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OUTSIDE JEB

Sharks swim side-stroke to save energy

Breaststroke, butterfly, front crawl and back crawl: many of us learnt these swimming styles as kids while splashing around in our local pool. These strokes all involve the swimmer lying on their back or front, much like the way most fish swim. Of course, some people prefer to swim tilted to one side rather than face down even though the side-stroke evokes images of elderly swimmers in bathing caps rather than speed and athletic prowess. However, a new study from a team of international researchers suggests that your grandparents' side-tilted swimming style may have something in common with a rather different type of sea creature: the great hammerhead shark.

Nicholas Payne from the University of Roehampton, UK, Gil Iosilevskii from the Israel Institute of Technology, and colleagues from various international institutions wanted to study the swimming behavior of these large predators in nature. They first fitted triaxial accelerometers, devices used to measure body pitch and roll angles, to the dorsal fins of two great hammerhead sharks, *Sphyrna mokarran*, in Australia and Belize. These devices recorded the body posture of each individual as it swam freely in the wild over the next 18–66 h. The team also attached body cameras to four individuals to get a shark's eye view of the fish's swimming position. Having recorded the fish's swimming styles, the group then tested the efficiency of various swimming postures using a miniature shark model positioned in a wind tunnel to mimic the drag forces acting on real sharks while swimming. By varying the tilt and rotation of the model, they calculated how much drag versus lift was produced in different positions for a given wind speed and estimated the most efficient angle for swimming.

Initially, the team was startled by the accelerometer data. The tagged sharks spent up to 90% of their time swimming at bank angles between 50 and 75 deg; in other words, rolled on their sides rather than upright. Video footage confirmed this side-stroke swimming preference. The researchers even observed videos of sharks swimming in public aquaria in the USA to verify that untagged, unhandled great hammerheads display the same tilted swimming behaviour, which they do. Interestingly, there is a real hydrodynamic advantage to this non-traditional stroke. As sharks are negatively buoyant, most species rely on long pectoral fins to generate lift and keep them from sinking. However, unlike most sharks, the great hammerhead's dorsal fin is significantly longer than its pectoral fins. This means that swimming with its dorsal fin tilted to one side allows the great hammerhead to generate more efficient lift than it would swimming ventrally. Simulations in the wind tunnel also showed that swimming side-stroke reduces drag, and therefore the cost of swimming, by about 10% compared with upright swimming.

Despite great hammerheads being such an iconic and easily recognizable shark, the team's study is the first to formally describe their peculiar tilted swimming behaviour. Whereas speed and agility might be best achieved by more traditional upright swimming, the advantages of the energy-savings provided by the unconventional side-stroke highlight the importance of efficient travel in the evolution of animal locomotion. Even though you may not see many side-strokers at the next Olympics, think about adding some sideways tilt to your swim the next time you're feeling tired in the water.

10.1242/jeb.130377

Payne, N. L., Iosilevskii, G., Barnett, A., Fischer, C., Graham, R. T., Gleiss, A. C. and Watanabe, Y. Y. (2016). Great hammerhead sharks swim on their side to reduce transport costs. *Nat. Commun.* **7**, 12289.

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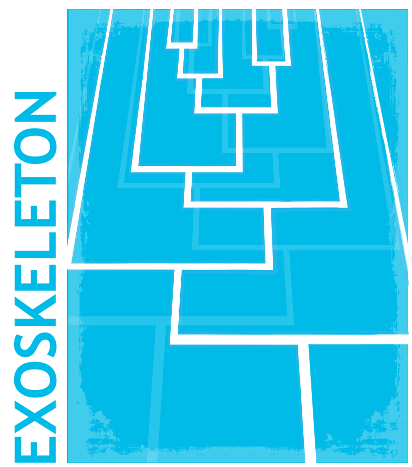
Tread lightly: insect tibias buckle under pressure



Skeletons need to be strong. If you're a terrestrial animal, they need to be strong enough to support the pull of muscles and the impact of steps, leaps and other gravity-defying feats. But being strong often has its drawbacks. Skeletal tissue that is too thick can burden an animal with unnecessary weight and hinder motion, so a fine balance has to be struck. Eoin Parle and his collaborators at Trinity College, Dublin, Ireland, wanted to understand how insect exoskeletons are designed to be strong enough to deal with daily forces they encounter, while being light enough for efficient mobility.

