



THE MULTI-FUNCTIONAL FOOT IN ATHLETIC MOVEMENT: EXTRAORDINARY FEATS BY OUR EXTRAORDINARY FEET

doi: 10.1515/humo-2016-0001

JENNIFER WILSON^{1*}, JOHN KIELY²

¹ University of Derby, College of Life & Natural Sciences: Sport, Outdoor & Exercise Science, Derby, United Kingdom

² University of Central Lancashire, Institute of Coaching & Performance, School of Sport, Tourism and the Outdoors, Preston, Lancashire, United Kingdom

ABSTRACT

The unique architecture of the foot system provides a sensitive, multi-tensional method of communicating with the surrounding environment. Within the premise of the paper, we discuss three themes: complexity, degeneracy and bio-tensegrity. Complex structures within the foot allow the human movement system to negotiate strategies for dynamic movement during athletic endeavours. We discuss such complex structures with particular attention to properties of a bio-tensegrity system. Degeneracy within the foot structure offers a distinctive solution to the problems posed by differing terrains and uneven surfaces allowing lower extremity structures to overcome perturbation as and when it occurs. This extraordinary structure offers a significant contribution to bipedalism through presenting a robust base of support and as such, should be given more consideration when designing athletic development programmes.

Key words: foot, degeneracy, bio-tensegrity, robustness

The overlooked role of the foot in dynamic sporting activities

Conventionally, when devising conditioning strategies to enhance ambulant, bipedal athletic movements – run, jump, pivot, turn, change direction – much training attention is dedicated to strengthening the large power-generating muscles of the hips and upper legs. Substantial research exists evidencing the positive contributions of various strength and conditioning strategies to athletic performance: to the extent that few would argue against the conventional perspective that, within reason, stronger muscles enhance movement capacity.

Within this conventional ‘muscle powers movement’ model there is, we suggest, an apparent omission. Specifically, observable power production, in dynamic locomotive activities, typically exceeds muscular force-generation capabilities. As an example, during the step phase of a triple-jump, impacts of up to 15 times bodyweight and above are commonly absorbed, controlled and the propulsive forces necessary to power the next jump phase are generated, within the abbreviated time-frame afforded by a short ground contact typically lasting less than one-fifth of a second [1]. Similarly, during running, impacts of multiple times bodyweight are comfortably accommodated, by runners of all abilities, for little discernible effort. In elite sprinters very forceful ground contacts must be managed in windows of as little as 80 ms⁻¹ [2]. In non-elite marathon runners, im-

pacts, while less forceful than those of the sprinter, nevertheless typically number beyond 21 thousand contacts, again of multiple times bodyweight per leg [3].

Furthermore, during the dynamic accelerating, decelerating, twisting and turning athletic movement permutations common across a broad range of sporting activities, the loadings imposed on joints and other structures appear similarly excessive: exposing tissues to high shock loads, in apparently unstable, ever-varying movement conditions. Despite the severe challenges imposed by such dynamically-shifting movement demands, we are capable of robustly and agilely executing a broad diversity of complex bipedal movements, under constantly shifting conditions.

A further interesting, if obvious, observation is that although many muscle groups must be skilfully activated to manage, buffer and generate propulsive powers, their net contribution to whole-body momentum can only be expressed through interaction with the ground. A feature of bipedal movement is that the large forces generated through the dynamic re-positioning of the limbs during flight must be transferred between body and ground via the relatively small surface area provided by the foot. The foot serves as our only interface with the ground during walking and running, but also in the endless variety of dynamic movement permutations encountered in athletic sporting activities. Hence the foot is exposed to high shock impacts and decelerations, while simultaneously and/or consecutively functioning as a brake, a spring, a buffer, a means of steering, and a stiff conduit for force transfer between the dynamically moving body, and the immovable environment. Yet despite this primacy, little consideration is typically afforded

* Corresponding author.

