

Inside JEB, formerly known as 'In this issue', is a twice monthly feature, which highlights the key developments in the *Journal of Experimental Biology*. Written by science journalists, the short reports give the inside view of the science in JEB.

# Inside JEB

## CRABS KEEP TABS WITH MENTAL MAP



Once you've had a tangle with the housing market, it's easy to understand why fiddler crabs are so determined to defend their real estate. Watching the tiny creatures rush home when an intruder threatens left Jochen Zeil and Jan Hemmi in no doubt that the crustacean's home is its castle. But how the crab saw the impending threat, and quickly decided on a course of action, wasn't clear. Travelling to the crab's home beaches in Queensland, Australia, Hemmi set up a bird's eye vigil, watching the crab's responses as a dummy crab threatened. But thinking from the defending crabs perspective, Hemmi couldn't find a defence triggering pattern in the dummy's movements, until he switched to a different point of view; the burrow's. No matter where the defender was relative to its home, as soon as an intruder came too close to the entrance the owner came scuttling home, even if the burrow was out of sight!

'Fiddler crabs are fantastic animals' says Hemmi; 'with a small camera above you see everything they do in a day out'. Snatching the brief periods between high tides, Hemmi rigged up a system of strings and pulleys to tow a crab dummy past a burrow's entrance as he filmed the home owner's reaction to the threat. The crabs were convinced enough to retreat to their burrows every time the dummy rolled past; some even abandon their homes after a prolonged series of dummy threats. But once Hemmi had gathered over 40 hours of defensive film footage, the real work started; looking for a pattern to the animal's behaviour.

At first Hemmi made little headway. He tried constructing spatial histograms of the dummy crab's movements, without success. But the break came when he thought of switching reference frames. Instead of thinking from the camera's view, he began thinking of the dummy's trajectory from the perspective of the crab and burrow. By drawing a vector between the crab and its

burrow, and superimposing many dummy paths on the calculated vector, Hemmi realised that the crabs weren't reacting to their attacker's proximity; it was the attacker's distance from the burrow that triggered a defensive run home (p. 3935)! Once the attacker came close to the burrow, the defender came running. And Hemmi and Zeil were amazed that the homeowners reacted even when their burrows were out of sight! Somehow they were working out the distance between the attacker and the burrow, but how? The tiny crabs were either calculating the distance from first principles, or they'd figured out another way to judge the aggressor's approach.

Hemmi quickly ruled out the arithmetic alternative. If the crabs were calculating the distance between the intruder and burrow, they'd need to know their distance to both objects, before they could complete the triangle and measure the intruders proximity to the burrow. Hemmi realised that the crabs would also have to measure an angle as well as being quadric equation solving geniuses; too tall an order for a 2 cm long crab.

But Hemmi and Zeil knew enough about the crab's simple visual system to plot a view of the world from a crab's eye height. They plotted how the beachscape looked when the crab was 10, 20 and 30 cm from the burrow (p. 3951). They realised that if the crab was to defend its burrow, it need only know its distance from home, call up the map that represented its view, and see where the intruder's position lay on the map. If the intruder was in the map's safe zone, the crab could rest easy, but as soon as the intruder stepped too close and into a danger zone, the threatened burrow owner could leap into action and protect its patch.

Hemmi says 'this is a wonderful example of an animal dealing with complexity in its environment... to achieve a task'. He explains that the crabs always keep a tally of their distance from the burrow, so the only extra information that they need to solve the mind boggling 3D problem is a set of neurons with preprogrammed maps to solve their home defence problem.

10.1242/jeb.00667

**Hemmi, J. M. and Zeil, J.** (2003). Burrow surveillance in fiddler crabs. I. Description of behaviour. *J. Exp. Biol.* **206**, 3935-3950.

**Hemmi, J. M. and Zeil, J.** (2003). Burrow surveillance in fiddler crabs. II. The sensory cues. *J. Exp. Biol.* **206**, 3951-3961.

