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Inside JEB

WHY WALKING FLAT-FOOTED HURTS AFTER HIGH HEELS

When it comes to shoes, some women will go through hell for a pair of Jimmy Choos. But what effect does wearing high heels have on our bodies? Clinicians have known for a long time that if you hold a limb in a shortened position over an extended period, the muscles shorten. High-heeled shoes push our heels up, which made Marco Narici from Manchester Metropolitan University wonder whether wearing heels on a regular basis could shorten our calf muscles. According to Narici, there was some anecdotal evidence that something changed because secretaries in the 1950s complained about discomfort when they took their heels off and walked flat-footed. 'I thought it was an experiment which was inadvertently being done by women. What we could do was test high heel wearers to see if we could find some changes in the calf muscle,' says Narici (p. 2582).

At that time, Robert Csapo, from the University of Vienna, Austria, was visiting Narici's Active Lifespan Lab, so Narici and Costis Maganaris asked Csapo to test the theory. Placing an advert in the Manchester Evening News asking for volunteers ranging in age from 20 to 50 years who had regularly worn 5 cm high heels for 2 years or more, Csapo attracted 80 recruits, which he whittled down to a final group of 11 who felt uncomfortable walking without their heels. Then he recruited a second group of women who did not wear high heels and teamed up with Olivier Seynnes to look at the internal workings of both groups' calf muscles.

Measuring the size of the women's calf muscles with MRI, the team found that the calf muscles of the high heel wearers were the same size as those of the women who preferred flat shoes; they hadn't shrunk. 'We were expecting slightly smaller muscle volumes in the high heel wearers because we thought that if the muscle is in a shortened position then you are loading it less and the muscle volume should be smaller,' explains Narici.

Next Csapo and Seynnes used ultrasound to measure the muscle fibre length in the women's calf muscles, and this time they did see a difference. The high heel wearers' muscle fibres were 13% shorter than those of the women who wore flat shoes. 'This confirmed the hypothesis,' says Narici, 'because when you place the muscle in a shorter position, the fibres become shorter.' However, by shortening the fibres, the muscles would have to contract more to shorten by the same length, and if this was the case the high heel fans' calf muscles could no longer function optimally and thus would produce less force than the flat shoe wearer's calf muscles. Had the shortened muscle fibres made it more difficult for high heel addicts to walk efficiently?

The team turned their attention to the tendons that attach the calf muscle to the heel. Scanning with MRI, the team could see that the Achilles' tendon was the same length in the two groups of women. The tendon had not lengthened to compensate for the shorter calf muscle. However, the high heel fans' tendons were much thicker and stiffer than the flat shoe wearers'. Narici and his team realised that by thickening and stiffening, the Achilles' tendon compensates for the shortened muscle fibres in the calf muscle, allowing the fashion addicts' calf muscles to function optimally as they walk, but causing discomfort when walking on flat feet because the tendon cannot stretch sufficiently.

So should women give up wearing high heels? Narici doesn't think so, but suggests that fashion addicts may want to try stretching exercises to avoid soreness when they kick off their heels at the end of the day.

10.1242/jeb.048454

Csapo, R., Maganaris, C. N., Seynnes, O. R. and Narici, M. V. (2010). On muscle, tendon and high heels. *J. Exp. Biol.* **213**, 2582-2588.

SEED EATERS BITE HARDER THAN RAPTORS

Diego Sustaita is fascinated by raptors. 'Most people are keen on raptors because of their flight capabilities, but for me its their shear carnivory,' says Sustaita. According to Sustaita, from the University of Connecticut, accipiter hawks tend to subdue and suffocate their prey with their talons, while falcons catch victims with their feet and sever the spinal cord with a neat bite to the neck. 'There have been studies describing the morphological characteristics that are presumed to be associated with differences in the way they attack, capture, kill and ultimately feed on their prey,' explains Sustaita, who adds, 'This study was an attempt to identify the performance or functional implications of these morphological characteristics'. Working with his Masters thesis supervisor, Fritz Hertel from California State University, Northridge, USA, Sustaita began measuring the forces generated by the beaks and talons of accipiter hawks and falcons as they attacked force transducers (p. 2617).

