PREVENTION & REHABILITATION: EDITORIAL

Toe-tal recall – What on Earth are our toes actually for?

When viewed through an evolutionary or naturalistic lens, to walk, run and move barefoot is, of course, the default human condition. Any alteration of this is an alteration of not just millions of years of bipedal hominid function, but hundreds of millions of years of natural selection’s honing and refining of foot structure.

The 2 papers featured in this section are, first, The effects of dorso-lumbar motion restriction on the ground reaction force components during running, by Moreley & Traum, and, second, Effect of spinal stabilization exercise on dynamic postural control and visual dependency in subjects with chronic non-specific low back pain by Salvati et al. The relevance of foot and, in particular, toe function, to these two papers will become clear as the editorial unfolds.

After researching evolutionary and comparative anatomy, and applying concepts from it clinically, such as barefoot conditioning, for around a decade, when this author first saw the commercial footwear product "Vibram Fivefingers" shortly after its 2006 market release in the US, he was inspired to both purchase a pair and, after a few days of use, to write to Vibram to ask if they would like their product featured as a viable rehabilitation tool in a Rehabilitation chapter that was being written in Leon Chaitow’s Naturopathic Physical Medicine (Elsevier Churchill-Livingstone, 2008). Vibram, who had developed the shoe for sailing and perhaps walking had no idea their product could provide any potential benefit from a medical, rehabilitation or conditioning perspective; so they agreed to have them featured, but asked for some references for these benefits. The end result was an opportunity for this author to serve as distributor of Vibram Fivefingers to the UK market. As a consequence for obvious reasons — a question that has been repeatedly been encountered is what are the toes actually for? Are they a necessary part of our foot function or some kind of evolutionary remnant we no longer need? It is clear that they are not utilised much in most footwear or sportswear.

Most anthropologists or holistically-orientate biomechanists would tell you that the toes are, indeed, important in optimal foot function. However, some people disagree. The biologist Heinrich (2007) wrote “for all practical purposes, all of our toes could as well be fused or our large toes could be enlarged and the others deleted, if we were uncompromisingly designed to be pure sprinters”. On the other hand (or foot), humans are actually particularly poor sprinters whereas they feature among the elite when it comes to endurance running; a fit human outpacing even endurance specialists such as wolves, horses and deer in the long run (Bramble and Lieberman, 2004) — and especially in the heat. And when it comes to economy, the toes may well have an important role in foot function and should not be so easily disregarded.

For the majority of time since Western medicine has developed, the appendix was viewed as a vestigial organ of a bygone digestive system; an irritating remnant particularly prone to inflammation that may become fatal. Even during training in internal medicine in the 1990’s were the pathologists and medical doctors towing the party line that the appendix was anachronistic and useless. It is only in the last few years that the function of the appendix as a storage pocket for beneficial bacteria that gets closed off when the gut swells with infection, so that, after the convulsions of diarrhoea have finished and the inflammation subsides, the neck of the appendix will open and allow the original beneficial bacteria to flourish once more; re-colonising the colon (Parker, 2007). The true reason for its predisposition to life-threatening inflammatory bouts is actually much more a product of our sedentary, nutritionally “refined” lifestyle with diuretics as our primary social drinks (alcohols, coffees, teas and sodas), and the constipation that ensues. And so perhaps there is a parallel here with the toes? Perhaps they do serve an important biological function? Perhaps the problems we have with our toes are related to our sedentary and culturally defined lifestyles. After all, when something that is both sensitive and vulnerable is retained by evolution (for example, eyes, appendices, testicles, breasts and … toes) they usually have an important biological role; why risk so much for so little?
Hi fives & low toes

Anthropometrically, it may come as little surprise that to give the foot a "high-five" and actually slot a finger between each toe results in a straightening of toes so that the digit aligns optimally with its preceding ray. To encourage patients to hold their feet in this way while relaxing in the evening may help them to reverse some of the damage caused by years of wearing shoes that have turned their feet "shoe-shaped" from feet that were once "foot-shaped". It was the picture below, from 1998 edition of the Journal of Bodywork & Movement Therapies that inspired this author to write to a large sports shoe manufacturer at the turn of the century to suggest they produce a highly tactile shoe with individual toe pockets, so that the toes hold the toes in a more neutral alignment whilst the user walks, runs, squats or moves in general.

or through disease processes, start to buckle, will alter the stresses going through the joint creating compression on one side and traction on the other and compromising overall performance. These aberrant stresses alter muscle firing around the joint, information feedback to the nervous system (Wyke, 1979) and the piezoelectric profile of the tissues under stress.

Simple Newtonian physics dictate that the broader any structures' base of support relative to its superincumbent profile, the more stable it will be. And the narrower the base of support (a biped versus a quadruped base of support, for example), the more exponential an effect that even small differences will make. Balance is not the only consideration, but also power generation and traction. So, from a human performance perspective, a broader base of support should, indeed, enhance performance. Research in this area is inconclusive (see below under Balance on your toes).

Of course, to view the foot as a simple platform however, is to miss the point. Beyond its platform function, it is highly adapted to both absorb and to store kinetic energy as potential (elastic) energy; to adapt to contours in the substrate; to provide feedback to the CNS about the characteristics of substrate; and the interaction of the foot with that substrate.

One often overlooked aspect of limb design is that the muscle mass is always situated primarily at the proximal end (Radinski, 1989) as any mass at the distal end will increase energetic costs of the inertial loads of swinging a limb back and forth. Since all animals occupy an energetic niche, the less energy they expend, in return for whatever energy they accumulate, the better. It may be of little surprise then that most elite runners have calf muscles where the mass is "high" in the lower leg, that running shoes are generally made of very light materials, and that barefoot running is generally found to be more efficient than shod running, in spite of poor habituation to this state by most tested (Divert et al., 2008; Squadrone and Gallozzi, 2009; Perl et al., 2012). Hence, the foot itself, and the toes as the terminal portion of the foot, are not highly muscled, nor especially strong, but the arrangement of the...
musculature and fascia is such that it would appear to make the foot compact when required while retaining flexibility. Clearly the foot must transfer large forces effectively between the descending body and the ground, yet perhaps its primary role (and the role of the digits) is the provision of information.

