News & views

Biomechanics

Ahead of the curve in the evolution of human feet

Glen A. Lichtwark & Luke A. Kelly

The longitudinal arch has long been considered a crucial structure that provides stiffness to the human foot. Now the transverse arch is stepping into the spotlight, with a proposed central role in the evolution of human foot stiffness. **See p.97**

Humans evolved to walk and run effectively on the ground using two feet. Our arched foot, which is not a characteristic of other primates, is a unique feature crucial for human bipedalism. The arch provides the foot with the stiffness necessary to act as a lever that transmits the forces generated by leg muscles as they push against the ground. The arch also retains sufficient flexibility to function like a spring to store and then release mechanical energy. On page 97, Venkadesan *et al.*[1] present a new view of how foot stiffness is regulated. Their finding not only has exciting implications for understanding foot evolution, but also provides a possible framework when considering foot health and how to design better footwear.

The foot's longitudinal arch (the arch that runs from the heel to the ball of the foot; Fig. 1) is often credited[2,3] with the leading role in foot stiffening. The ligaments spanning this arch, including the plantar fascia (or plantar aponeurosis), act like a bowstring to resist arch collapse when force is applied. Moreover, the spring-like mechanical properties of these ligaments contribute substantially to the foot's ability to store and return energy[4].

However, Venkadesan and colleagues present the idea that another arch component, the transverse arch (the part of the arch that curves across the foot at the base of the metatarsal bones; Fig. 1) is at least as important for foot stiffness as is the longitudinal arch, if not more so. The authors provide evidence for how transverse-arch curvature might help prevent foot bending and therefore increase foot stiffness. An analogy for this proposed stiffening mechanism is the way that a pizza slice becomes less floppy if the slice's outer crust is curled up.

Venkadesan *et al.* initially took a theoretical approach to investigate the role of transverse curvature in stiffening the foot. Modelling an elastic shell, the authors demonstrated that, if the transverse curvature of the shell increased, this increased the stiffness of the shell in the longitudinal direction. Venkadesan and colleagues derived a parameter for curvature and longitudinal stiffness (independent of other factors such as shell size and thickness), and show that a distinct transition point exists beyond which the amount of curvature directly influences the longitudinal stiffness. A similar relationship exists for a physical model consisting of discrete rigid elements (analogous to the metatarsal bones) connected by springs (corresponding to ligaments).

To test whether this model might be relevant to the stiffness of the human foot arch, the authors examined human cadaver specimens (frozen after death and then thawed to combat stiffening due to rigor mortis) and cut ligaments in the transverse arch that are expected to be crucial for coupling the curvature of this arch to foot stiffness. Venkadesan *et al.* then assessed the foot's vertical deformation when loads were applied. Cutting the transverse ligaments reduced foot stiffness by the remarkable value of more than 40%. By comparison, previous research[4] indicates that cutting the foot's plantar fascia, which spans the longitudinal arch, reduces stiffness by just 23%. Venkadesan and colleagues' data therefore suggest that transverse ligaments make a substantial contribution to overall foot stiffness. When bearing a load, the foot's transverse ligaments are presumably stretched by the resultant spreading out of the metatarsals at the ball of the foot. The authors suggest that this ligament stretching is a direct result of transverse-arch curvature.

Venkadesan and co-workers examined the evolution of the transverse arch across different primates, including various species of extinct hominin (those species more closely related to humans than to chimpanzees). As in other work[5] investigating foot evolution, Venkadesan *et al.* focused on the amount of torsion (twist) in the fourth metatarsal bone. They estimated the curvature of the transverse arch and determined which species would probably have had sufficient

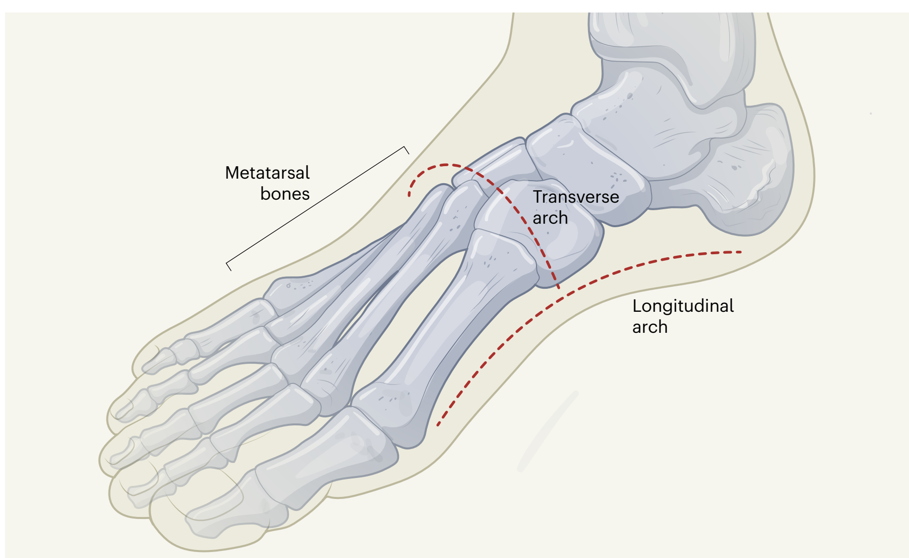

Figure 1 | Human foot arches. The longitudinal arch of the human foot has been proposed[2,3] to have a key role in providing stiffness for the foot, an attribute that enables humans to walk on the ground on two feet. Venkadesan *et al.*[1] report that another foot arch – the transverse arch, which is in the vicinity of the metatarsal bones – makes a major contribution to foot stiffness.