'Gaining access to the raptors was the most difficult part of this study,' remembers Sustaita. Working with raptor rehabilitation organizations in California and Hawkwatch International in New Mexico, the duo had access to four species of falcon and two accipiter species. Designing a force transducer built from strain gauges and a crescent wrench, Hertel restrained the birds while Sustaita offered them the force transducer to bite on or grip with their talons. Sustaita admits that this was sometimes risky and says, 'It helps if you trust the person holding the bird,' and adds that sometimes his fingers got nipped but says, 'It was worth it to get the data'.

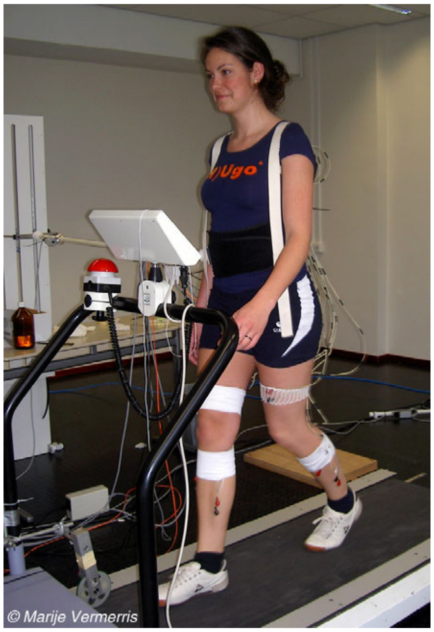
Analysing the data, Sustaita found that the falcons bit with greater force than the hawks, while the hawks gripped tighter than the falcons. However, the grip forces produced by the birds were consistently lower than Sustaita and Hertel had predicted based on the bird's musculature and smaller falcons' grips were much weaker than they had predicted. 'Smaller falcons may be capable of producing higher grip forces, but they tend not to as far as we can measure,' says Sustaita.

The duo also compared the raptors' bite forces with those of other birds and mammals and was surprised to find that the raptors' bites were at the weaker end of the spectrum. 'Based on data that have been published for seed eaters these forces are comparatively low, absolutely and relative to body size, which may be due to real functional differences,' says Sustaita. 'For example, some of the birds adapted to crush seeds have skulls built to deliver force and the forces that raptors may contend with in nature may be different because raptors are dealing with skin tissue, muscle and bone. There might not be such strong selection for crushing as for ripping and tearing, and these capabilities involve a different suite of modifications that involve not only muscular strength but also sharpness of the beak and talons,' explains Sustaita. 'There is a whole list of things that might explain the low bite force away and we would need to look at a greater diversity of birds to get at the heart of that,' he adds.

10.1242/jeb.048447

Sustaita, D. and Hertel, F. (2010). *In vivo* bite and grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae). *J. Exp. Biol.* **213**, 2617-2628.

WALKERS TAKE SIDE COLLISIONS IN THEIR STRIDE



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Rushing through the underground or getting jostled in the street, minor bumps hardly knock us off course. But what strategies do we use to recover without stumbling? At Hof from the University of Groningen, The Netherlands, explains that our reflexes help us to regain our balance after a bump from behind, but it wasn't clear how we recover after a jostle from the side. Hof had built a mathematical model that suggested that we regain our balance within one step, but would this theory stand the test? Could walkers recover from a minor sideways collision without stumbling and in one graceful step as Hof's theory predicted (p. 2655)?