The foot is massively sensory, in much the same way as its homologue, the hand. A review of the homunculus helps to illustrate how the foot is perceived on the cortical map (see Fig. 2A) and how, like the hand, it occupies a significant proportion of sensory awareness. Hence the combination of tiny musculature, densely packed with spindle cells, with low torque production capacities, yet high afferent drive and fine-tuning capabilities all point to the notion of the foot and toes in particular as sensory devices who’s primary role is to conform to the ground and provide feedback to the CNS about the substrate characteristics. As such, perhaps toe function is primarily linked to balance?

In their featured paper, "Effect of spinal stabilization exercise on dynamic postural control and visual dependency in subjects with chronic non-specific low back pain" Salavati et al. show that patients with persistent non-specific low back pain appear to respond slightly better to treatment when balance training was included as part of their rehabilitation protocol. In particular, the group that were given physiotherapy and balance trained (versus just receiving physiotherapy treatment) responded with lower disability scoring and better general balance — and, specifically, their balance with eyes closed was statistically superior to the control group. Whenever vision is impaired (as discussed below under Apical ectodermal ridge) greater dependence on proprioceptive information occurs. Since the prime sensory placodes\(^1\) of the body are the eyes, when vision is either deliberately or incidentally compromised, awareness through the feet (and the entire proprioceptive net) must be facilitated.

Overall then, Salvati et al.’s work found that balance training with deliberate visual compromise, seemed to enhance balance greater than balance training with eyes open. This may be because muting vision, which accounts for somewhere between 30% and 83% of sensory processing, results in a focus on the next most significant senses, hearing and touch (accounting for between 1.5 and 11% each). This channelling of attention, as Janda suggested, probably facilitates activation of the tonic nervous system (Janda and Vávrova, 1996). Being so large on the cortical map, the sole of the foot and, it would seem, independent toe function should assist in optimizing balance. Is there much evidence to support this notion?

**Balance on your toes**

Perhaps surprisingly, there is very little evidence to support the notion that independent toe function facilitates balance. For example, one study looking specifically at toe shoes compared to barefoot and shod conditions (Smith et al., 2015), found that although the toe shoes and barefoot conditions were very similar in profile, they were both

\[^{1}\text{A neurogenic placode is an area of thickening of the epithelium in the embryonic head ectoderm layer that gives rise to neurons and other structures of the sensory nervous system.}\]
worse for static balance than wearing standard shoes. Another looking at toe-socks compared to normal socks and barefoot (Shinohara and Gribble, 2009) seemed to identify that static balance fared best when barefoot (as you might expect), slightly worse in normal socks and worse again in toed socks. However, neither of the studies allowed for any kind of acclimatization to the conditions, so it might be argued that the most unfamiliar state is the one in which balance would be most compromised.

One year later, Shinohara & Gribble (2010a, 2010b, 2010c) revisited the research and with one week’s worth of acclimatization found that the toe-sock group had statistically significant better balance measures than the barefoot group and the group wearing normal socks. Could it be the adaptation period that’s key?

The adaptation period is probably important, and there are various papers that suggest that adapting to either barefoot or simulated barefoot conditions may take some time (as one would expect), however, there is also evidence that it is the condition itself that changes the way the body is recruited, more so than the pre-existing motor patterns that it is the condition itself that changes the way the body

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were using 5-toed shoes were on average 0.4 s quicker than

speed, agility and quickness found that those troops who

predicted outcome?

2010c) revisited the research and with one week’s worth

of acclimatization found that the toe-sock group had sta-

rheological development marks them as digits two, three, and

four of the full ancestral complement (Gould, 1991). The hundreds of millions of years of development resulting in almost ubiquitous presence of five digits in most vertebrates (from lobe-finned fish, to reptile feet, from bird wings, to mammalian paws and primate hands), carries with

it a strong implication that this pentadactyl arrangement is an optimal solution of sorts.

Such is the influence of our five fingers that the entire number-based system of decimal counting is derived from them. Jarvik, the great Swedish anatomist wrote: “The most prominent feature of man is no doubt his large and elaborate brain. However, this big brain would certainly never have arisen — and what purpose would it have served — if our arm and hand had become specialized as strongly as has, for instance, the foreleg of a horse ... We can say, with some justification, that it was when the basic pattern of our five-fingered hand for some unaccountable reason was laid down in the ancestors ... that the prerequisite for the origin of man and the human culture arose” (Gould, 1991).

But it hasn’t always been that way. Of the very earliest land animals; the only three Devonian tetrapods known, none has five toes. They bore, respectively, six, seven, and eight digits, yet, it seems five digits seems to be where evolution has settled; representing a secondary stabilization, as opposed to an original state (Gould, 1991). Reduction from these higher digit patterns to the more familiar arrangements of five (or less) digits accompanied the evolution of sophisticated wrist and ankle joints — both in terms of the number of bones present and the complex articulations among the constituent parts (Coates, 2005).

So, perhaps this provides some insight as to why five is a useful number; as any animal moving in the sagittal plane (which is common to most animals with one or two exceptions, such as crabs who move in the frontal plane), the motion options of a multi-planar wrist or ankle complex would need optimal ground feedback and stability. Essentially a 5-digit arrangement allows a sagittal plane (or “north”) a frontal plane east—west and an intermediary north-east/north—west information processing and traction option. Gould (1991) echo’s this sentiment, but goes on to question if five (with symmetry about a strong central toe) is advantageous, then why do Homo sapiens retain five, require great strength in using mainly one leg at a time against gravity, yet only primarily utilise the first toe for weight bearing? And why do the most successful of all large mammals, the “cloven-hoofed” artiodactyls, or even-toed ungulates (cows, deer, giraffes, camels, sheep, pigs etc)
bear an even number of toes, with the central axis running through a space between the digits?