curvature to induce stiffening of this arch to an extent similar to that of modern humans. For example, the authors examined the species *Australopithecus afarensis*. This species existed more than three million years ago, and whether it walked upright in a human-like fashion is debated[6–8]. Venkadesan *et al.* report that the transverse arch of *A. afarensis* was less curved than that of a human foot and thus, according to their model, probably less stiff. However, the authors correctly emphasize that such curvature alone cannot be used reliably to infer movement capabilities, and other mechanisms might stiffen the foot sufficiently to allow a human-like gait.

The curvature of transverse arches in human populations probably spans a wide range of values. Some people have noticeably flat feet whereas others have a high arch. Perhaps those with flat feet have less curvature of their transverse arch and thus potentially reduced stiffness in their feet compared with those whose feet are less flat. But it is also possible that people with flat feet have sufficient transverse-arch curvature to compensate for their low longitudinal arch, thereby maintaining sufficient stiffness for effective walking and running. Given that Venkadesan and colleagues' work did not directly test whether there is a relationship between transverse-arch curvature and the stiffness of the human foot, it remains to be determined whether the range of differences in human transverse-arch curvature is a crucial functional parameter to explain foot stiffness.

The range of curvature of the arch of human feet suggested by Venkadesan *et al.* would indicate that a nearly twofold change in stiffness is possible as a result of natural variation in curvature of the trans verse arch from one person to the next. However, any relationship between transverse-arch curvature and stiffness is probably not enough to completely explain the regulation of foot stiffness, and other factors will also need to be considered — for example, the stiffness of the plantar fascia or the potential for muscles to actively regulate arch stiffness. As such, caution is necessary before relying on this curvature parameter alone as the key variable in assessing human foot stiffness.

The fields of evolutionary biology, sports science and medicine have largely neglected the transverse arch when trying to explain the managements of loads applied to the foot. Venkadesan and colleagues' research suggests a new mechanism that links foot form and function and sets the scene for a possible shift in how the human foot is considered. More research will be needed to better understand how the transverse arch contributes to human locomotor performance, including determining what its contribution is to an individual's foot stiffness and whether this provides any mechanical or energetic benefits. It is conceivable that new treatments that take advantage of transverse-arch curvature to modulate foot stiffness could be developed for various foot disorders. Perhaps even more exciting are the implications of this work for efforts to mimic a human foot when designing prosthetic limbs or legged robots.

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Artificial intelligence

In-sensor computing for machine vision

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An image-sensor array has been developed that acts as its own artificial neural network to capture and identify optical images simultaneously, processing the information rapidly without needing to convert it to a digital format. **See p.62**

Sight is one of our most vital senses. Biologically inspired machine vision has developed rapidly in the past decade, to the point that artificial systems can 'see' in the sense of gaining valuable information from images and videos[1,2], although human vision remains much more efficient. On page 62, Mennel *et al.*[3] report a design for a visual system that, rather like the brain, can be trained to classify simple images in nanoseconds.

Modern image sensors such as those in digital cameras are based on semiconductor (solid-state) technology and were developed in the early 1970s; they fall into two main types, known as charge-coupled devices and active-pixel sensors[4]. These sensors can faithfully capture visual information from the environment, but generate a lot of redundant data. This vast amount of optical information is usually converted to a digital electronic format and passed to a computing unit for image processing.

The resulting movement of massive amounts of data between sensor and processing unit results in delays (latency) and high power consumption. As imaging rates and numbers of pixels grow, bandwidth limitations make it difficult to send everything back to a centralized or cloud-based computer rapidly enough for real-time processing and decision-making — which is especially important for delay-sensitive applications such as driverless vehicles, robotics or industrial manufacturing.

A better solution would be to shift some of the computational tasks to the sensory devices at the outer edges of the computer system, reducing unnecessary data movement. And because sensors normally produce analog (continuously varying) outputs, analog processing would be preferable to digital: analog-to-digital conversion is notoriously time- and energy-consuming.

To mimic the brain's efficient processing of information, biologically inspired neuromorphic engineering adopts a computing architecture that has highly interconnected elements (neurons, connected by synapses), allowing parallel computing (Fig. 1a). These artificial neural networks can learn from their surroundings by iteration — for instance, learning to classify something after being shown known examples (supervised learning), or to recognize a characteristic structure of an object from input data without extra information (unsupervised learning). During learning, an algorithm repeatedly makes predictions and strengthens or weakens each synapse in the network until it reaches an optimum setting.

Mennel and co-workers implement an artificial neural network directly in their image sensor. On a chip, they construct a network of photodiodes — tiny, light-sensitive units, each consisting of a few atomic layers of tungsten diselenide. This semiconductor's response