Hof teamed up with students Marije Vermerris and Welmoed Gjaltema to test some walkers' reactions. Recruiting 10 fit undergraduate students to walk on a treadmill, the team tied a belt attached to a piston around each student's waist. After every 10 strides, the piston gently tugged or pushed the walker while the team measured the forces acting on the walker's feet. Subtly adjusting the piston's timing so that it jostled the student at different points during the stride cycle Hof also increased the strength of the push from 2.7 to 12.4 $\mathrm{kg\,m\,s^{-1}}$. Collecting force measurements for 5000 steps over a 2 h period as each student was jostled 400 times, Hof also filmed the first minutes of each walking experiment and was impressed by how well the students reacted to the disturbance. Their arms and trunks barely moved; 'I measured the trunk movements with a gyroscope and they were so small that they were not interesting,' says Hof.

Analysing the ground reaction forces as the students recovered from each bump, Hof saw the walkers use two strategies. In the first strategy they simply recovered by stepping wide of the position where they would normally have placed their feet. For example, if a walker that was standing on the right foot was jostled from the right, then the left foot was free to be placed wide to brace the walker. However, when the walker was standing on his left foot and pushed towards the left, the walker had to cross his right leg over his left before continuing on his way. What is more, the students were completely unaware of the dramatic step they took. 'The subjects saw their own videos after doing the experiments and they said, "Did I do that strange stepping crossing over?" They didn't realise how complicated the things were that they were doing,' says Hof.

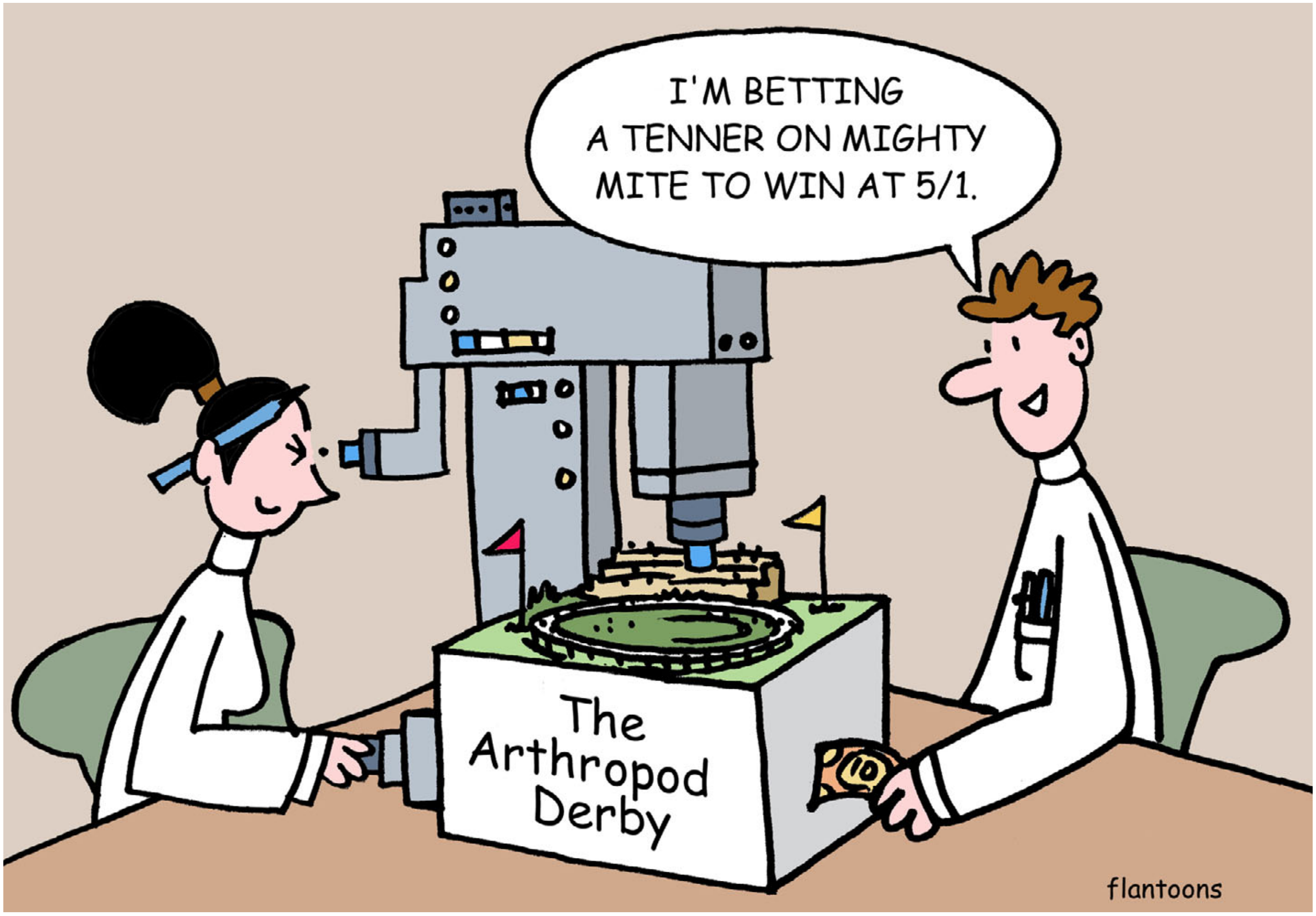
However, the walkers only used the 'step' strategy when jostled early in a stride and had to resort to the second strategy, rolling the ankle, when bumped toward the end of each step. 'The stepping strategy needs at least 300 ms (30%) before foot placement to be successful,' explains Hof, but walkers can roll their ankles at any stage of a stride to recover. He also noticed that on the occasions when a walker did not recover sufficiently in a single stride, they rolled the ankle slightly to complete the correction.