This is discussed further below, and in a previous paper (Walden, 2014), but simply would seem to support the train of thought regarding toes being key for bipedal multidirectional movement.

The story of “Why five?” may not have reached a complete conclusion, but Gould (1991) points out that, once attained, by whatever means, the fact that the five digit arrangement is so stubbornly intractable as an upper limit thereafter — so that any lineage again evolving six or more must do so by a different path, leads to a larger overall question. This issue of digits is a microcosm for the grandest question of all about the history of animal life: why, following a burst of anatomical exploration in the Cambrian explosion some 550 million years ago, have anatomies so stabilized that not a single new major body plan has evolved since? He leaves this question for the reader to ponder, but one might guess it could have to do with a level of biological optimization that has reached a threshold for the planet niche we inhabit.

Based on this, should the expectation be that the literature would support greater freedom of the toes?

Perhaps; but, then again, perhaps not. Despite penta-dactyly’s near ubiquity, as discussed, many mammals especially have adapted their digits to form hoofs or paws with pads. Toes tend to be flexible but vulnerable, adaptable but weak; yet their orientation, origins and embryology can provide further insight into their role. Some of the oldest known footprints of our bipedal ancestors, famously left in the volcanic ashes at Laetoli in Africa, have been dated to 3.6 million years old and are literally solidified that not a single new major body plan has evolved since? He leaves this question for the reader to ponder, but one might guess it could have to do with a level of biological optimization that has reached a threshold for the planet niche we inhabit.

Looking backwards to move forwards

A useful way to understand function in the human body is to investigate how evolutionary pressures shaped it. Since toe function seems key to the windlass mechanism (see below), and Heinrich (2007) suggests that the toes may as well lengthen and be fused, a look at the evolutionary record may help provide insight. Rolian et al. (2006) investigated the evolution of hominid toes to understand how natural selection molded the foot. They found that early hominids, such as Australopithecus, had longer toes than later hominids, such as Cro-Magnon. In applying biomechanical modeling to this finding, Rolian et al. were able to identify

that shorter toes are associated with greater bipedal efficiency; in particular, in running, but also in the stance phase of walking gait. It may be relevant to note, therefore, that since most modern shoe design effectively serves to lengthen the toes again; going counter to the evolutionary process, this may compromise gait efficiency (see Fig. 3 below). Rolian et al. (2006) found that even as little as 20% increase in toe length would double the peak loads on the toe flexors and the mechanical work during running gait. Not only this, but with increased loading, the ability to resist such doubling of load could only be matched through hypertrophy of the toe flexors; something that may be counterproductive in terms of movement efficiency.

Grip & grab

Our primate origins also provide interesting insight into the origins of toes from the perspective of grip, grab and conforming to the substrate. Watching our primate cousins it seems clear that the next most recent function of our feet, prior to being solely for walking on, was as grasping appendages. This prehensile function is commonly reclaimed in people who find themselves without functional upper limbs to pick up phones, write, type or paint; so it is not entirely lost to humans function, it just remains undeveloped in most through lack of necessity. Those who are experienced in barefoot running or running with toe shoes will also note the use of the toes for grasping the ground; much in the same way a dog would dig its claws in for traction in mud, sand or snow. The first time this author ran in thick mud wearing toe shoes, his toe flexors actually cramped due to the reflexive action to attempt to dig the toes into the slippery substrate; an exercise that would be futile in a conventional shoe.

This led to consideration of what is this reflexive response that creates a sense of slip and therefore the reflex to “toe grab” the ground? When investigating reflexes there are 3 key reflexes — the M1, M2 and M3 reflexes as well as a 4th that is described as the triggered response or wine-glass reflex (see Table 1).

Simply, the M1 reflex is monosynaptic and therefore mediated at the spinal cord only; the kind of reflex you get to a patella hammer striking your patella tendon — or even a stone striking a tendon in the sole of your foot... What would this mean? The flexor muscles would reflexively flex around the ground level object lifting the foot away from (or wrapping it around) the potentially injurious protrusion. The Babinski response is an example of how a stimulus to the sole of the mature foot should result in a flexor response of the toes (an extensor response being an indication of myelination pathology). The M2 reflex is a conditioned reflex; one in which a highly skilled and experienced athlete — a goal-keeper, for example — reads the body language of the unfolding situation and anticipates the direction of the shot carrying out a “reflexive save”. In other words, they have responded based on a familiar set of stimuli to carry out an appropriate response that is quicker than true reaction time. The M3 reflex is true response time; the time it would take for someone who had never played in goal before to respond to a shot — or to respond to a random noise or sound to hit a timer-button,
for example. There is no anticipation, just pure response time.

However, between the M2 and M3 reflexes there is a response known as the triggered response or wine-glass reflex. This is a response to a tactile stimulus — such as a wine-glass slipping between the fingers perhaps because of an alcoholic induced miscalculation of the grip strength required! The relevance of this response to a primate is very high, especially when one considers what the consequences of the slippage of the grip might mean for an arboreal species... So, not only has the wine-glass reflex been retained in the hands — now primarily used to pick objects up (more so than to hold the body off a branch), but it is also retained in the foot so that, as the skin of the foot perceives a slippage on the ground, so the toes will attempt to “grip” and will dig into the ground to facilitate traction.

In addition to the sensation of slipping the natural gait mechanism helps identify the importance of toe function. During the stance phase, as the Tibia of the stance foot moves anteriorly, creating dorsiflexion at the ankle, so the flexor hallucis longus and flexor digitorum longus, which run up behind the tibia via medial malleolus become tensioned. This tensioning creates a flexion through the distal phalanx so that the toe digs into the ground for toe-off. This mechanism is lost or redundant in conventional footwear; so all grip depends entirely on the traction properties of the outsole of the footwear. The beauty of natural foot design is that grip and traction properties can be adjusted based on the requirements.