The authors explored this question with three insects: the desert locust (*Schistocerca gregaria*), American

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cockroach (*Periplaneta americana*) and death's head cockroach (*Blaberus discoidalis* – which is more than twice the size of the American cockroach). To understand the structural aspects of each insect exoskeleton, they measured tibia geometry, stiffness and the force required to bend the tibia to the point of breaking (strength). Then they estimated the ecologically relevant stresses encountered by each species by using previously published forces incurred by the tibia during common activities such as walking, running and jumping, as well as those of more strenuous survival activities – usually performed during an emergency – such as pushing through small holes and crevices (wedging) and righting when overturned (both performed by the death's head cockroach), and anti-predator jumping by the locust.

Parle and his collaborators found that tibia strength did not differ across insects, even though they varied in material properties (composition, orientation and amount of each component). One reason for this, the authors state, is that exoskeletons bend before they break, unlike materials such as wood. In a previous study, the authors suggested that the thin-walled tubular legs of insects are similar to many engineered structures in that they are light and strong, but will buckle when their strength is tested.

Not surprisingly, running generated more stress than walking for all three insects, and all emergency maneuvers generated more stress than routine activities. The authors found that of all the emergency maneuvers, jumping in the locust generated the most stress. In addition, wedging through a tight space generated more stress than righting in the cockroach. And although these emergency maneuvers appear to place limbs at perilous risk, Parle and his colleagues state that the insects only take these extreme chances on a small number of occasions.

Interestingly, although the death's head cockroach is larger and heavier than the American cockroach, and had larger and thicker tibia, there was no difference in tibia strength or stiffness between the two. The authors propose that this is because the American cockroach runs more and generates proportionally greater daily forces than its ghoulishly named cousin. So, the similarity in strength and stiffness of the smaller cockroach to the larger compensates for the greater forces it has to endure.

The authors also found that safety factors – essentially the margin of extra protection built into a design or material – were lowest for the emergency maneuvers, particularly for jumping in the locust. This, the authors say, suggests that insects have evolved to have light limbs that allow economic movement, which they trade off by avoiding riskier behaviors that may cause their limbs to buckle.

10.1242/jeb.130385

Parle, E., Larmon, H. and Taylor, D. (2016). Biomechanical factors in the adaptations of insect tibia cuticle. *PLoS ONE* **11**, e0159262.

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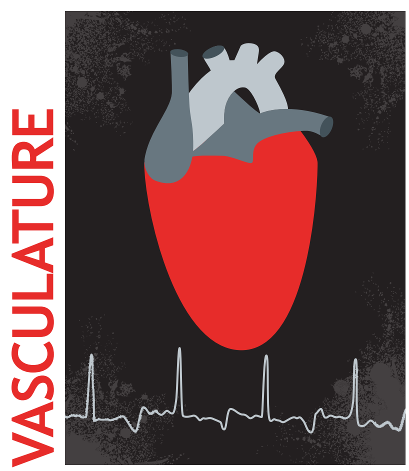
The shark heart crowned



The heart works tirelessly to pump blood around the body. But, ironically, heart muscle itself is one of the tissues most reliant on an uninterrupted oxygen supply. Conventionally, there are two routes via which oxygen may reach the heart: a dedicated coronary supply or the residual oxygen in returning venous blood. In mammals such as us, the coronary arteries – regally named because of their resemblance to a crown enveloping the heart – supply the vast majority of oxygen to the heart. They immediately branch off the aorta, carrying fully oxygenated blood, and penetrate throughout the heart muscle. Their importance is revealed by the devastation that ensues if one of these channels becomes blocked, resulting in a heart attack. Yet, most bony fishes do not have a dedicated coronary supply. In those that do, the crown more closely resembles a delicate tiara and only supplies blood to the superficial compact layer of the heart. The majority of the heart is spongy and scavenges the leftover oxygen from venous blood returning after circulating around the body.

Whilst the hearts of bony fishes have been well characterised, much less is known about cartilaginous fishes, such as sharks, which are even more distantly related to mammals. However, gross morphological studies, spanning over a century, suggested that their coronary vessels are more extensive than those of bony fishes and enter the spongy myocardium. To provide the first quantification of coronary vasculature in sharks, Georgina Cox and her colleagues at the University of British Columbia meticulously compared vascularisation of the heart in a shark, the Pacific spiny dogfish, with that of a representative bony fish, the rainbow trout.

Under the microscope, Cox and her colleagues saw what they expected in trout hearts; the atrium and spongy myocardium were devoid of coronary vessels, which only decorated the peripheral compact layer. In the dogfish, however, the coronary arteries uniformly permeated the entire heart, including the atrium and spongy core of the ventricle. Also, the vessels in the trout heart were slightly narrower than those in the dogfish, which is probably because they have smaller red blood cells.