But what does all this mean for Hof's theory? Well, the walkers behaved exactly as the theory predicted. By stepping and rolling their ankles the walkers were always able to track their moving centre of mass (which Hof refers to as the extrapolated centre of mass) with the centre of pressure exerted by their feet on the ground by shifting their weight from one foot to the other. Next Hof is keen to find out which muscles the walkers use when recovering and whether the reaction is a true reflex.

10.1242/jeb.048470

Hof, A. L., Vermerris, S. M. and Gjaltema, W. A. (2010). Balance responses to lateral perturbations in human treadmill walking. *J. Exp. Biol.* **213**, 2655-2664.

MITES' SUPERFAST MUSCLES



Most muscles don't contract very fast. A few exceptional creatures have specialised muscles that register contraction frequencies of several hundred Hertz for sound production, but most muscles involved in walking don't come close to that. Jonathan Wright, working with Grace Wu and other colleagues from Pomona College and Harvey Mudd College, USA, explains that muscles trade off contraction frequency against force: fast contracting muscles cannot produce much force, while high force-producing weight-bearing muscles only contract slowly. So what about minute teneriffiid mites? Their leg muscles must be strong enough to carry their weight, but the smaller you are, the higher your stride frequency. Could mite leg muscles break the rule and contract super fast to produce a high speed stride while still carrying the arthropod's weight? Wright and his colleagues collected two new species of mite from the Californian sage scrub, weighed them and filmed the arthropods at 1000 frames s^{-1} as they scuttled around to see how fast they could run (p. 2551).

The first species weighed in at 182 μg and hit colossal speeds up to 133 body lengths s^{-1} with leg stride frequencies of up to 90 Hz at 50°C. Meanwhile, the second smaller species, weighing in at 30 μg, got up to a similar relative speed (129 body lengths s^{-1}) and stride frequencies of up to 112 Hz. So the mites' leg muscles can contact super fast while still carrying their body weight and the stride frequency is similar to the values that you would predict based on the arthropods' size relative to that of other creatures. Calculating that the muscle contraction phase of a stride could last as little as 4–5 ms and knowing that the mites only run in 4–5 s bursts, the team speculate that the muscles may be anaerobic, allowing them to pack more muscle fibres in at the expense of aerobic energy-producing mitochondria to increase force production despite their superfast contraction rate.

10.1242/jeb.048462

Wu, G. C., Wright, J. C., Whitaker, D. L. and Ahn, A. N. (2010). Kinematic evidence for superfast locomotory muscle in two species of teneriffiid mites. *J. Exp. Biol.* **213**, 2551-2556.

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