Also, during the latter part of the stance phase, the midfoot and forefoot must be relatively stable or rigid to transfer loads associated with push-off. As the heel lifts and bodyweight shifts anteriorly, the plantar fascia is strongly tight raising the arch and rigidifying the foot for force transfer (Neumann, 2002), in a windlass-style of mechanism. This requires 65° of extension of the great toe to fully engage it; something that many forms of footwear limit. Footwear aside, the description always focuses on the connection of the plantar aponeurosis to the great toe, and all-but ignores the attachment of the plantar aponeurosis to the other digits. This may be because the great toe is so important in direct sagittal plane motion, yet, as soon as there is a deviation in direction of travel; as would occur frequently in natural environments or sports, the other toes become dominant in engaging the windlass effect (see Fig. 4).

In terms of power, the Great Toe, or hallux, accounts for around 80% of power output of the toes related, in part, to the density of the flexor hallucis brevis tendon. Yet it is important to recognise that the lesser toes are seen clinically to compensate when the hallux is fused or isn’t present and that the tendons are fully capable of hypertrophying under conditions of increased load (Kartik: Personal Communication).

### Digital development

Toes develop, embryologically, from the lateral plate mesoderm. At around the 5th week IU (intra-uterine), the limb buds form and begin to grow out of the lateral body wall. This “bud” gradually differentiates into a limb and, at the end of it, there is a “paddle-like” arrangement (week 8), similar to the fin of a fish (see Fig. 5). However, at around 12 weeks IU a cleaving process causes differentiation of the toes and each of the rays become distinct. The hands form just slightly earlier than the feet (by about 1 week), but both

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**Table 1** Response types and times: The triggered reaction is key in preventing slipping and falling, but will only work when the ground can be “felt” either barefoot or through a very thin material that allows the perception of movement of the foot over the ground.

<table>
<thead>
<tr>
<th>Response type</th>
<th>Latency (ms)</th>
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<tbody>
<tr>
<td>M1</td>
<td>30–50</td>
</tr>
<tr>
<td>M2</td>
<td>50–80</td>
</tr>
<tr>
<td>Triggered reaction</td>
<td>80–120</td>
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<tr>
<td>M3</td>
<td>120–180</td>
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hands and feet have a distinct pre-axial border (along the big
toe/thumb side of the limb) and post-axial border (along the
little toe/little finger side of the limb); yet their functional
axis of rotation differs. For the hand, the functional axis of
rotation is the middle finger, as you might predict, but in the
foot it is the second toe. This, according to O’Rahilly and
Mueller (2003) is due to differing arrangement of the
intrinsic muscles of hand and foot.

The second toe as central axis corresponds with what is
known mechanistically that the pinnacle of the transverse
arch of the foot is found by tracing a line back down the 2nd
digit and its ray all the way to the medial cuneiform (Norkin
and Levangie, 1992). It also has some relevance clinically,
as in the typical anatomical configuration, we would expect
during gait or squatting or lunging that the centre of the
knee would track directly over the second toe; and, indeed,
this is exactly what is observed most commonly in young
children. However, as people reach maturity in the modern
environment, it seems the combination of potential factors,
from injury, to deconditioning, to inhibition, result in a
decreased capacity to resist gravity effectively resulting in
the knee tracking increasingly inside the line of the central
functional axis (2nd toe) and toward or inside the big toe
(pre-axial border). The result of this is stress to the great
toe, which can force it into a valgus position, stressing the
1st MTP in particular and accompanying collapse of the
medial longitudinal arch of the foot; compromising the
windlass energy-saving mechanism of gait with it.

Clinically, this descending over-pronation pattern is
almost universal in cases of flat foot; with lower abdominal
strength, anterior oblique sling strength and gluteus medius
and maximus strength in particular testing as weak on the
more overpronated foot (or bilaterally in many cases). See
The Middle Crossed Syndrome (Wallden, 2014) for further
details.

Reciprocally, the valgus positioning of the great toe
through use of ill-fitting footwear may drive a further
collapse of the medial longitudinal arch, as described by
sports podiatrist Maclarnon (Personal Communication,
2016; www.youtube.com/watch?v=O-g8-D_1VrQ), as the
bony deviation results in both a passive insufficiency of the
flexor hallucis brevis, and displacement of the sesamoid
bones normally present to optimise torque.

Apical ectodermal ridge

One point of interest here is that, although the somatic
tissues of the hands and feet are formed from lateral plate
mesoderm, as the limb bud pushes out through the body
wall at that early 5-week mark, it pushes through a struc-
ture called the apical ectodermal ridge (see Fig. 2B).

Ectoderm, of course, goes on to form skin, nerve and brain,
but the apical ectodermal ridge is highly specialized and
goes on to specifically form all the special sensory tissues;
the eyes, ears, nose, mouth, tongue, lips nipples, genitals
and … the finger tips and toe tips (with some influence over
the palmar and plantar skin too). So here there are some clues as to the way the body
develops the special sensory tissues that are so key for the
maintenance and perpetuation of life. In a pattern akin to
MacLean’s (Cory 2002) description of the 3 hierarchical
“Reptilian Reflexes” (see Table 2 below), the structures of
apical ectodermal ridge help disclose the way these re-
flexes are activated and executed.

Simply, the special senses are early detection devices,
warning the animal of threat before that danger is immi-
nent; including cliffs (visual), rivers (visual, auditory),
predators (visual, auditory, olfactory), food that has gone
off or is poisonous (visual, olfactory, taste). They also work
to identify opportunity; the fruit on this tree looks ripe,
smells ripe and tastes ripe, the way that person moves,
looks, sounds and smells all make them attractive as a
potential mate.

