitting counter rotation of the trunk and legs, long legs that lengthen the stride so reducing energy cost per unit of distance, large proximal hip muscles (gluteals) to control forward pitch of the torso at ground contact, long Achilles tendons and plantar arches to facilitate energy storage and return, and short-straight toes that minimise toe flexion moments and smooth the forward trajectory of body weight over the supporting foot [1-3]. Many of these adaptations benefit running only, suggesting that

this activity was an important species-specific movement pattern for survival, and that these adaptations were retained by selective pressure [2,3,8-10].

Mismatch Hypothesis

Evolutionary adaptations can be phylogenetic (of a species) or ontogenic (within an individual's lifespan). Both are responses to the habitat in which the organism lives. The phylogenetic evolution of humans occurred over 200,000 years as hunter gatherers in Africa [10]. The anatomical adaptations discussed above reflect the demands of that lifestyle and habitat. By comparison, modern lifestyles and habitats are a blink of an evolutionary eye to which our species is yet to phylogenetically adapt, but to which we do ontogenically adapt (Figure 1a and Figure 1b). Deformations of foot structure and subsequent impaired foot function are examples of ontogenic adaptation known to relate to years of narrow footwear use [11,12]. A mismatch between what humans are adapted for and the habitat in which we now exist is suggested to underpin many health and injury problems [10,13]. We propose that the design features of conventional footwear, and the structure and function for which feet are adapted could be considered a mismatch. We further suggest that ontogenic adaptations to this mismatch (deformed toe position in particular) could compromise foot function and increase risk of injury in endurance running. For the purpose of this opinion piece, we define foot structure and function congruent with phylogenetic adaptation as 'biologically normal'. Foot structure and function at odds with evolutionary

heritage and resulting from unfavourable ontogenic adaptation are defined as 'culturally normal'.

Foot Structure and Function

In an upright biped, the purpose of the foot is to support and control the direction of the body weight as it falls forwards during the stance phase of locomotion [3,14,15]. With this and fundamental principles of physics in mind, a reverse-engineering approach suggests a larger base of support (i.e. the effective area of the supporting foot), that is widest at the front, would serve both purposes. Unsurprisingly, comparisons of habitually-unshod with habitually-shod populations consistently show wider (particularly at the front) feet in unshod populations, in agreement with that predicted by fundamental principles governing stability [12,16-19]. Observational studies on habitually-barefoot populations also demonstrate the benefits of a wide foot in the form of more uniform distribution of pressure through the entire plantar surface of the supporting foot during walking [18], and reduced peak pressure and pressure-time integral under the forefoot when running [20]. Given that pressure is force divided by area of contact, these observations support the natural selection of a wide foot to serve a support function.

Of importance to forefoot width and the stabilisation role of the foot is the position and function of the great toe. The notable spread and abducted position of this toe from the others characterises habitually-barefoot populations [16,18,19]. Increased thickness and an abducted position of the great toe in humans

