

INSIDE JEB

Paralympic sprinters' prostheses impair curve-running performance



A Paralympic sprinter. Photo credit: Applied Biomechanics Lab.

The debate about Paralympic athletes competing against able-bodied athletes has raged since before Oscar Pistorius took to the track on his Flex-Foot Cheetah prosthetic leg at the London Olympics in 2012. Some biomechanists suggest that prosthetic limbs give Paralympians an unfair advantage, while others argued that prostheses restrict athletes as they power away from the blocks. 'When I saw Paralympians using these devices I said, "I really want to understand how these prostheses function during sprinting"', recalls Paolo Taboga, from the University of Colorado, USA. All of the previous studies had investigated sprinters running straight, however, 200 m and 400 m competitions are run on curves. 'We wanted to see what happens for these athletes with unilateral [one-sided] amputations when they run on a curve', explains Taboga, who teamed up with Rodger Kram and Alena Grabowski to learn more about the effects of prostheses on cornering.

However, instead of testing local recreational runners, the scientists aimed for the top and recruited members of the US and German Paralympic teams. 'It's like in Formula 1 races – you push the limits of cars', smiles Taboga, who wanted the athletes to give their prosthetic limbs the ultimate workout as they sprinted around a flat curve on an indoor track.

The scientists flew athletes with left and right below-the-knee amputations to the

University of Colorado Boulder, where they asked the sprinters to run at top speed around a 17.2 m radius curve in both the clockwise and anti-clockwise directions as they filmed the trials. Taboga admits that running around the clockwise curve was challenging. 'Nobody trains to run in that direction, so it is a bit weird', he says, remembering that everyone eventually got the knack.

However, when the team analysed the sprinters' performances, they were surprised to discover that the athletes that were running with their prosthesis on the inside of the curve were 4% slower than the athletes that were sprinting with the prosthesis on the outside. 'It was a measurable difference', says Taboga, adding that this could add up to two-tenths of a second to a sprint over 200 m. 'That means you could win the race, or get fourth and not even get on the podium', shrugs Taboga.

Admitting that the extent of the impairment was unexpected, Taboga explains that Paralympic sprinters produce less force when running straight, which probably means that the force is also reduced when they go around a bend. In addition, the athletes slowed more as they took the curve with the affected leg on the inside. 'So you have two limiting factors that sum up', he says. And when he broke the news to the athletes, Taboga recalls, 'A lot of athletes with a left leg amputation said, "Oh yes, when I have to run on curves I don't really like running in lane 1 or 2"'.

But what does all this mean for sprinters competing at the next Paralympic Games? Taboga suspects that athletes with a left leg amputation may be slightly disadvantaged, although he adds 'The calibre of the athletes is the main difference'. He suggests, 'To make a fair competition, let the left leg amputees run on the outside, lanes 5–8'. And he is keen to design new prosthetic limbs that handle corners better. 'Then people who don't normally like prostheses will use them more and get more active, improving their quality of life', he hopes.

10.1242/jeb.139600

Taboga, P., Kram, R. and Grabowski, A. M. (2016). Maximum-speed curve-running biomechanics of sprinters with and without unilateral leg amputations. *J. Exp. Biol.* **219**, 851-858.

Kathryn Knight

Famished foragers suffer malnutrition faster than fat workers



Black garden ants (*Lasius niger*) on a cotton bridge. Photo credit: Audrey Dussutour.

Every family has a picky eater, but imagine feeding a family of 20,000, where some siblings eat nothing but pasta and others expect steak. This is the situation faced by forager ants on a daily basis. 'The queen and larvae want protein for growth, but the workers want carbohydrates for energy,' explains Audrey Dussutour from the University of Toulouse, France. This is fine when food is plentiful, but Dussutour and her colleague Stephen Simpson, from the University of Sydney, Australia, wondered how well ant colonies cope when a staple vanishes from the menu and they are threatened with starvation.