The team further investigated the vessel density in the trout compact layer and found that it was about twice that in the dogfish heart. They believe that this is a sign of the much higher heart rate, and therefore oxygen demand, in trout and suggest that it may be interesting for future studies to compare other sharks and bony fishes with varying heart rates to verify the hypothesis. Nonetheless, it was clear that the coronary arteries in the dogfish heart, whilst less dense, are more far reaching and play a more general role in oxygenating the entirety of the heart.

Because the hearts of bony fishes are so reliant on oxygen in venous blood, but

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mammals and birds have extensive coronary networks, it has been tempting to speculate that coronary arteries only rose to prominence relatively recently, possibly during the evolution of endothermy. However, by detailing the important crown of vessels in the dogfish heart, Cox and her colleagues suggest that an expansive coronary circulation is likely to have evolved earlier in some of the more ancient vertebrates.

10.1242/jeb.130393

Cox, G. K., Kennedy, G. E. and Farrell, A. P. (2016). Morphological arrangement of the coronary vasculature in a shark (*Squalus suckleyi*) and a teleost (*Oncorhynchus mykiss*). *J. Morphol.* **277**, 896-905.

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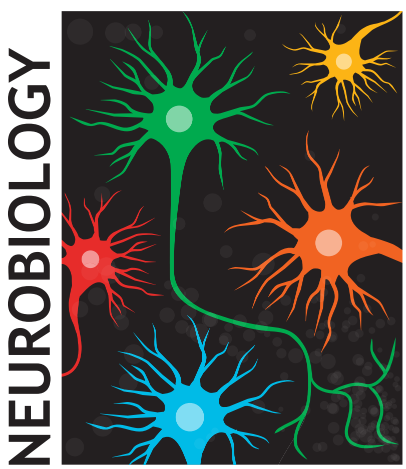
Brain wiring explains sex differences in *Drosophila* behaviour



Males and females sometimes look and behave so differently that they could be mistaken for different species. Males often display vibrant pigmentation and striking ornaments to court inconspicuous females, who accept or reject male advances. How did such differences evolve? After all, the sexes share a genome and so selection must shape this diversity from shared genes. Carolina Rezával and colleagues at the University of Oxford wanted to understand what differences in male and female brains control these sex differences in behaviour. To answer this question, the team studied the courtship display in *Drosophila melanogaster* fruit flies, where males (but not females) sing and dance to court potential mates.

The team knew that in *D. melanogaster*, reproductive behaviour is controlled by *doublesex* neurons. But it was unclear whether sex-differences in these neurons explain why males court and females do not. To find out, Rezával and colleagues artificially activated *doublesex* neurons in the brains of female *Drosophila* and found that this caused the females to act like courting males, following, tapping and serenading other flies. This result shows that female brains have latent neurons that, when activated, trigger male-like behaviours.

If females have circuity that allows them to act like males, why don't we see male-like behaviours in females more often? The team found two clues that may hint at the answer. First, when the team turned on different bundles of neurons in turn using a temperature-dependent molecular switch, they found that activating just one neuron cluster (called pC1) caused females to act like males.

Second, females with activated *doublesex* neurons did not perform courtship displays when housed alone, while males with activated neurons sang and danced even without an audience. This suggests that females require additional stimuli to begin courting. By systematically blocking different senses in females paired with male flies, the team found that females only failed to court when their antennae were removed and so they had no sense of smell. By exposing flies to different compounds, the team showed that females only begin courting once they get a whiff of pheromones.

Taken together, these data suggest that differences in the pC1 node may explain why females do not court, even though they can. Males and females have different numbers of both PC1 neurons and projections from these neurons. Perhaps there are too few pC1 neurons to trigger male-specific courtship behaviours in females. Or perhaps these neurons are less excitable or less well connected and so receive less excitation (or more inhibition) than in males, so females only begin acting like males when their pC1 neurons are activated outside of their normal range.

Sex differences in behaviour have been attributed to neurons that are unique to each sex. However, these results show that females actually have neurons capable of triggering male-specific behaviour and that, instead, differences in how each sex uses shared circuitry can explain why males woo females and females choose amongst them.

10.1242/jeb.130369

Rezával, C., Pattnaik, S., Pavlou, H. J., Nojima, T., Brüggemeier, B., D'Souza, L. A. D., Dweck, H. K. M. and Goodwin, S. F. (2016). Activation of latent courtship circuitry in the brain of *Drosophila* females induces male-like behaviors. *Current Biol.* **26**, 2508-2515.

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