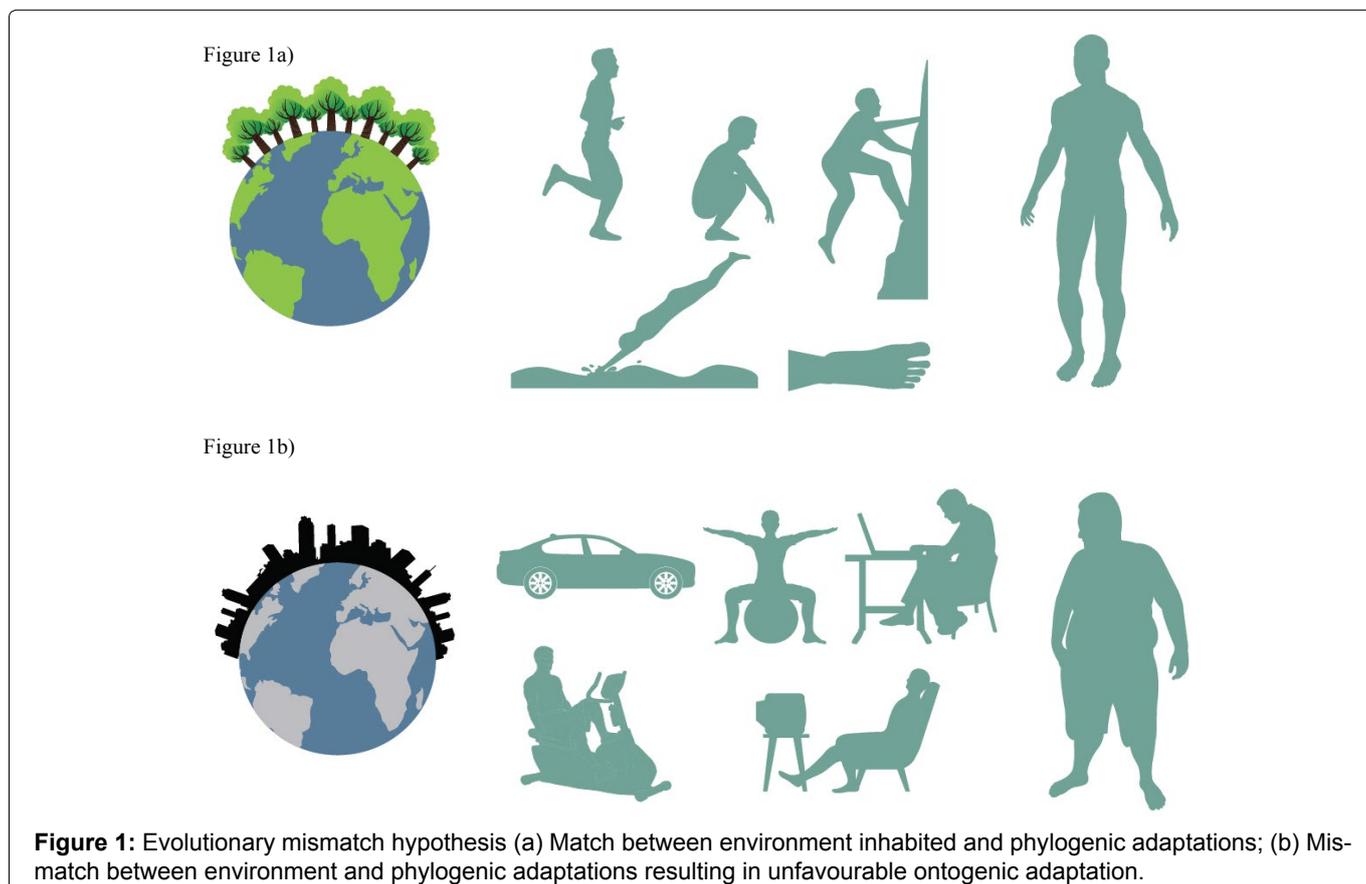


Figure 1: Evolutionary mismatch hypothesis (a) Match between environment inhabited and phylogenetic adaptations; (b) Mismatch between environment and phylogenetic adaptations resulting in unfavourable ontogenic adaptation.

are evolved-functional adaptations providing directional stability in bipedal locomotion [20-22]. These adaptations are important considering that direction of ground-reaction forces (and the resulting joint moments created) contribute to injury [20,23-25].

The main function of the great toe is to direct body weight through the axis of leverage of the foot, while facilitating the windlass mechanism and creating a rigid lever for force transfer in terminal stance [9,21,22,26]. The stabilising role was demonstrated by Chou, et al. [22]. Directional stability, quantified as % of centre-of-pressure movement in the intended direction, was significantly worse when the great toe was splinted into 30° of dorsiflexion. These results and other investigations of static-unipedal balance, suggest that a reduced-forefoot width results in a smaller mechanical lever to control directional stability [22,27]. Morton [21] and Plank [28] also demonstrated a compromised-functional capacity of the foot with a valgus (adducted) position of the great toe in walking trials. Both authors reported excessive pronation in feet with great-toe valgus. So, positioned, the toe cannot oppose the inward role of the foot due to reduced lever arm length. Increased loading in the transverse and frontal plane at joints above the foot is a likely consequence of instability at the foot, and might explain the high injury rates observed at the knee in runners lacking biologically-normal foot structure and function [4].