'I love collecting ants, it's like digging for treasure', chuckles Dussutour, who remembers returning from the nearby village of Marquefave with 24 colonies of black garden ants (*Lasius niger*), ready to test their resilience when their diets became unbalanced. Dussutour established 64 well-fed mini colonies – with 200 residents each – and then assigned each colony to one of four diets: a high carbohydrate/low protein diet that was perfectly balanced for the ant's nutrition; a poorly balanced diet of low carbohydrate and high protein that would produce malnutrition; a dilute well-balanced diet – the ant equivalent of thin

soup; and a starvation diet. Then she waited to see how well they fared.

However, Dussutour was in for a shock. 'Usually we use foragers to do these studies because they are supposed to be older so they are supposed to die earlier', she says. However, the foragers that were fed the optimal diet lived for almost as long as the inner nest workers, with one surviving an incredible 409 days while the last worker held out for 436 days. And some of the foragers on the well-balanced thin soup diet even survived for 300 days. However, the foragers on the high protein malnutrition diet struggled, only surviving an average of 21 days, and the foragers that were placed on a starvation diet were decimated. 'They lasted a week and a half, but the inner nest workers survived for over 100 days', says Dussutour. So, when their diet took a turn for the worse, the foragers were always the first to die, even though they were the colony's sole supplier of nutrition.

But why did the foragers suffer first? Dussutour was puzzled: 'We wondered if it was because they had different tasks or if it was because they were different ages'. Foragers are usually the oldest ants in the nest and workers are the youngest, so Dussutour used a cunning trick to create youthful foragers and elderly nest workers to test whether age or role was the cause of the forager's demise. Testing the ants' longevity on a starvation diet, Dussutour was amazed to discover that the foragers always died first. 'Even the foragers that were young died earlier than the inner nest workers that were old', she says.

Having ruled out age as the cause of the foragers' deaths, Dussutour wondered whether they were more vulnerable to starvation because they carry less fat than worker ants. She measured the fat content of foragers' and workers' bodies as they switched between roles, and no sooner had a worker switched to become a forager than its body fat content dropped to 15%. Meanwhile, the fat content of foragers that assumed a worker's role rocketed to 30%. 'The colonies that had consumed more carbohydrates were more fat and we were able to show that [for ants] the fatter you are the better it is for your survival,' chuckles Dussutour.

So it seems that lean foragers die first when food is scarce, although Dussutour explains that foragers have to be skinny: 'If they are not starving, they won't be motivated to go out to forage', she laughs.

10.1242/jeb.139576

Dussutour, A., Poissonnier, L.-A., Buhl, C. and Simpson, S. J. (2016). Resistance to nutritional stress in ants: when being fat is advantageous.

J. Exp. Biol. **219**, 824-833.

Kathryn Knight

Bats have leaky intestines like birds to fuel flight



Leptonycteris yerbabuena on Don Panchito Island, Mexico. Photo credit: Romeo Saldaña.

No matter how hard a terrestrial animal pushes itself, its exertions are negligible in comparison with those of a hovering hummingbird. Sustaining metabolic rates (per gram of body mass) that are approximately 10 times those of elite human athletes, hummingbirds directly fuel their flight muscles with sugar from their nectar diet. William Karasov, from the University of Wisconsin-Madison, USA, and Enrique Caviedes-Vidal, from Universidad Nacional de San Luis, Argentina, explain that birds have smaller guts than mammals of the same size, to reduce their cargo costs. However, it also turns out that their intestines are leakier – water-soluble nutrients pass through the junctions between gut cells (in a process known as paracellular absorption) to compensate for the smaller surface area – in addition to using molecules embedded in the intestine surface to transport nutrients into the blood. Could the same hold true for other fliers? 'The only other living vertebrates that actively fly are bats', says Karasov, so would their intestines be as leaky as those of hummingbirds?

Karasov recalls that Nelly Rodriguez-Peña arrived in his lab at just the right time to test the theory. He says, 'She did a wonderful job of identifying a practical, catchable population of bats', adding that Eddy Price taught her how to feed sugar solutions to small animals and then collect the minute blood samples that would be needed to determine how leaky the bats' intestines

were. 'Then she took the method and equipment and set up a makeshift field lab [in Mexico] to do the work', says Karasov.