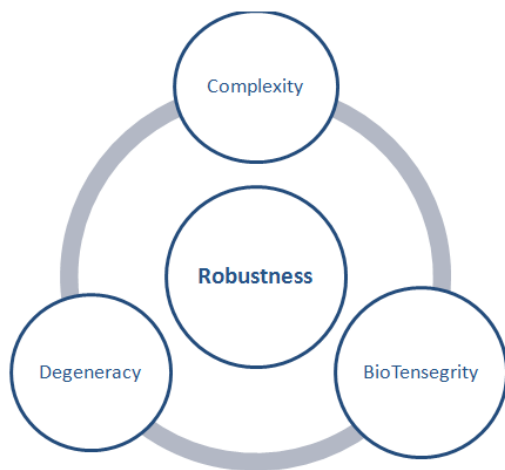


Figure 1. A depiction of the three evolutionary innovations that contribute to 'robustness' within the foot structure

to foot conditioning within our conventional training theory or practices.

Over the course of our evolutionary history, the architecture of the foot has been progressively shaped by ever-present evolutionary imperatives, constantly striving to increase movement proficiency, for minimum uptake of energetic and neural resources, while simultaneously reducing exposure to negative sensory feedback indicative of the mounting risk of 'damage' [4–8]. The aim of this piece is to highlight three evolutionary innovations which, in combination, underpin the remarkable robustness of the human foot during dynamic impact activities (see Figure 1).

Extraordinary feats by our extraordinary feet

Neurobiological complexity of the human foot

As the only habitually upright bipedal primate, human foot architecture differs substantially from that of our nearest relatives. With three strong arches; over 100 muscles; 26 separate skeletal elements (exempting the sesamoids) linked through 33 joints, fastened by 3 layers of ligaments; dextrously manipulated by numerous intrinsic and extrinsic muscle-tendon units, the human foot constitutes a uniquely complex bio-composite anatomical module [9–11]. This design complexity is not only structural but also sensory. During locomotion the various tissues and structures of the foot are subjected to considerable deformations, in three dimensions. Sensory information, arising from local foot deformations, emanates from multiple somatosensory receptors in the foot arch ligaments, joint capsules, intrinsic foot muscles, and cutaneous mechanoreceptors on the plantar soles: such that deformations instantaneously affect afferent outflow [9, 12–14,]. This neurobiological design complexity is matched by a similarly expansive functional complexity, as the foot adapts to the expansive diver-

sity of tasks imposed by the physics of landing on unpredictable surfaces.

In the past, this seemingly needless complex design was frequently considered an unfortunate legacy from our evolutionary past. Yet, despite the intricate nature of its multi-tissue, multiple sensory organ, bio-composite structure, the foot remains highly functional and adaptable. It is remarkably robust, across an unusually diverse range of dynamic movement activities: walking, running, climbing, turning, pivoting, hopping, bounding. Furthermore, not only does the foot adapt to changing movement demands, it also is capable of fulfilling multiple roles, frequently simultaneously, in multiple movement contexts. For example, even under the abbreviated ground contacts afforded during run/jump activities, the foot functions as a flexible structure in early stance, buffering, braking, and stabilizing, yet milliseconds later is a rigid structure, stiffly channelling propulsive forces; directing momentums and contributing to push-off efficiency [14].

Certainly, the foot is not simply a passive, rigid base of support but a flexibly adapting, exquisitely adaptive functional unit: enabling precise control of multiple functions. And, far from being a potentially problematic evolutionary hangover, the complexity of the human foot endows us with a rich repository of robustness and efficiency-enabling movement innovations.

Degeneracy: the adaptive agility of the 'nearly decomposable' human foot

The early complexity theorist Herbert Simon suggested biological organisms could be meaningfully approximated as 'nearly decomposable' complex systems. A purely mechanical system is, in contrast, fully decomposable, in that each component fulfils a tightly designated role within a given context [15]. Within a 'nearly decomposable' biological system there is obvious cross-over, overlap and integrated interplay between the functionality of different tissues and structures in different contexts. Yet, the entire organism is not haphazardly complex and instead exhibiting a modular design: whereby each module is composed of collections of elements more densely networked to each other than to elements within other modules.