Further evidence for the importance of the great toe in the control of bipedal locomotion comes from neurophysiology and comparative anatomy. The ratio of sensory to motor nerves in humans is reported between 9:1 and 40:1, highlighting the importance of sensory feedback for movement control [29,30]. Hashimoto, et al. [31] mapped the neural and somatic representation of the fingers and toes in living humans and monkeys. While monkeys and humans represented fingers separately in the primary-sensorimotor cortex, the toes in monkeys were not differentiated. In contrast, humans had independent-cortical representation of the great toe from the other toes. Moreover, Aiello, Dean and Cameron [32] report that unlike chimpanzees and orang-utans, humans have a separate and distinct primary-flexor muscle (flexor hallucis longus) that inserts only to the great toe. The independent representation and muscular control of the great toe in humans, absent in non-bipedal primates, underlines its importance in the control of bipedal locomotion.

Evidence suggests that selective pressure for success in endurance running has adapted the structure and function of the great toe to direct and control the forces associated with this gait. There is also evidence that misalignment of this toe compromises control of body weight through the longitudinal axis of the foot, leading to excessive loading in the transverse and frontal planes. Such patterns could produce injurious loading at joints proximal to the foot, particularly the primarily-sagittal

knee joint. Evidence also suggests that constraining forefoot width and preventing direct contact of the great toe with the ground impairs directional stability and balance, and increases plantar pressure, both of which are known to increase ankle and overuse injuries [18,33,34].

Foot Structure and Energy Return

The medial-longitudinal arch of the foot represents one of most important evolutionary-lower-limb adaptations for endurance running in humans [1,8,9]. Humans are the only primate to have evolved this structure. Compression of the medial-longitudinal arch contributes to the return of elastic energy captured in the first half of stance [8,24,35-37]. Stearne, et al. [8] recently demonstrated this *in vivo* by restricting compression of the arch and reporting an adverse effect on the metabolic cost of running. Running with a 'full arch' insole (decreasing arch compression by 80%) reduced elastic energy storage by 8.8% and increased the cost of transport by 6%. Recent work also suggests that elastic contributions increase with running speed [38]. A substantial energy saving is made with biologically-normal functioning of the longitudinal arch.

Sensory Role of the Foot

The plantar surface contains slow-adapting mechanoreceptors, providing feedback about the spatial distribution of pressure, and rapid-adapting mechanoreceptors that sense magnitude and change in magnitude of pressure [39,40]. Evidence suggests that plantar-sensory feedback is used to modify running technique to avoid painful and potentially injurious impacts [24,41,42]. Increasing plantar sensation via textured insoles has recently been shown to reduce vertical loading rate by a magnitude equal to the difference between injured and non-injured runners by reducing stride length [43]. In other work, Gruber, et al. [42] investigated whether heel striking, a landing pattern associated with injury [6] and commonly seen in western populations, was related to impaired plantar-sensory feedback. When running barefoot on a soft-cushioned material similar to a running shoe, 80% of participants landed on their heel. Only 35% retained a heel strike, with 27.5% and 37.5% changing to midfoot and forefoot landings respectively when the cushioning was removed. Gruber, et al. [42] suggested that the change in foot strike pattern was a response to the change in surface compliance and perceived increase in the sense of impact when running barefoot on a hard surface. Similar responses were observed by Liberman, et al. [44]. After adjusting for speed and stride frequency, there was greater variability in foot strike pattern between soft and hard surfaces in habitually barefoot than in shod runners. There was a significant trend to heel strike on a compliant surface and an increased likelihood to land on the mid or forefoot on a hard surface in participants that habitually ran barefoot. Hatala, et al. [45] had previously reported a switch from heel to forefoot striking with increasing running speed in

a population of habitually-barefoot Kenyans. Together, these results confirm the importance of plantar-sensory feedback to modify technique according to speed and substrate underfoot, and show cushioned footwear to reduce adaptability in technique in response to changes in impact with speed and surface compliance.

Evidence suggests that sensitivity of the plantar surface has evolved for avoidance of injury. It follows that compromised sensory feedback might increase injury risk. However, unlike other cursorial mammals, humans have not evolved thick keratinous protection against puncture or thermal injury such as hooves or pads, hence humans have used footwear for this purpose, with early examples dating back 10000 years [46]. A record of the characteristics of such early footwear show that they were mostly types of sandal, offering simple protection without interfering with biologically-normal foot function. In contrast, common design features of modern footwear such as heavy cushioning, elevated heels, arch supports, a tapered and narrow toe box and a toe spring (upward curve of the sole at the front of the shoe) that flexes the great toe off the ground, are at odds with biologically-normal foot structure and function. Ontogenic adaptations to this mismatch and the functional implications are discussed next.