Having gently trapped nectar-sipping Saussure's long-nosed bats in nets at dusk as they left their cave roost on Don Panchito Island, Rodriguez-Peña then worked through the night. First she fed the animals with a solution made from several sugars, including L-rhamnose (which can only enter the bat's bloodstream by paracellular absorption because there are no protein transporters to carry the sugar across the intestine wall) and D-(+)-cellobiose (a large sugar that also enters the bloodstream by paracellular absorption, but at a slower rate). Then she patiently collected minute blood samples (28 μ l) from the animals over a 2 h period. After releasing the bats, Rodriguez-Peña relocated to Cesar Flores-Ortiz's lab at the Universidad Nacional Autonoma de México with the blood samples to find out how much of each sugar was in the bats' blood.

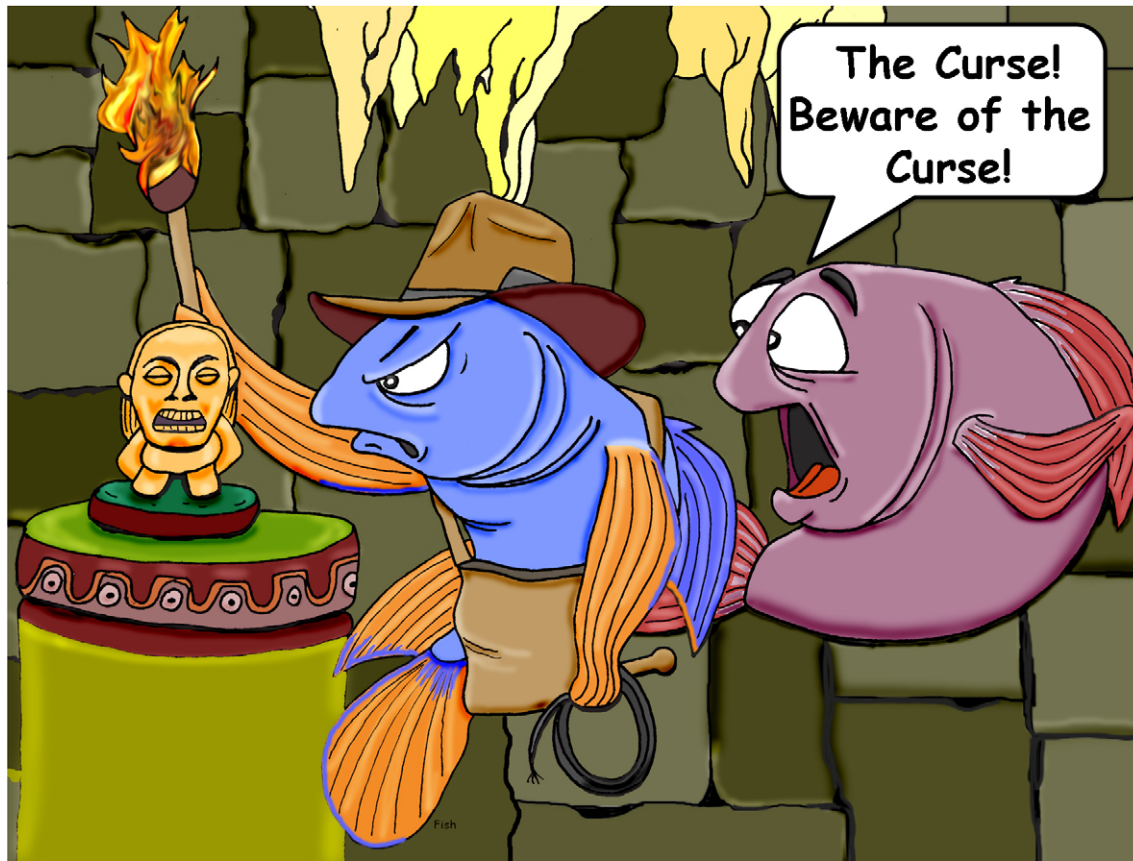
Using high-performance liquid chromatography to analyse the blood samples, Rodriguez-Peña saw the rhamnose levels increased substantially; the intestines were leaky and the animals were using paracellular routes to absorb sugar into the blood. And when she measured the amount of cellobiose in the blood samples, she found that the molecule also crossed the intestine, but at much lower levels. 'It [the junction between adjacent intestine wall cells] is almost like a filter, and if molecules are too big they cannot get through; that is what makes the junction tight against large foreign molecules', explains Karasov. In fact, the junctions were so leaky that almost as much rhamnose appeared in the bats' blood as if it had been injected directly.