So the apical ectodermal ridge incorporates the special
senses, for safety, security and sustenance, and it also

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**Figure 4** The Plantar Fascia is most commonly described as being important in storing energy as part of the windlass mechanism which is activated when the big toe is extended (ideally to ~65°). However, all of the toes are inserted into the plantar fascia, and there may be an over-focus on the big toe, in part, because most gait assessment is done on treadmills or walkways when moving in a straight line. The other toes are likely to become of greater significance when a) movement is non-linear, such as in sports or on natural terrains and b) in sagittal gaits using to the “low gear” mechanism, which may occur as initial phase of a forefoot strike in running; stabilizing the longitudinal aspect of the foot dome (see McKeon et al., 2014) moving sequentially across from lateral to medial.
incorporates the genitals and nipples for sex and perpetuation of the species, but of course the organism needs to be able to both move away from danger or threat and towards opportunity. For this gait is required.

During gait, an organism reads its environment via a combination of its visual, vestibulo-auditory, and proprioceptive input. In some circumstances, when one sense is compromised, for example if light levels are low, or vision is impaired, the other sensory components may be facilitated as illustrated in the accompanying paper by Salavati et al. (2016). In gait, the eyes are primarily predictive (scanning for what’s coming up, but not actually the ground beneath the feet), the vestibular-system is primarily reactive (if you begin to fall or slip, it will tell you), while the feet are the sense that are providing real-time feedback.

It may come of little surprise, then, that the apical ectodermal ridge incorporates both the palms of the hands and the soles of the feet, which is why they are far more

Table 2  The notion with Maclean’s reptilian reflexes is that if a reptile is sat in his home, say, a hole in the sand, and is hungry, but senses danger, he will prioritise safety and security and will sacrifice the idea of exploring for food. When he senses the danger is gone he will cautiously emerge and search for food, even bypassing the opportunity to pursue a potential mate if he is hungry; and, should danger appear, both food and sex are off the menu and he will make for his place of safety in the sand. Assuming he is safe, he will go ahead and search for food and only after food has been obtained will he entertain the notion of the potential mate. This reptilian brain underlies neomammalian limbic-emotional brain and the neocortex. Maclean’s model, while obviously having some room for flexibility is useful clinically in understanding behaviour and even physiological prioritization.

<table>
<thead>
<tr>
<th>Maclean’s reptilian reflexes</th>
<th>Safety &amp; Security (fight, fright, flight)</th>
<th>Sustenance (food)</th>
<th>Sex (fornication)</th>
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<tbody>
<tr>
<td>1st Reptilian Reflex</td>
<td></td>
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<tr>
<td>2nd Reptilian Reflex</td>
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<tr>
<td>3rd Reptilian Reflex</td>
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sensory than the dorsal aspects. Their evolutionary function was, first and foremost, to read the contours of the ground; to provide feedback about the substrate the animal is traversing. Since human anatomy has evolved from a quadrupedal design, it is clear that the reason both the hands and the feet are equally sensitive (see Fig. 2A) relates to their shared function as ground contact points.

Much like the difference between a quad bike and a push bike, quadrupedal gait, with 4 ground contact points, is a relatively stable configuration, with less likelihood of mishap than bipedal gait with 2 ground contact points (and, in fact, only one ground contact point for most of the walking gait cycle and all of the running gait cycle). However, for an animal to rear-up and stand on its hind legs, not only has it halved it’s ground contact points from 4 to 2 and halved the information coming in regarding the substrate, but it has narrowed its base of support down to (in our case) about 10% of the previous base. Then, in our infinite wisdom, we have shut down almost all proprioception from our feet, but putting thick chocks of polyurethane (as an example), which restrict motion at 32 of the 33 joints of the foot and almost nullify sensation, between the sole and the substrate. Is it any wonder that a creature evolved for running, as Homo Sapiens appear to be, get injured at rate of around 75 to 80% per year (Fredericks et al. 2015; Hrynýiak et al., 2014)? It would seem surprising if fish or birds had an up to 75% injury rate per year for moving in the niche that they are adapted for.

Could this high injury rate be something to do with the shod environment most runners find themselves in as a cultural default? Possibly. Could it be related to a general deconditioning of the adult population compared to our hunter-gatherer past? Almost certainly. And could the hard modern substrates we run over also be a part of this injurious recipe? The answer here is most probably both "yes" and "no".

A common misperception of the ancestral environment is that our hominid forbearers had the luxury of soft-bedded forest floors to walk and run over. The perhaps harsher reality is that, not only has Africa (a continent known today for its hard sun-baked lands) gotten wetter over the last 2 million years, but that most of the ancestral fossil finds there have been in rocky or volcanic regions such as the Rift Valley, Olduvai Gorge or Laetoli. Marry that with the various contours and they are typically the first part of the foot to touch the ground when running barefoot on hard surfaces. The toes are also hugely sensory, adaptable to ground contours and they are typically the first part of the foot to touch the ground when running barefoot on hard surfaces. The forefoot is roughly twice as sensitive as the hindfoot, preventing them from effectively splaying. It is this splaying movement that not only absorbs shock, but it eccentrically loads the lumbricales and the dorsal and plantar interossei. These muscles help to not only control the splay of the toes, but to store kinetic energy as elastic (potential) energy and to recoil it as the foot is unloaded. They also serve to stiffen the foot under load, this stiffening being a large part of how the foot is able to transform from a flexible 33-joint structure into a rigid lever to effectively transfer force for toe-off and forward propulsion.

In addition, a conditioned, functional foot with all of its spring mechanisms intact has tensegrity properties similar to a deflated basketball. If this is the case it doesn’t matter too much what the surface is like underfoot, the recoil will be severely compromised. For too long now the focus has been on the footwear — even the substrate to a much lesser degree — and not the foot itself. The reality however is that the foot is the real technology that needs addressing.

Hence, the notion that asphalt is “too hard” is the “no” part of the question posed above. The notion that asphalt is too flat, well this may have more mileage as an etiological factor in injury.

Looking at ground hardness is where the next paper included in this Rehabilitation & Prevention section “The effects of dorso-lumbar motion restriction on the ground reaction force components during running” by Moreley & Traum will feature. Before it does, however, consideration of ground reaction force is important.