Implications of Footwear Design on Foot Structure

Research reporting the detrimental effects of footwear on the structural development of the foot spans

over 100 years [16,24,47-50]. Studies show that biologically-normal flexibility and width of the forefoot, and longitudinal arch development are compromised by non-anatomically-shaped footwear [1,8,47,50,51].

The plasticity of foot structure was well known and exploited by the Chinese in the ancient cultural practice of foot binding [16,52]. The timescale of structural alterations appears to be rapid, particularly in the young, where bones have yet to fully ossify [50]. Hoffman [16] observed hallux deformation in a habitually-barefoot teenager required to wear shoes for just six weeks. In an adult-case-study patient, Knowles [53] showed reversal of great toe valgus after two years wearing anatomically-shaped shoes (i.e. tip of shoe medial to the medial border of the great toe). Other observational research [12] reported a significant relationship between years of shoe wear and great-toe-valgus angle in shoe-wearing communities, with valgus angle increasing in a linear fashion with years of shoe wear. The observed adaptation of foot structure to shoe wear is in accord with Wolff's law, as is the reversal of deformity observed by Knowles [53].

Highly cushioned, narrow, stiff-soled and toe-sprung footwear characteristic of the modern-running shoe could potentially compromise foot structure and function. Indeed, altered gait patterns, increased maximum impact force, reduced arch deformation and toe flexion have been reported in children running in conventional-running shoes compared to barefoot [54,55]. Moreover, a comparison of shod and barefoot populations

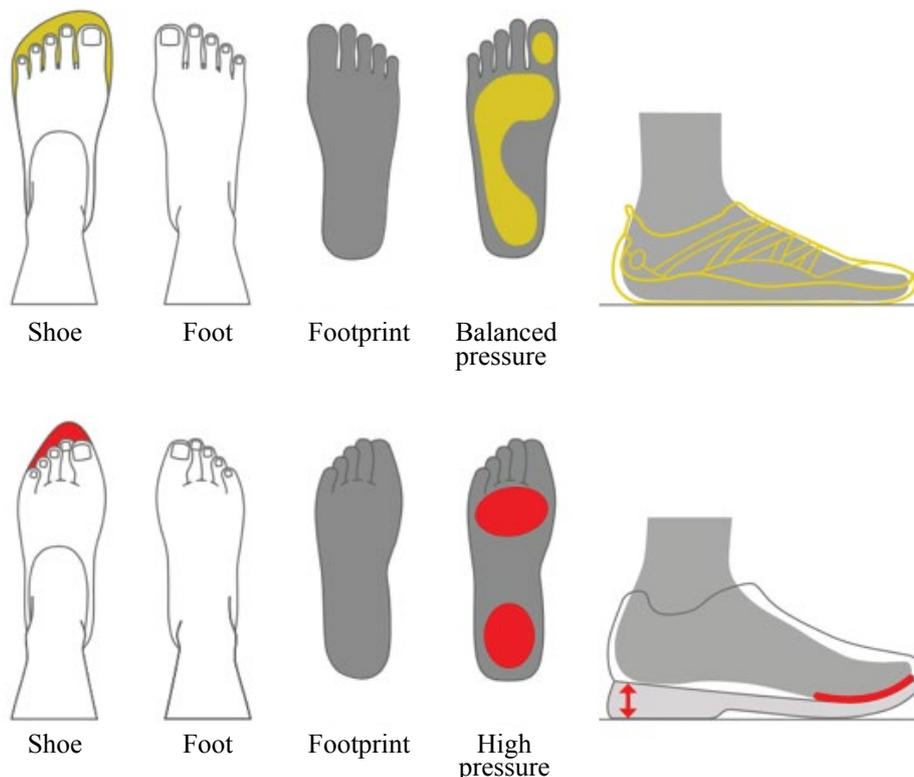


Figure 2: Anatomically-shaped shoes permit biologically-normal structure and function whereas non-anatomically-shaped shoes produce 'shoe-shaped' feet.

suggested that habitual-western-footwear use leads to stiffer feet with impaired function [47]. There is a dearth of longitudinal studies examining the effects of long-term shoe wear on foot function. However, a recent prospective, long-term follow up, study using large samples of mono and dizygotic twins provided strong evidence that development of great toe deformity (hallux valgus) is not genetic, but is significantly associated with years of wearing narrow shoes, with frequent use increasing risk of developing toe deformity by almost three fold [11].