Modularity is a crucial organizing principle, pervasive throughout biology, greatly simplifying what would otherwise be overwhelmingly disordered complexity. Although all modules are inter-connected, they are simultaneously partially-insulated and functionally semi-autonomous. Hence modularity facilitates robustness as modules can evolve, reshape, rewire and repair in tandem, or independently, without necessarily jeopardizing the survivability of the entire organism [16–18].

This 'nearly decomposable' architecture enables complex neurobiological systems to reap the benefits of structural specialization while simultaneously retaining

the adaptive agility essential to coping with demands imposed by a chaotic, ever-changing environment. Such design characteristics underpin an essential prerequisite of biological robustness: degeneracy [19].

Degeneracy is the capacity, of alliances of modules, to collectively modify behaviours and re-combine outputs in differing permutations to collaboratively realize equivalent outcomes through a diversity of pathways [20–24]. In biological terms, degeneracy is similar to, but differs from, the classical concept of redundancy, in that it enables collaborating communities of fundamentally different components to produce consistently reliable outputs under diversely fluctuating conditions [19, 21].

The bio-composite design of the human foot provides a prime example of a highly-degenerate biological architecture. The complex ‘nearly decomposable’ architecture of the foot enables instantaneous structural re-configuration to dynamically changing contexts. Most obviously in circumstances imposed by environmental variations, such as encountered during running over broken terrains but also during the various permutations of accelerations, decelerations, pivots, turns and changes of direction implicit in dynamic sporting activities. Thus the ‘nearly decomposable’ architecture of the foot facilitates immediate and flexible adaptation to changing context.

A further feature of this highly degenerate configuration is that seemingly identical movement cycles, resulting in equivalent movement outcomes, can be achieved through a multiplicity of subtly varying pathways. Thereby enabling the mechanical stresses imposed by repetitive impacts, such as that encountered during a marathon, to be dispersed amongst a broad network of collaborating structural and material components. Hence degeneracy facilitates robustness.

Degeneracy within the foot ensures that subtle modifications, in multiple permutations of positioning and/or pre-tensioning of foot structures, channels mechanical stress through ever-varying routes, thus spreading the work burden imposed by impact and diminishing the probability of repetitive strain, and subsequent tissue damage. The impact of which plays a significant role in ambulant athletic performance.

Resisting deformation and channelling momentums: the bio-tensegrity solution

The foot is commonly subjected to both frequent, and large, impacts during athletic movements. The degenerate design of the foot substantially contributes to its structural robustness in the face of repetitive shock loadings, yet does not operate in isolation, and is irreparably entwined with another evolutionary design innovation.

The architect Buckminster Fuller originally defined tensegrity systems as structures that stabilize shape

through continuous tension rather than by continuous compression such as employed, for example, in the construction of a stone arch [25]. In contrast, tensegrity systems innately self-stabilize and resist structural distortion purely by balancing tension-imposing and compression-resisting structural components within a self-stabilizing web of tensioning and stiffening forces [26].

The strikingly energy-efficient, perturbation-repelling simplicity of tensegrity designs has, recently, been recognised as a pervasive evolutionary innovation evident across biological scales, from the cellular to the whole-body level [26, 27].

The bio-tensegrity model depicts the skeletal system as a non-random arrangement of compression elements knitted into the tensional fabric of the fascia [28]. Fascia provides a constant inherent tension maintaining a background tautness that allows the system to respond and adapt to external force without losing the structural integrity of the organism whilst simultaneously serving as a mechano-sensitive signalling system, receptive to pressure changes [29].

The running bio-tensegrity system is composed of a hierarchy of nested subsystems. During dynamic activities, the athletes body acts as a tensegrity system; as does each leg, each muscle-tendon unit (MTU), each muscle, each muscular sub-compartment, each motor unit, each muscle fiber, each myofibril and so on [30–31]. In essence, serving as a sequence of nested tensegrity structures extending down to the level of the individual cell, and beyond. Each nested structure lies within greater, and is comprised of lesser, bio-tensegrity architectures; each evolutionarily designed, structurally and materially, to advantageously respond to the loadings and deformations most relevant to our species survival. Each sub-system innately responds to deformation by striving to rebound to a state of homeostatic mechanical equilibrium: linking from the micro-level of the cell, through the various tissue collectives, to the macro-level of the entire organism [26, 28, 32–35].