A simple practical demonstration to understand how toes are important in managing ground reaction force is to kneel down in a high-knee position with hands out in front ready to fall forward into a push-up position. Falling forward into that push-up position on the ground note how your hands land (see tinurl.com/primalfingersplay). You will note all of your fingers are splayed out laterally. Now, repeat the same maneuver, but deliberately keep your fingers together. Most participants get a sense, before they even start to fall forward with their fingers together, that they simply do not want to go through with it; there is an instinct that this is going to jar and instinctive resistance to fall forwards... And yet this is exactly what shoes do to the toes, preventing them from effectively splaying. It is this splaying movement that not only absorbs shock, but it eccentrically loads the lumbricales and the dorsal and plantar interossei. These muscles help to not only control the splay of the toes, but to store kinetic energy as elastic (potential) energy and to recoil it as the foot is unloaded. They also serve to stiffen the foot under load, this stiffening being a large part of how the foot is able to transform from a flexible 33-joint structure into a rigid lever to effectively transfer force for toe-off and forward propulsion.

In conjunction with this splaying action, the dorsal & plantar digital veins become effectively compressed with each step ensuring venous blood is returned effectively from the forefoot back into general circulation.

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In conclusion, we should be paying more attention to our feet and proprioception. A conditioned foot is more likely to adapt to the terrain and risk injury. In contrast, a deconditioned foot with a general lack of adequate proprioceptive awareness is at high risk for overuse injuries. Research focusing on the mechanics of ground reaction forces and the role of the foot in injury prevention is needed.
As McKeon et al. (2014) state, “Human runners are unique in needing to control balance during single leg support and for this reason (unlike quadrupeds) require a foot that is reasonably mobile, able to accommodate uneven substrates, and actively controlled.” As illustrated in The Overpronated Foot — A New Paradigm (Wallden, 2010, 2014; Figs. 5 and 6), not only does hominid bipedal gait require greater external rotator mass at the hip, but it also needs a mechanism at the foot end to provide adequate traction to counter this force — especially in the acceleration phase, or in turning (see accompanying practical paper). This is more likely where toe function becomes most relevant and may explain why the hoof or paw is uniquely found in quadruped gait, but not in bipedal gait. The bipedal dinosaurs, such as tyrannosaurus or the troodontids retained toes, and, as their descendants, so do the birds; the only other extant true biped (albeit not their primary form of locomotion).

That said, much like the toe splay discussion above, the hoof of the horse is also designed to splay as it contacts the ground and, preceding the recent focus on minimalist/barefoot function in human performance the same debate was being had in the equine world (Strasser, 1999; Cook, 2001). Simply, as with human gait, horses have evolved unshod, they have adapted to the unshod state and adding an artificially restrictive device to the hoof’s function similarly compromises load transfer properties through the limbs of horses as it does the limbs of humans.

Looking at our closer relatives, the arboreal apes, the spring mechanisms of the foot are minimal; a key distinction between a creature evolved for walking (and swinging) versus running. These springs include a prominent Achilles tendon, which inserts into the plantar aponeurosis, and the spring ligaments on the inferior aspect of the foot. All are absent in apes and were either lacking or minimally developed in the earliest hominids, such as Australopithecus (McKeon et al., 2014). These primarily sagittal spring mechanisms, as well as the transverse arch spring associated with toe splay are key considerations in any discussion of ground reaction force and running economy.

For example, Perl et al. (2012) who compared forefoot striking (typical of barefoot running) with heel-striking (typical of running in cushioned shoes or on soft substrates; Lieberman et al., 2014) comment that the plantar aponeurosis and Achilles tendon naturally recover, respectively, around 17% and 35% of the mechanical energy of ground strike in running gait. However, if there is a material blockage to the plantar aponeurosis from an “arch support” and a lack of eccentric loading to the Achilles due to a heel-strike gait, these mechanisms will be compromised. Eccentric loading to the Achilles and triceps surae complex have been utilized as a mainstay of rehabilitation to Achilles Tendinopathy since Alfredson’s classic paper was first published in 1999; and it may be that Alfredson accidentally stumbled upon the phase of the natural human gait cycle that is largely missing in shod runners ...

**Impact transient**

Aside from efficiency concerns, studies have identified that running in a cushioned running shoe tends to result in a heel-strike in between 89 and 100% of cases (Fleming et al., 2015). Further, this heel strike is associated with what is termed an impact transient (or pressure spike) that has been correlated with various lower limb injury, such as tibial stress syndrome (Samaan et al., 2014). A simple explanation for this pressure spike is that it is a sudden deceleration, associated with heel strike while the centre of mass of the body is moving over the outstretched foot (see Fig. 7); much akin to a pole vaulter’s mass being behind the strike point of the pole, until he or she vaults over the top of it.

Being a deceleration force, the presence of the impact transient in heel-strike running may partly explain how the majority of research assessing running efficiency, shod

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**Figure 6** One role of the toes is to both adjust the body’s platform to the contours of an underlying substrate that, in nature, is highly variable; while also providing valuable feedback to the central nervous system that can instruct the musculature to respond appropriately. Here you can see that when a ground-lying object, such as a stick, stone or root falls under the great toe, the 2nd toe, the middle toe or the lateral toes it will do very little to alter stability of the foot as a platform. A rigid shoe sole, on the other hand, will result in a tilt of the foot and increase potential for ankle sprain - a particular risk for a biped. It is interesting to note that 23 of the 26 bones and 26 of the 33 joints of the foot are directly related to, and affected by, independent toe movement. See tinyurl.com/dynamictoefunction for video footage.
versus barefoot, identifies barefoot as more efficient. This discussion has been heavily focused upon elsewhere (Lieberman, 2010; Divert et al., 2008; Squadron and Gallozzi, 2009; Fleming et al., 2015) and so it is not the objective of this editorial to rehash that information, nevertheless, areas that are less discussed elsewhere will be presented.