From an evolutionary perspective, footwear makes sense, particularly given the range of environments in which humans thrive. However, the mechanics and evolution of the foot dictate that such footwear should be anatomically shaped to allow biologically-normal toe position and function, and also flat and flexible enough to allow unimpeded movement of the foot and toes during locomotion. Such characteristics have been previously recommended [49,52] (Figure 2).

It is notable that a review of injury-reducing benefits of conventional-cushioned-elevated-heel-running shoes could find no supporting evidence [56]. Cushioned-elevated heels are marketed to offer protection from large impact forces and high loading rates characteristic of a heel-strike strategy [24,57]. This marketing is largely based on machine testing protocols that do not account for proprioceptive feedback and human-behavioural responses to compliant materials [58]. Furthermore, a heel-toe drop has been argued to encourage running mechanics associated with injury [6,57].

Heel elevation produces a dorsiflexion off-set and encourages the commonly-observed heel strike pattern associated with increased effective mass, impact transients and higher injury rates [6,24,59]. Moreover, the sensory dampening created by the cushioning leads to additional kinetic consequences.

Implications of Footwear Design on Sensory Feedback

Plantar-sensory feedback provides key information about the location and magnitude of forces under the foot [39,40]. The cushioning in modern footwear impairs sensory input in static and dynamic tasks [42,58,60]. As previously discussed, Gruber, et al. [42] showed a strong relationship between change in foot-strike strategy (heel strike to mid/forefoot strike) and change in surface conditions (compliant to hard). This agrees with the biological imperative i.e. the subconscious drive to minimise energy cost subject to also minimising injury risk [61,62]. The energetic cost of running is inversely related to ground-contact time and is also paid for 'per step' i.e. when body weight is supported against gravity [63]. It is energetically favourable to cover a given distance with a longer ground contact time and stride length. However, while economical, over stride relative

to the knee is associated with increased joint loading at the knee and hip [64] and the potential for overuse injuries. The cushioned heel masks the true forces acting upon the foot allowing runners to perceive over stride as safe [58,65].

Biologically Normal Versus Culturally Normal and the Injured Running Specialist

There is evidence that humans are uniquely adapted to perform endurance running with minimum energy expenditure and injury risk. Natural-human cultures that still practice persistence hunting wear traditional footwear that adapts to the foot, offering only puncture wound and thermal protection [66]. Such cultures are characterised by wide, flat and flexible feet, even plantar-pressure distributions, and running styles with higher stride frequency and lower propensity to heel strike, particularly at higher speeds and on harder surfaces. By contrast, western populations that grow up and run in conventional, tapered, toe-sprung, stiff and cushioned footwear, have narrower feet, higher incidence of great-toe deformity that worsens with years of shoe wear, uneven distribution of plantar pressure, and running styles characterised by lower stride frequency and high propensity to heel strike regardless of speed or running surface. There are few data on injury rates in natural-running populations. However, based on the mismatch hypothesis and the evidence reviewed here in relation to foot development, structure, function and the effects of conventional footwear on these, we propose that the high-injury rates in western runners could be (in part) related to acute and chronic loss of biologically-normal form and function of the feet, due to habitual use of conventionally-shaped-cushioned footwear. This suggestion could add to the list of factors currently thought to explain injury risk in runners, but requires further study.

Summary, Implications and Recommendations

Evidence suggests that a biologically-normal human foot is well adapted to deal with the loads and dynamic-instability challenges of endurance running. However, it is susceptible to puncture and thermal injury from the range of environments that humans inhabit. This provides the rationale for footwear. The design features of conventional footwear can compromise the structure and function of a biologically-normal foot. Chronic use of conventional footwear and the associated maladaptation could be irreversible, or take years to undo. This could explain the findings of studies reporting negative effects for acute minimal-shoe interventions in habitual-conventional-shoe wearing runners [67,68] that possibly began these studies with compromised foot structure and function.