## MALE HOUSEFLIES CLEARLY SEE BETTER



When a male housefly sets his sights on a female, there's a lot at stake. In a high-speed chase, he's got to get his gal, or loose his chance of genetic immortality. The stakes are high enough for male flies to have developed a specialised eye structure, the 'lovespot', that is adapted to improve his chances of capturing a dodging and weaving female. But what is it about the male's eye that gives him the tactical edge? Brian Burton and Simon Laughlin started playing female fly escape sequences to photoreceptors in the male's lovespot to find out what was special about the insects ommatidia, and discovered that while the male has better optics and neural responses, he also has the ability to de-blur his vision as the female flashes past; he simply sees more clearly (p. 3963)!

A male fly's visual perception isn't bad. With his acute photoreceptors, the male can register small targets moving at the high angular speeds that an escaping female reaches. Burton explains that while a lot was already known about the male fly's high-speed tactics to trap a mate, no one had ever recorded the remarkable visual system's response to a fleeing female. Laughlin and Burton knew that if they could simulate the visual input at the male's eye, they could record the resulting neural responses at individual photoreceptors, and reconstruct the neural image on the retina to get the male's perspective.

Laughlin explains that at the photoreceptor level, a passing female is simply a succession of dimming events, as her image moves across the retina. By programming an LED to dim and glow in the same way as the passing image, and shining it on individual photoreceptors, Burton was able to record the neural signals that the LED triggered. Laughlin explains that they played 54 different pursuit trials, ranging from a female that was practically stationary at close range, up to a long distance high speed encounter;  $10,000^{\circ}\text{s}^{-1}$ , 76 cm away! Burton also tested the female's neural responses to the same suite of aeronautical encounters, to see how

well her eyes fared compared with the males.

At 40 cm, female eyes could hardly see the moving target even when it was practically stationary. But the males had no problems with their long distance vision at any speed. Laughlin explains that the male's visual responses were much stronger because their neurons had a much larger gain than the females'. The neural signals had a higher amplitude and a shorter sharper duration. As well as having superior neural responses, the male's optics are better too, as the lovespot's ommatidia have larger, higher quality lenses than the female's eyes.

But Burton and Laughlin were really amazed when they reconstructed the neural signals in the male fly's eye; the retina was de-blurring the image! Laughlin admits that this was completely unexpected and he was 'knocked out' when he saw the male's sharp view. Using a combination of high gain and rapid damping of the signal, the male's photoreceptor's response lags the visual image on the eye by only 7.8 ms! Which explains why there's no escape once she's in the lovespot's focus.

10.1242/jeb.00629

**Burton, B. G. and Laughlin, S. B.** (2003). Neural images of pursuit targets in the photoreceptor arrays of male and female houseflies *Musca domestica*. *J. Exp. Biol.* **206**, 3963-3977.

## EGG COUNTING SNAILS

Laying eggs is hard work, and risky with the next generation's future invested in a single clutch. So snails only ovulate when the time and place is right. But how land snails control this costly process wasn't clear until Ronald Chase began investigating a branch of the intestinal nerve that runs close to the mollusc's ovotestis. Working with Tomasz Antkowiak, he discovered that the nerve effectively counts the number of ripe eggs a snail is carrying, triggering the snail's egg laying preparations when the clutch is large enough to warrant the investment (p. 3913).

Chase explains that the snail's tiny nerve was first discovered shortly after the turn of the 20th century, but no one had clearly pinned its function down. Almost a century later, Chase noticed that the nerve passed close to the mollusc's gonad, in fact it looked as if it might innervate the snail's seminal vesicle. But on closer inspection, he realised that the nerve innervated the mollusc's ovotestis. Knowing that most

mammalian ovaries are innervated, Chase decided to test whether the nerve might play a sensory role or trigger some of the physical activities needed as the snail produces its eggs, but first he needed a steady supply of snails. Fortunately several volunteers from California were perfectly happy to rid themselves of the gardener's scourge, keeping Chase well supplied with the voracious molluscs.

Testing the nerve's sensory capacity, Antkowiak gently prodded a snail's ovotestis, to see whether the intestinal nerve detected the disturbance and produced a signal. Chase remembers that the work was very fiddly, as the nerve is only  $20\mu\text{m}$  wide, and covered in tissue that Antkowiak had to gently remove before making his nerve recordings. Antkowiak's patience was rewarded; the nerve began sending signals as he gently prodded the ovotestis.