So hovering nectar-feeding bats use the same leaky intestine mechanism as hummingbirds to absorb as much sugar as possible into the blood to meet their immense metabolic demands. Karasov says, 'I don't know if this is a phenomenon of small bats and small birds, or all bats and birds, so we need to study some really big bats next'.

10.1242/jeb.139584

Rodriguez-Peña, N., Price, E. R., Caviedes-Vidal, E., Flores-Ortiz C. M. and Karasov, W. H. (2016). Intestinal paracellular absorption is necessary to support the sugar oxidation cascade in nectarivorous bats. *J. Exp. Biol.* **219**, 779-782.

Prozac makes Siamese fighting fish timid



Oliver was too scared to raid the tomb and steal the idol because of the Prozac he had taken

Hailed as a wonder drug since the mid-1980s, fluoxetine – the drug in Prozac – is on the World Health Organisation List of Essential Medicines. Used to treat human psychiatric disorders such as depression and post-traumatic stress disorder, fluoxetine is believed to increase levels of the neurotransmitter serotonin in the synapse between nerves by reducing reabsorption into nerve cells to relieve symptoms. But humans may not be the only animals on the doctor's prescription. Teresa Dzieveczynski and colleagues from the University of New England, USA, explain that the drug is turning up in our river systems, thanks to its resistance to breakdown, and seems to be affecting the behaviour of aquatic residents, reducing aggression and risk-taking, and affecting how often animals feed. But little is known about the longer-term effects of exposure or how the drug may alter behaviour in different settings. As female Siamese fighting fish are known to

be less aggressive and inquisitive after a dose of the drug, Dzieveczynski and her colleagues Brennah Campbell and Jessica Kane decided to find out how male Siamese fighting fish that had not been exposed to the fluoxetine and those that had experienced a week-long low ($0.5 \mu\text{g l}^{-1}$ – similar to the levels found in effluent water) or high dose ($5 \mu\text{g l}^{-1}$ – similar to levels found in body fluids of human patients) of fluoxetine responded to situations that were designed to challenge their courage, and how their reactions changed over time.

Right from the start, it was clear that fish that had not been exposed to fluoxetine were much keener to explore a novel empty tank than the fish that had been swimming in water laced with the anti-depressant, and the fish that had received the highest dose were the most timid. However, the fish that had been exposed to $0.5 \mu\text{g l}^{-1}$ of the drug were bolder on

some occasions than others. And when the team tested the fish's reactions to an unfamiliar tank furnished with intriguing stones and plants, or the presence of a shoal of lady Siamese fighting fish, the two sets of drugged males were equally disinterested in exploring; the strength of the drug did not affect them differently. The team says, 'Perhaps most importantly and alarmingly, the effects of exposure lasted even after fluoxetine was removed', and they warn, 'Even brief periods of exposure could potentially produce chronic effects, especially as boldness is important in migration, aggression and predator evasion'.

10.1242/jeb.139592

Dzieveczynski, T. L., Campbell, B. A. and Kane, J. L. (2016). Dose-dependent fluoxetine effects on boldness in male Siamese fighting fish. *J. Exp. Biol.* **219**, 797-804.

Kathryn Knight
kathryn.knight@biologists.com