One example of this is the discussion around what is "right" or what is "natural" in terms of foot-strike, yet there is rarely focus on the substrate the individual is traversing; nor the direction they are traversing it. Anyone playing a ball sport, for example, or running in a natural setting will rarely a) run in a straight line for very long, nor b) run at the same speed for very long, nor c) necessarily run on a flat surface. Yet the vast majority of research conducted into foot function is conducted running straight ahead, at a pre-defined speed on a treadmill or in a lab. This would be like only ever testing the tyres and suspension system of a 4 × 4 (a vehicle that has evolved for off-road use) on a flat, straight road at only one speed. Admittedly this may be the easiest way to test, but hardly very relevant to its actual function. Perhaps this is why we know so little about the toes in human function. The relevance of toe function; particularly on rough or cambered surfaces and with cutting and planting especially when specific trajectories are optimal (such as on a narrow mountain trail, or to cut and reach for a shot in tennis) is likely to be significant. Other aspects of foot function that are relatively under investigated are, for example, the contrasting function of feet in those who have grown up unshod, versus those who have grown up shod. There is some discussion of this in the literature, but there is a lot less accessibility to habitually unshod populations, than there is to habitually shod populations in proximity to university labs.

A barefoot person running across soft grass or sand tends to heel strike due to the give of the surface acting much like a the give of a soft running shoe, yet as soon as they hit some hard ground or a concrete path, it should encourage them to switch strategies to a more forefoot strike. This is not a 100% correlation, but it is a strong likelihood; assuming there are no neural deficits or kinesthetic dysfunction. Why might this be so?

The answer may be that the foot and leg are not so much a simple interface with the ground, but moreover a sophisticated mechanical filter (Gracovetsky, 2001). When one considers the range of motion (from plantar-to-dorsiflexion) at the ankle in forefoot strike alone (that is lost in heel-strike) then it is clear that the ability to filter, store and recoil ground reaction forces is significant in the natural state. Why would this be important? According to Gracovetsky (1988), throughout the evolution of animal locomotion, the spine has been the point of power generation to drive the appendages forward and these appendages are merely amplifications of spinal movement. This can be clearly seen in the fish, lizards and even into mammalian locomotion to some degree. In human locomotion, much attention has been focused on the lower limb, yet Gracovetsky's "Spinal Engine" theory remains unchallenged nearly 30 years later.

As one runs, there is clearly a ground reaction force which, in forefoot running, is nicely dampened and controlled by the eccentric loading of the triceps surae complex initially, then the flexion of the knee and hip before it reaches the spine. This ground reaction force is filtered and stored by the various visco-elastic tissues within the lower limb and into the pelvis where the force travels up the spine "derotating" each segment of the spine as it passes until, it is finally expressed out the upper limb and the head is able to travel with almost zero vibrational effect from gait allowing optimal visual function. (See The Neutral Spine Principle, Wallden, 2009, for more detail.) This whole process is modulated and either down-regulated or up-regulated (decreased or increased tone/
stiffness) via the afferent neural drives reading the loading profile and feeding back into the muscle system. Note, part of the challenge for the body with an impact transient is that it occurs in a time period less than 40 ms (see Figure 1, bottom left in Moreley & Traum’s paper), which has potentially major ramifications when reviewing the data in Table 1 above.

Gracovetsky explains that this process described above reshapes the ground impact pulse to perfectly drive derotation of the spine, which, in turn, serves to swing the opposite leg through into the next step of the gait cycle. This process happens very naturally during running on firm surfaces, however, when the surface becomes very soft, such as in mud or on soft sand then a different phenomenon occurs. Because there is significantly decreased ground reaction force, there is not a large enough pulse to de-rotate the spine. In order to achieve this de-rotation, therefore, the abdominal oblique muscles must increase their recruitment level to spin the spine actively (rather than using the “free” or passive energy from the ground reaction pulse), which is both fatiguing in and of itself, and also compromises the breathing mechanism creating earlier fatigue. This is why elite sprinters often do “sand training” as a form of core conditioning. As Morely and Traum (2016) state in their accompanying paper, “clear transmission of sensory messages is critical for mechano-receptive and proprioceptive coordination of the internal forces that allow the body to adapt to the external forces influencing the foot and ankle through ground reaction force”.

In other words, the nervous system’s reading of the ground reaction impulse is key for adapting the locomotor strategy employed. The greater the movement ability and movement skill of the runner, the better their strategy is likely to be. And skill acquisition is derived from feedback; the better the feedback, the better the skill development, within certain genetic limits.

But what if the skill is limited? What if the runner has never had to develop a great deal of body awareness and locomotor resilience; either through their lack of movement history and/or their protection from the environment? As insinuated above, even someone with movement skill may not be able to react quickly enough to a large impact transient due to the speed at which it happens. Could this be why low back pain is commonly reported in runners, and, in contrast, commonly reported as minimized by barefoot running (Hryniak et al., 2014)? An interesting statistic from a study of 509 barefoot/minimalist runners is that more than half of all respondents stated that they began this style of running to get over an old injury, and 14% of the respondents finding that it improved their low back pain. The discussion around impact transient and ground-strike above and in the paper by Daoud et al. (2012) described below may be part of the explanation for this decrease.

Daoud et al. (2012) reviewed the injury history and running style of 52 competitive runners across 4 years of records. They predicted that, due to the well-documented impact transient in those runners who favoured a rear foot strike, they would find that injuries of the knee and hip, lower back pain, plantar fasciitis, medial tibial stress syndrome, and stress fractures of bones of lower limb excluding the metatarsals would have a higher incidence. This they found to be correct; by a factor of greater than 2:1 (rearfoot strike to forefoot strike). However, they also predicted that due to the increased loading, they would find a different injury profile in forefoot strikers, to include injuries such as Achilles tendinopathies, injuries of the foot, and stress fractures of the metatarsals. This, however, was found not to be the case with no significant difference between the two groups. Other studies of army recruits didn’t show this same trend; so while the demands in terms of mileage, loading, motivation and footwear is very different between these groups, the strike pattern may not be quite as significant as the Daoud et al. (2012) study would first suggest. What other factors could be at play?