But how did the nerve respond as eggs matured and the ovotestis swelled? First Antkowiak recorded the neural activity in the nerve and then counted the number of mature eggs in the snail's gonad. As the number of eggs increased, the nerve's response grew stronger. And when Antkowiak simulated oocyte maturation by gently expanding the gonad with minuscule injections, the nerve's sensory signals increased again. The nerve was 'counting' the number of ripe oocytes that the snail was carrying.

Pleased that the nerve was effectively counting, Chase wondered whether it also triggered the snail's preparations to produce a clutch? Suspecting that the snail's heart rate rises to maintain its hydrostatic pressure during oviposition, Antkowiak tested whether signals sent by the ovotestis' branch of the intestinal nerve might affect the heart rate regulating pericardial nerve. Electrically stimulating the ovotestis branch, he recorded the pericardial nerve's activity and found an immediate and dramatic increase. 'The ovotestis influences the heart rate' says Chase, which is an essential behaviour for snail egg laying.

Chase explains that although other molluscs regulate their egg laying behaviour with hormonal signals, this is the first time that a single nerve has been found to be responsible for sensing the state of the snail's ovotestis, as well as triggering some egg laying reflexes.

10.1242/jeb.00668

**Antkowiak, T. and Chase, R.** (2003). Sensory innervation of the ovotestis in the snail *Helix aspersa*. *J. Exp. Biol.* **206**, 3913-3921.

## ANCIENT ALTERNATIVE FOR ADHESION



It's one of the oldest scenes in the 'Horror' repertoire; a spider's web brushing a passing face! But spiders and their webs have been around longer than humans have been afraid of them. Today, most spiders' webs are coated in a sticky glue to ensnare flies and other victims. But a few ancient species stuck to an older, drier alternative. They produce cribellar threads; thousands of minute filaments coating a supporting thread that snag insects by their setae, like Velcro hoops over loops. Remarkably, the silk also sticks to glass and metal sheer surfaces through van der Waals molecular forces. But not all dry webbed spiders produce the same types of microscopic fibril. Some species produce lumpy fibrils, while the most ancient member of the cribellar family, the rare Hypochilidae, produce smooth fibrils. Intrigued by the

differences between both types of silk, Brent Opell and his student Anya Hawthorn noticed that the lumpy fibre's adhesive properties improved under damp conditions, while the smooth fibres didn't. Wondering whether the knobbly fibres picked up water and adhered through hygroscopic forces, the team modelled the fibre's adhesive qualities under dry and damp conditions (p. 3905).

First they needed fresh spider silk, but *Hypochilus* refused to spin its smooth fibred webs in the lab, even though Hawthorn and Opell built them cosy cliffs to make their homes on. So the team headed south to the spider's home in North Carolina to gather the unusual silk. Fortunately, *Hyptiotes* was more cooperative, contented to construct their knobbly silk webs in plastics boxes in the lab.

With a steady supply of web silk, the team began measuring both fibres' stickiness as the humidity rose. Although the 'sticky-o-meter' was straightforward to use in the field, operating it inside a humidity-controlled chamber was tedious, but Hawthorn persevered. As the humidity rose, the knobbly silk became stickier, while *Hypochilus*' remained the same.

But was the increased stickiness due to humidity, or some other physical property?

Hawthorn and Opell modelled the effects of van der Waals and hygroscopic forces on the smooth and lumpy silks. After measuring the area of both fibres that peeled away from the sticky-o-meter's plate, and calculating the resulting van der Waals and hygroscopic forces, the team realised that the increased humidity was giving *Hyptiotes* the sticky edge.

Which probably gives *Hyptiotes* the mechanical edge too. When the conditions are right, their silk becomes stickier by freeloading on the moist fibre's hygroscopic attachment. But if *Hypochilus* want to increase their threads' stickability, they have to coat their threads with more smooth fibrils, at a significant metabolic cost. Which probably explains why most dry webbed spiders have upgraded to hygroscopic knobbly fibres as a low-cost alternative adhesive, leaving the Hypochilidae as the sole surviving link to the spiders' silky past.

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Hawthorn, A. C. and Opell, B. D. (2003). van der Waals and hygroscopic forces of adhesion generated by spider capture threads. *J. Exp. Biol.* **206**, 3905-3911.

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