The foot, as the structure exposed to the highest impact deceleration, is an exquisitely evolved bio-tensegrity structure. The foot is itself formed by a number of bio-tensegrity systems encased within the foot architecture, and in turn serves as a sub-system of the integrated systemic whole. The foot is often described as being made up of floating compression elements (such as the skeletal structures of the midfoot [36]) supported by a tensional fabric (the plantar aponeurosis being the most cited [37]). Although it is typically considered as having two functional aims – to support body weight and to act as a lever during propulsive phases of locomotion [9] –, thanks to its complex multi-tissue design the foot system is capable of fulfilling a wide diversity of functions: variously absorbing, decelerating, transferring, steering and recycling movement powers.

As with any bio-tensegrity system, effective dispersal of forces alleviates risks of exceeding critical tissue loading

limits. To move efficiently these forces must be channelled and re-deployed to optimally contribute to stabilisation and propulsive power demands. Within the hierarchy of tensional systems, compression of local structures creates a ‘non-linear wave’ through the tensional fabric of the global construct resulting in a modification to internal forces through a ‘preflexive’ response [27]. Driven by evolutionary imperatives and repeat practice, we progressively become more skilled at exploiting these built-in mechanical efficiencies. We gradually become more proficient at poising ‘tensioned’ or prestressed tensegrity structures to more productively capitalise on ‘cheap’ sources of control and propulsion merely by matching the physics of the situation to innate deformation-repelling features of our integrated bio-tensegrity design [38].

Furthermore, simply by leveraging properties of the mechanical system, the coordinated harnessing of our nested bio-tensegrity design remedies the inherent information-processing and perturbation-prediction deficits implicit in top-down control [39]. This provides an instantaneous non-neurological, yet skilled, response to sudden perturbation: automatically buffering, re-directing and re-cycling momentums and stabilizing movement, for little energetic or neurological investment.

Locally, the foot must respond instantaneously, with zero delay, to variations in contact conditions [38]. When moving at speed, where conditions underfoot are predictable, the variable component may assume a stiffly set posture (i.e. high efficiency but high impact). Under more uncertain conditions, the foot will be less stiffly pre-set, allowing for more flexible absorption of contact to overcome external perturbations.

The robust human foot: a collaboration of evolutionary innovations

During dynamic loading activities the complex, ‘nearly decomposable’ structure of the human foot provides a robust means of absorbing, distributing, channelling and re-directing the shock loads imposed by violent collision with the external environment. Upon impact the foot deforms as tissue structures variously collapse, compress and stretch under the integrated influence of gravity and ground reaction forces. These deforming forces provide both a challenge and an opportunity.

Degeneracy exploits the multi-functionality bestowed by our nested bio-tensegrity architecture, enabling us to solve inevitably unique movement problems through ever-varying movement solutions. Hence, movement variability is an outcome of degeneracy, accounting for the flexible and adaptive behaviours seen in a bio-tensegrity structure.

As with any system demonstrating degeneracy, exploitation of variable configurations and behaviours promotes mechanical efficiency as the system strives for the most economical outcome. By offering more movement options, a degenerate system is able to facilitate stress management through variable permutations. At the level of the foot, the seamless integration of tensional properties regulates the poising and pre-activation of hierarchical structures so as to optimally contribute to the stabilization and energetic requirements of movement. In locomotive activities, particularly those that incur repetitive impacts, the foot serves multiple functional roles. A multi-functionality built among a platform of structural complexity. The generous movement degeneracy, afforded by the human foot, is underpinned by this structural complexity. Together this blend of bio-tensegrity and degeneracy enable the human foot to adjust, deform, dampen, absorb and productively harness the deformations imposed by ground contact (see Figure 2).

Theoretical implications

Conventional performance training models are built upon a theoretical assumption that improving strength – specifically of the large lower limb muscles – inevitably enhances bipedal movement proficiency. Our purpose is not to dispute this presumption but to highlight its fundamental limitations as an overarching conceptual framework: specifically in relation to the role of the foot in dynamic bipedal movements.