To promote and maintain biologically-normal foot function, footwear should be anatomically shaped, flat, flexible and of sufficient thickness to allow sensation

appropriate to the terrain, while protecting the plantar surface of the foot. These features facilitate biologically-normal alignment of the great toe, contact of the great toe with the ground, spreading and flattening of the loaded foot, free flexion of the toes, and appropriate sensory feedback. Where necessary, shoes with these features should be worn from childhood. However, there is a caveat to these recommendations. In maladapted adults, switching from conventional shoes to shoes with these features should be made with caution. Exposing a compromised foot to the demands of endurance running without the support on which it has come to depend is a mismatch that is likely to lead to problems. Gradually exposing compromised feet to the lower demands of standing and walking in anatomically-shaped, flat and flexible shoes is probably a sensible starting point to regain biologically-normal structure and function. Future research should explore these suggestions.

References

- Bramble DM, Lieberman DE (2004) Endurance running and the evolution of Homo. *Nature* 432: 345-352.
- Lieberman DE, Raichlen DA, Pontzer H, Bramble DM, Cutright-Smith E (2006) The human gluteus maximus and its role in running. *J Exp Biol* 209: 2143-2155.
- Rolian C, Lieberman DE, Hamill J, Scott JW, Werbel W (2009) Walking, running and the evolution of short toes in humans. *J Exp Biol* 212: 713-721.
- Taunton J, Ryan M, Clement D, McKenzie D, Lloyd-Smith D, et al. (2003) A prospective study of running injuries: the Vancouver Sun Run "In Training" clinics. *Br J Sports Med* 37: 239-244.
- van Gent RN, Siem D, van Middlekoop M, van Os AG, Bierma-Zeinstra SMA, et al. (2007) Incidence and determinants of lower extremity running injuries in long distance runners: a systematic review. *Br J Sports Med* 41: 469-480.
- Daoud AI, Geissler GJ, Wang F, Saretsky J, Daoud YA, et al. (2012) Foot strike and injury rates in endurance runners: a retrospective study. *Med Sci Sports Exerc* 44: 1325-1334.
- Wilkinson M, Saxby L (2016) Form determines function: Forgotten application to the human foot? *Foot and Ankle Online Journal* 9: 5-8.
- Stearne SM, McDonald KA, Alderson JA, North I, Oxnard CE, et al. (2016) The Foot's Arch and the Energetics of Human Locomotion. *Sci Rep* 6: 19403.
- Lieberman DE (2012) Human evolution: Those feet in ancient times. *Nature* 483: 550-551.
- Lieberman DE (2016) The Story of the Human Body: Evolution, Health and Disease. *Fam Med* 48: 822-823.
- Munteanu SE, Menz HB, Wark JD, Christie JJ, Scurrah KJ, et al. (2017) Hallux Valgus, By Nature or Nurture? A Twin Study. *Arthritis Care Res (Hoboken)* 69: 1421-1428.
- Shine Ib (1965) Incidence of Hallux Valgus In A Partially Shoe-Wearing Community. *Br Med J* 1: 1648-1650.
- Lieberman DE (2015) Is exercise really medicine? An evolutionary perspective. *Curr Sports Med Rep* 14: 313-319.
- mann R, Inman Vt (1964) Phasic Activity of Intrinsic Muscles of The Foot. *J Bone Joint Surg Am* 46: 469-481.