Sole sensation

A brief review of the wiring of the foot (and the hands) may provide some insight. As discussed above, the hand and foot are homologues of each other and form via the apical ectodermal ridge for specialized sensory awareness. The sole of the foot is fed by the L4, L5 and S1 nerves primarily. Hence the sole is feeding afferent information directly into the spinal cord segments that innervate musculature of the lumbo-sacral junction. Any junctional area compromises stability for mobility, and the lumbo-sacral junction is no exception. According to McKenzie and May (2006), 98% of posterio-lateral disc bulge occurs between the segments L4, L5 and S1. This may come as little surprise since they are the lowest part of the mobile spine and therefore under greatest load, however, it is unlikely to minimize injury if the very part of the body that is designed to feed information back into the those spinal segments is muffed or desensitized by an artificial, mundane and unchanging afferent awareness. Similarly, the palms of the hands are fed by the C6, C7 and C8 nerves that span the cervico-thoracic junction — the second most injured part of the spine; so the original quadrupedal arrangement is actually designed to provide information into these most vulnerable junctional areas of the animal’s spinal column.

Is it really, then, about heel strike versus forefoot strike, or is it more about having a functional (and attentive) nervous system that is able to read the variability of the ground and to adjust according? After all, you only need to look at the trabecular pattern of the foot bones to note that they are structured to take load both from the heel forwards and from the midfoot backwards; the structure betrays the flexibility of the function. Similarly, van Wingerden et al.’s (1996) deep longitudinal system seems to only work with a heel strike, while an alternative system, akin to Myer’s (2001) superficial back line, described in Chains, Trains & Contractile Fields (Walldén, 2010), may provide a viable forefoot-striking alternative.

To extrapolate what has been known in the field of strength and conditioning (and, perhaps unconsciously, in the world of fashion) for many years; that loading the
forefoot facilitates quadriceps activation and loading the heel facilitates gluteal activation, may provide further insight into the gait action.

If, as the foot strikes the ground, it is out in front of the centre of mass of the body then the heel will tend to strike first (as in walking or running in cushioned shoes), therefore the first concern of the body is to extend the hip to relatively pull the body over the planted foot. Hence a heel strike serves that function well; to stimulate the gluteus maximus to extend the hip and pull the centre of mass over the planted foot; finally, when the centre of mass is ahead of the foot, the quadriceps are stimulated to extend the knee and drive the runner forward. Whereas, if the forefoot strikes the ground first (as tends to occur in barefoot running), the centre of mass tends to be more over the planted foot (see Fig. 7). This forefoot landing will facilitate the quadriceps group, to counter the downward loading of the trunk through the leg initially and as the heel descends from a plantar flexed position to "kiss the ground" the hip extensors will fire to propel the individual forward (note, there is some corroborative evidence for this in unpublished EMG studies from University College London; Personal Communication: Newey, 2013). Further, the rectus femoris is a pennate muscle, and therefore ideally suited for resisting heavy gravitational loading, while the gluteus maximus is a longitudinal or strap muscle and therefore ideally suited for stretch-shortening power generation; so both contexts work, though one might expect the forefoot strike to (resisting gravity first, then extending the hip) to be the most efficient way to generate forward momentum in a gravitational field. See Fig. 7.

With this background, it is interesting then to consider the accompanying paper in this section by Morley & Traum, The effects of dorso-lumbar motion restriction on the ground reaction force components during running.

This research was designed to assess how restricting range of motion of the trunk would affect the ground reaction forces due to a forced restriction in the ability to utilize the myofascial slings of the trunk to derotate the spine. If Gracovetsky’s interpretation of the Spinal Engine were correct, one would expect that an inability to store energy through these elastic tissues would result in a requirement for greater ground reaction forces to propel the spine and, with it, heel strike.

While the results, indeed confirmed this, the runners all wore conventional shoes (which would imply a 95% rate of heel strike in any instance); certainly the ground reaction force data illustrated showed an impact transient and therefore a heel-strike ... These findings suggest that a restriction of natural trunk motion in running gait (or, indeed, how deconditioning or inhibition of the trunk musculature, so common in modern society) may result in a greater requirement for ground reaction forces to propel the spine and, with it, heel strike.

To summarize, then, it would seem that the toes are involved in gait efficiency from mechanisms creating adjustable grip, rigidifying the foot for toe off, but also to provide accommodation to the substrate, potentially minimizing injury risk — particularly in the frontal plane. The toes also are highly sensitive, providing information about the substrate directly to the nervous system in order that it may both react reflexively in cases of slippage or uneven surfaces and respond strategically in terms of ground reaction forces. When unrestricted, the toes appear to disperse forces in landing and, a shorter toe configuration aids efficiency. Their role in multidirectional, cambered or uneven substrate locomotion to create an effective adaptable interface and intelligent mechanical filter may be key and somewhat unconsidered due to research constraints and ease of repeatability.

Concluding thoughts from UltraRunner, Ted McDonald (Personal Communication, 2010) — also known as "Barefoot Ted":

"If I were to develop the optimal shoe it would not constrain the motion of any of the 33 joints of the foot, nor the toes independent or gripping action; it would encourage activation of the innate musculature of the foot, would be self-regenerating and would adapt to use by getting thicker and stronger rather than getting weaker or wearing away, and it would be wired directly into the user's nervous system ..."

So if the question is ever posed "What on Earth are the toes actually for?" the short, but accurate response answer could be "Our toes are for being on the Earth".

**Conflict of interest**

The author of this piece is the owner of the Primal Lifestyle Ltd, a company set up to distribute Vibram Fivefingers to the UK Market in 2007 — described more fully on the opening page of this editorial.

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