In activities that require the athlete to run, jump, land, accelerate, brake and pivot, the foot must instantaneously respond, to inevitably idiosyncratic permutations of internal and external constraints, in a manner resolving the twin demands of robustness and efficiency. The capacity of the foot to simultaneously fulfil multiple demands is enabled by its design complexity. A complexity underpinning the foot’s highly degenerate capacity to

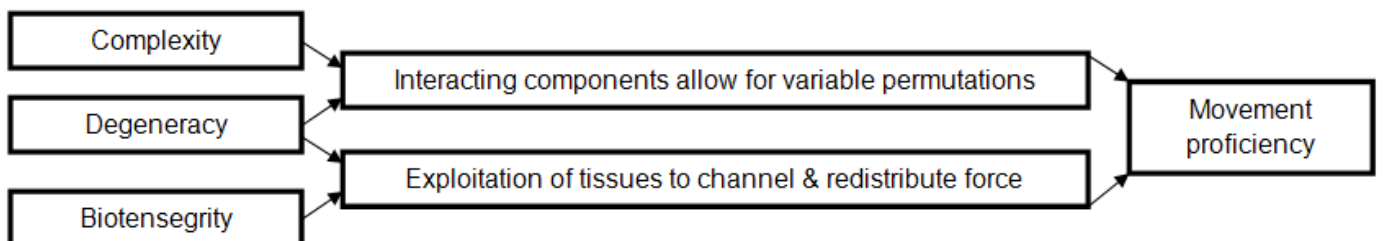


Figure 2. Collaboration between three evolutionary innovations

accomplish similar outcomes through a multiplicity of ever-varying movement permutations. A complexity which, thanks to its nested bio-tensegrity design, innately responds to imposed perturbation by first absorbing, and subsequently repelling, structural and material deformations: thus contributing to self-stabilization and momentum re-cycling.

This extraordinary structure plays a fundamental role in damping, dissipating and dispersing shock impacts; in channelling and directing momentums; in seamlessly adapting to movement errors or changing surface conditions; in contributing to energy re-cycling through deformation and restitution. Yet despite the criticality of foot function in bipedal athletic activities, our foot conditioning philosophies remain poorly evolved and the potential importance of developing strategies to optimise foot functionality remain commonly overlooked. As our appreciation of the architectural and functional complexity of the foot continues to grow, so too does an awareness that perhaps conventional foot conditioning and therapy strategies need to evolve in tandem? Certainly, given the importance of optimised foot function to athletic bipedal movement, it seems remiss not to reflect on how we conventionally consider, or fail to consider, how we might design conditioning and therapeutic interventions to specifically target the on-going health of these extraordinary structures.