- Reeser LA, Susman RL, Stern JT Jr (1983) Electromyographic studies of the human foot: experimental approaches to hominid evolution. *Foot Ankle* 3: 391-407.
- Hoffman P (1905) Conclusions drawn for a comparative study of the feet of barefooted and shoe-wearing peoples. *The Journal of Bone and Joint Surgery* 3: 105-136.
- Morioka M, Miura T, Kimura K (1974) Morphological and functional changes of feet and toes of Japanese forestry workers. *J Hum Ergol (Tokyo)* 3: 87-94.
- D'Aout K, Pataky TC, De Clercq D, Aerts P (2009) The effects of habitual footwear use: foot shape and function in native barefoot walkers. *Footwear Science* 1: 81-94.
- Shu Y, Mei Q, Fernandez J, Li Z, Feng N, et al. (2015) Foot Morphological Difference between Habitually Shod and Unshod Runners. *PLoS One* 10: e0131385.
- Mei Q, Fernandez J, Fu W, Feng N, Gu Y (2015) A comparative biomechanical analysis of habitually unshod and shod runners based on foot morphological difference. *Human Mov Sci* 42: 38-53.
- Morton DJ (1935) *The Human Foot: its evolution, physiology and functional disorders*. New York: Columbia University Press.
- Chou SW, Cheng HY, Chen JH, Ju YY, Lin YC, et al. (2009) The role of the great toe in balance performance. *J Orthop Res* 27: 549-554.
- Edwards WB, Taylor D, Rudolph TJ, Gillette JC, Derrick TR (2010) Effects of running speed on a probabilistic stress fracture model. *Clin Biomech* 25: 372-377.
- Lieberman DE (2012) What we can learn about running from barefoot running: an evolutionary medical perspective. *Exerc Sport Sci Rev* 40: 63-72.
- Lopes AD, Hespanhol Júnior LC, Yeung SS, Costa LO (2012) What are the main running-related musculoskeletal injuries? A Systematic Review. *Sports Med* 42: 891-905.
- Yavuz M, Hetherington VJ, Botek G, Hirschman GB, Bardsley L, et al. (2009) Forefoot plantar shear stress distribution in hallux valgus patients. *Gait Posture* 30: 257-259.
- Hoogvliet P, van Duyl WA, de Bakker JV, Mulder PG, Stam HJ (1997) Variations in foot breadth: effect on aspects of postural control during one-leg stance. *Arch Phys Med Rehabil* 78: 284-289.
- Plank M (1995) The pattern of forefoot pressure distribution in hallux valgus. *The Foot* 5: 8-14.
- Gesslbauer B, Hruba LA, Roche AD, Farina D, Blumer R, et al. (2017) Axonal components of nerves innervating the human arm. *Ann Neurol* 82: 396-408.
- O'Uchi T, Hisatome H, Ri K, Maki S (1998) Wallerian degeneration of pontocerebellar tracts after pontine hemorrhage. *International Journal of Neuroradiology* 4: 171-177.
- Hashimoto T, Ueno K, Ogawa A, Asamizuya T, Suzuki C, et al. (2013) Hand before foot? Cortical somatotopy suggests manual dexterity is primitive and evolved independently of bipedalism. *Philos Trans R Soc Lond B Biol Sci* 368: 20120417.
- Aiello L, Dean C, Cameron J (1990) *An Introduction to Human Evolutionary Anatomy*. Elsevier Science.
- Willems TM, Witvrouw E, Delbaere K, Mahieu N, De Bourdeaudhuij I, et al. (2005) Intrinsic risk factors for inversion ankle sprains in male subjects: a prospective study. *Am J Sports Med* 33: 415-423.
- Hrysomallis C (2007) Relationship between balance ability, training and sports injury risk. *Sports Med* 37: 547-556.