References

- Perttunen J.O., Kyröläinen H., Komi P.V., Heinonen A., Biomechanical loading in the triple jump. *J Sports Sci*, 2000, 18 (5), 363–370, doi: 10.1080/026404100402421.
- Richmond J., In search of the 70 kph human: challenging the limits of human muscle contraction time – a pilot investigation. *Hypothesis*, 2011, 9 (1), e3. Available from: <http://www.hypothesisjournal.com/?p=980>.
- Perl D.P., Daoud A.I., Lieberman D.E., Effects of footwear and strike type on running economy. *Med Sci Sports Exerc*, 2012, 44(7), 1335–1343, doi: 10.1249/MSS.0b013e318247989e.
- Kitano H., Biological robustness. *Nat Rev Genet*, 2004, 5 (11), 826–837, doi: 10.1038/nrg1471.
- Todorov E., Optimality principles in sensorimotor control. *Nat Neurosci*, 2004, 7 (9), 907–915, doi: 10.1038/nn1309.
- Niven J.E., Laughlin S.B., Energy limitation as a selective pressure on the evolution of sensory systems. *J Exp Biol*, 2008, 211 (11), 1792–1804, doi: 10.1242/jeb.017574.
- Miller R.H., Umberger B.R., Hamill J., Caldwell G.E., Evaluation of the minimum energy hypothesis and other potential optimality criteria for human running. *Proc Biol Sci*, 2012, 279 (1733), 1498–1505, doi: 10.1098/rspb.2011.2015.
- Raichlen D.A., Polk J.D., Linking brains and brawn: exercise and the evolution of human neurobiology. *Proc Biol Sci*, 2013, 280 (1750), 20122250, doi: 10.1098/rspb.2012.2250.
- Wright W.G., Ivanenko Y.P., Gurfinkel V.S., Foot anatomy specialization for postural sensation and control. *J Neurophysiol*, 2011, 107 (5), 1513–1521, doi: 10.1152/jn.00256.2011.
- Hillstrom H.J., Song J., Kraszewski A.P., Hafer J.F., Mootanah R., Dufour A.B. et al., Foot type biomechanics part 1: structure and function of the asymptomatic foot. *Gait Posture*, 2013, 37 (3), 445–451, doi: 10.1016/j.gaitpost.2012.09.007.
- McKeon P.O., Hertel J., Bramble D., Davis I., The foot core system: a new paradigm for understanding intrinsic foot muscle function. *Br J Sports Med*, 2015, 49 (5), 290, doi: 10.1136/bjsports-2013-092690.
- Saltzman C.L., Nawoczenski D.A., Complexities of foot architecture as a base of support. *J Orthop Sports Phys Ther*, 1995, 21 (6), 354–360, doi: 10.2519/jospt.1995.21.6.354.
- Nurse M.A., Nigg B.M., The effect of changes in foot sensation on plantar pressure and muscle activity. *Clin Biomech (Bristol, Avon)*, 2001, 16 (9), 719–727, doi: 10.1016/S0268-0033(01)00090-0.
- Kennedy P.M., Inglis J.T., Distribution and behaviour of glabrous cutaneous receptors in the human foot sole. *J Physiol*, 2002, 538 (3), 995–1002, doi: 10.1013/jphysiol.2001.013087.
- Simon H., The architecture of complexity. *Proc Am Philos Soc*, 1962, 106 (6), 467–482, Available from: <http://www2.econ.iastate.edu/tesfatsi/ArchitectureOfComplexity.HSimon1962.pdf>.
- Meunier D., Lambiotte R., Bullmore E.T., Modular and hierarchically modular organization of brain networks. *Front Neurosci*, 2010, 4, 200, doi: 10.3389/fnins.2010.00200.
- Bassett D.S., Gazzaniga M.S., Understanding complexity in the human brain. *Trends Cogn Sci*, 2011, 15 (5), 200–209, doi: 10.1016/j.tics.2011.03.006.
- Clune J., Mouret J.B., Lipson H., The evolutionary origins of modularity. *Proc Biol Sci*, 2013, 280 (1755), 20122863, doi: 10.1098/rspb.2012.2863.
- Whitacre J.M., Degeneracy: A link between evolvability, robustness and complexity in biological systems. *Theor Biol Med Model*, 2010, doi: 10.1186/1742-4682-7-6.
- Tononi G., Sporns O., Edelman G.M., Measures of degeneracy and redundancy in biological networks. *Proc Natl Acad Sci USA*, 1999, 96 (6), 3257–3262, doi: 10.1073/pnas.96.6.3257.
- Edelman G.M., Gally J.A., Degeneracy and complexity in biological systems. *Proc Natl Acad Sci USA*, 2001, 98 (24), 13763–13768, doi: 10.1073/pnas.231499798.
- Whitacre J., Bender A., Degeneracy: a design principle for achieving robustness and evolvability. *J Theor Biol*, 2010, 263 (1), 143–153, doi: 10.1016/j.jtbi.2009.11.008.
- Mason P.H., Degeneracy: demystifying and destigmatizing a core concept in systems biology. *Complexity*, 2015, 20 (3) 12–21, doi: 10.1002/cplx.21534.
- Komar J., Chow J.Y., Chollet D., Seifert L., Neurobiological degeneracy: supporting stability, flexibility and pluripotentiality in complex motor skill. *Acta Psychol (Amst)*, 2015, 154, 26–35, doi: 10.1016/j.actpsy.2014.11.002.
- Fuller B., Tensegrity. *Portfolio Art News Ann*, 1961, 4, 112–127.
- Ingber D.E., Tensegrity I., Cell structure and hierarchical systems biology. *J Cell Sci*, 2003, 116 (7), 1157–1173, doi: 10.1242/jcs.00359.
- Levin S.M., Our internal universe. *J Mot Behav*, 2014, 46 (3), 195–196, doi: 10.1080/00222895.2014.880307.
- Levin S.M., Martin D.C., Biotensegrity: the mechanics of fascia. In: Schleich R., Findlay T.W., Chaitow L., Huijings P.A. (eds.), *Fascia: the tensional network of the hu-*

- man body. Churchill Livingstone, Elsevier, London 2012, 137–142.
29. van der Wal J.C., Proprioception. In: Schleip R., Findlay T.W., Chaitow L., Huijing P.A. (eds.), *Fascia: the tensional network of the human body*. Churchill Livingstone, Elsevier, London 2012, 81–87.
 30. Wickham J.B., Brown J.M., Muscles within muscles: the neuromotor control of intra-muscular segments. *Eur J Appl Physiol Occup Physiol*, 1998, 78 (3), 219–225, doi: 10.1007/s004210050410.
 31. Wilson A., Lichtwark G., The anatomical arrangement of muscle and tendon enhances limb versatility and locomotor performance. *Philos Trans R Soc Lond B Biol*, 2011, 366 (1570), 1540–1553, doi: 10.1098/rstb.2010.0361.
 32. Myers T., Anatomy trains and force transmission. In: Schleip R., Findlay T.W., Chaitow L., Huijing P.A. (eds.), *Fascia: the tensional network of the human body*. Churchill Livingstone, Elsevier, London 2012, 131–136.
 33. Swanson R.L., Biotensegrity: a unifying theory of biological architecture with applications to osteopathic practice, education and research – a review and analysis. *J Am Osteopath Assoc*, 2013, 113 (1), 34–52. Available from: <http://jaoa.org/article.aspx?articleid=2094459>.
 34. Turvey M.T., Fonseca S.T., The medium of haptic perception: a tensegrity hypothesis. *J Mot Behav*, 2014, 46 (3), 143–187, doi: 10.1080/00222895.2013.798252.
 35. Boehler Q., Vedrines M., Abdelaziz S., Poignet P., Renaud P., Influence of spring characteristics on the behaviour of tensegrity mechanisms. In: Lenarčič J., Khatib O. (eds.), *Advances in robot kinematics*, Springer International Publishing, Switzerland 2014, 161–169, doi: 10.1007/978-3-319-06698-1_18.
 36. Okita N., Meyers S.A., Challis J.H., Sharkey N.A., Mid-tarsal joint locking: new perspectives on an old paradigm. *J Orthop Res*, 2014, 32 (1), 110–115, doi: 10.1002/jor.22477.
 37. Kim W., Voloshin A.S., Role of plantar fascia in the load bearing capacity of the human foot. *J Biomech*, 1995, 28 (9), 1025–1033, doi: 10.1016/0021-9290(94)00163-X.
 38. Brown I.E., Loeb G.E., A reductionist approach to creating and using neuromusculoskeletal models. In: Winters J.M., Crago P.E. (eds.), *Biomechanics and neural control of posture and movement*. Springer-Verlag, New York 2000, 148–163.
 39. Biewener A.A., Daley M.A., Unsteady locomotion: integrating muscle function with whole body dynamics and neuromuscular control. *J Exp Biol*, 2007, 210 (17), 2949–2960, doi: 10.1242/jeb.005801.

Paper received by the Editor: January 18, 2016

Paper accepted for publication: March 30, 2016

Correspondence address

Jennifer Wilson
 University of Derby
 College of Life & Natural Sciences:
 Sport, Outdoor & Exercise Science
 Kedleston Road
 Derby, DE22 1GB
 e-mail: j.wilson1@derby.ac.uk