35. Kelly LA, Cresswell AG, Racinais S, Whiteley R, Lichtwark G (2014) Intrinsic foot muscles have the capacity to control deformation of the longitudinal arch. *Journal of The Royal Society Interface* 11: 20131188.
36. Ker RF, Bennett MB, Bibby SR, Kester RC, Alexander RM (1987) The spring in the arch of the human foot. *Nature* 325: 147-149.
37. Rodgers MM (1988) Dynamic biomechanics of the normal foot and ankle during walking and running. *Phys Ther* 68: 1822-1830.
38. Lai A, Schache AG, Lin YC, Pandy MG (2014) Tendon elastic strain energy in the human ankle plantar-flexors and its role with increased running speed. *J Exp Biol* 217: 3159-3168.
39. Kavounoudias A, Roll R, Roll JP (1998) The plantar sole is a 'dynamometric map' for human balance control. *Neuroreport* 9: 3247-3252.
40. Patel M, Fransson P-A, Johansson R, Magnusson M (2011) Foam posturography: standing on foam is not equivalent to standing with decreased rapidly adapting mechanoreceptive sensation. *Exp Brain Res* 208: 519-527.
41. Derrick TR (2004) The effects of knee contact angle on impact forces and accelerations. *Med Sci Sports Exerc* 36: 832-837.
42. Gruber AH, Silvernail JF, Brueggemann P, Rohr E, Hamill J (2012) Footfall patterns during barefoot running on harder and softer surfaces. *Footwear Science* 5: 39-44.
43. Wilkinson M, Ewen A, Caplan N, O'Leary D, Smith N, et al. (2018) Textured insoles reduce vertical loading rate and increase subjective plantar sensation in overground running. *Eur J Sport Sci* 12: 1-7.
44. Lieberman DE, Castillo ER, Otarola-Castillo E, Sang MK, Sigei TK, et al. (2015) Variation in foot strike patterns among habitually barefoot and shod runners in Kenya. *PLoS One* 10: e0131354.
45. Hatala KG, Dingwall HL, Wunderlich RE, Richmond BG (2013) Variation in foot strike patterns during running among habitually barefoot populations. *PLoS One* 8: e52548.
46. Pinhasi R, Gasparian B, Areshian G, Zardaryan D, Smith A, et al. (2010) First direct evidence of chalcolithic footwear from the near eastern highlands. *PLoS One* 5: e10984.
47. Kadambande S, Khurana A, Debnath U, Bansal M, Hariharan K (2006) Comparative anthropometric analysis of shod and unshod feet. *The Foot* 16: 188-191.
48. Hsu AR (2012) Topical review: barefoot running. *Foot Ankle Int* 33: 787-794.
49. Miller EE, Whitcome KK, Lieberman DE, Norton HL, Dyer RE (2014) The effect of minimal shoes on arch structure and intrinsic foot muscle strength. *Journal of Sport and Health Science* 3: 74-85.
50. Walther M, Herold D, Sinderhauf A, Morrison R (2008) Children sport shoes--a systematic review of current literature. *Foot Ankle Surg* 14: 180-189.
51. Rao UB, Joseph B (1992) The influence of footwear on the prevalence of flat foot. A survey of 2300 children. *J Bone Joint Surg Br* 74: 525-527.
52. Stewart SF (1972) Footgear--its history, uses and abuses. *Clin Orthop Relat Res* 88: 119-130.
53. Knowles FW (1953) Effects of shoes on foot form: an anatomical experiment. *Med J Aust* 1: 579-581.
54. Wegener C, Hunt AE, Vanwanseele B, Burns J, Smith RM (2011) Effects of children's shoes on gait: a systematic review and meta analysis. *J Foot Ankle Res* 4: 1-13.
55. Hollander K, Riebe D, Campe S, Braumann KM, Zech A (2014) Effects of footwear on treadmill running biomechanics in preadolescent children. *Gait Posture* 40: 381-385.
56. Richards CE, Magin PJ, Callister R (2009) Is your prescription of distance running shoes evidence-based? *Br J Sports Med* 43: 159-162.
57. Kerrigan DC, Franz JR, Keenan GS, Dicharry J, Della Croce U, et al. (2009) The effect of running shoes on lower extremity joint torques. *PM R* 1: 1058-1063.
58. Robbins S, Waked E, Gouw GJ, McClaran J (1994) Athletic footwear affects balance in men. *Br J Sports Med* 28: 117-122.
59. Lieberman DE, Venkadesan M, Werbel WA, Daoud AI, D'Andrea S, et al. (2010) Foot strike patterns and collision forces in habitually barefoot versus shod runners. *Nature* 463: 531-535.
60. Rose W, Bowser B, McGrath R, Salerno J, Wallace J, et al. (2011) Effect of footwear on balance. *American Society of Biomechanics Annual Meeting*. Long Beach.
61. Sparrow WA (2000) *Energetics of Human Activity*. Human Kinetics.
62. Alexander RM (1989) Optimization and gaits in the locomotion of vertebrates. *Physiol Rev* 69: 1199-1227.
63. Kram R, Taylor CR (1990) Energetics of running: a new perspective. *Nature* 346: 265-267.
64. Lieberman DE, Warrener AG, Wang J, Castillo ER (2015) Effects of stride frequency and foot position at landing on braking force, hip torque, impact peak force and the metabolic cost of running in humans. *J Exp Biol* 218: 3406-3414.
65. Robbins SE, Gouw GJ (1991) Athletic footwear: unsafe due to perceptual illusions. *Med Sci Sports Exerc* 23: 217-224.
66. Wallace IJ, Koch E, Holowka NB, Lieberman DE (2018) Heel impact forces during barefoot versus minimally shod walking among Tarahumara subsistence farmers and urban Americans. *R Soc Open Sci* 5: 180044.
67. Bergstra SA, Kluitenberg B, Dekker R, Bredeweg SW, Postema K, et al. (2015) Running with a minimalist shoe increases plantar pressure in the forefoot region of healthy female runners. *J Sci Med Sport* 18: 463-468.
68. Ridge ST, Johnson AW, Mitchell UH, Hunter I, Robinson E, et al. (2013) Foot bone marrow edema after a 10-wk transition to minimalist running shoes. *Med Sci Sports Exerc* 45: 1363-1368.