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BEE VISUAL PROCESSING MORE COMPLEX THAN THOUGHT

A. G. Dyer
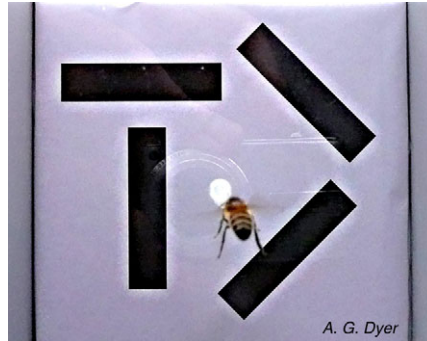
Bees live in a fantastically complex visual world, visiting luscious flowers and navigating through meadows and woods. But it wasn't clear how bees process complex images from their cluttered visual environment. Adrian Dyer, from RMIT University, Australia, explains that there were two competing theories of how bees process visual images.

In the first, the bees simply learn the shape of an image, such as a flower, on the retina and then recognise it by matching their current view with the image that they learned previously. However, the second theory suggested that bees' brains are capable of more complex visual processing: that they might be able to learn the relative configuration of features in an image so that they can still recognise the object even when approaching from different angles. With evidence stacking up for both theories, Dyer wondered whether the bees might actually use both tactics. Intrigued, he developed two different training procedures to find out which mechanism they use and when (p. 397).

First, Dyer painstakingly taught individual foraging bees to visit a specially designed Y-shaped maze where the bee could choose to visit one of two images. Then, he trained them to see if they could learn a memory of a simple image by rewarding them with sucrose solution when they visited a target four-block image and punishing them with a bitter taste of quinine when they visited a second four-block image (the distractor) that he did not want them to learn. Finally, he removed the sucrose and quinine and tested whether the bees would keep returning to the first block image. They did, and when he tried to confuse them by placing the image on a tree background, they still recognised it.

But the real test was to see whether the bees would recognise the four-block image when it was enlarged. If they did not, then they must be using the image matching

visual processing mechanism. Scaling up the image, Dyer realised that the bees no longer recognised it. The bees were using the retina image mechanism because of the simple training regime. But which mechanism would the bees use after more complex training?

To test this, he showed the bees a series of four-block images that all shared the same overall layout but varied subtly. Using the same training procedure – where visits to the target images in the maze were rewarded with sucrose, while visits to the distractor were punished with a dose of quinine – Dyer tested whether the bees could learn the shape of an image based on the configuration of key features by showing them an enlarged version of the four-block image.

This time, the bees passed the enlarged image test; they had no problem picking the correct image. They were using the more sophisticated configuration mechanism to recognise the image.

So the bees were using both mechanisms to recognise images depending on how they had been trained and Dyer adds that this makes perfect ecological sense. 'A bee lives in a tree of a certain shape. As it is flying it sees the tree from a variety of different distances and then it is valuable to use the configural mechanism. But if it is foraging from flowers and always views the same flowers from 5 cm, then maybe it just wants to use a retinotopic match because it is much faster and easier to learn', he says.

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Dyer, A. G. and Griffiths, D. W. (2012). Seeing near and seeing far; behavioural evidence for dual mechanisms of pattern vision in the honeybee (*Apis mellifera*). *J. Exp. Biol.* **215**, 397-404.

Kathryn Knight

TEMPERATURE GRADIENT PRODUCES TWO-STROKE MUSCLE

Warm-blooded mammals don't realise how easy life is. Before any cold-blooded creature can get going, they either have to sit in the sun or shiver to generate heat. Nicole George, from the University of Washington, USA, explains that *Manduca sexta* moths have to warm their muscles to about 32°C before take off, and regularly run their flight muscles at a sizzling 40°C. But when George's thesis advisor, Tom Daniel, and Michael Tu inserted a thermocouple in the insect's main flight muscle (the dorsolongitudinal muscle) during flight, they were amazed to see that the temperature in the muscle was not uniform. There was a gradient running from

the warmest tissue on the ventral side to the coolest on the dorsal. But how would this temperature gradient affect the muscle's function? Knowing that temperature can dramatically affect the power output of a muscle, George and Daniel decided to find out how the temperature gradient affects the muscle (p. 471).

'We used the work-loop method to replicate *in vivo* muscle contraction', says George. Leaving the insect's thorax intact and attaching a motor to the muscle to simulate its natural 25 Hz contraction cycle, George electrically stimulated the muscle and measured the force that it exerted over the course of each contraction. By plotting the force generated by the muscle against muscle length – as it varied over a contraction cycle – and calculating the area under the curve, George could calculate the amount of power generated by the muscle.

Admitting that the measurements were fiddly, George says, 'It took three repeats to do this. The setup changed dramatically from a very homemade setup to a second round using bought equipment and then we found out that extra muscles were being stimulated so I had to do another round where I removed the extra muscles.' However, after perfecting her technique with the help of Simon Sponberg, George was able to measure the power produced by the muscle at temperatures ranging from 25°C up to 40°C.

At the highest temperatures, the muscle produced high power output in the region of 100 W kg^{-1}. However, as the temperature decreased, so too did the power output, until at 30°C, the power output became negative. 'The muscle's negative power output doesn't make sense, it doesn't help the moth to fly, it doesn't achieve lift so it really suggested that the cooler regions that produced zero or negative power output are functioning differently', says George. She adds, 'Negative power output is reflective of muscles that act as a break, so it may be a damping element that stabilises the oscillation of the thorax.'

George also repeated the experiments stimulating just the dorsal and ventral sections of the muscle. She found that the power output again switched from positive values at higher temperatures to negative at the lower temperatures, and suggests a possible alternative function for the cooler dorsal portion of the muscle. 'Our theory suggests that since the cool muscle is contracting a lot slower, then myosin cross-bridges will remain deformed and bound to the thin filament, which will mean they can store energy in their deformation and they

can release that in the next part of the cycle.'

So the *Manduca* dorsolongitudinal muscle could function as a two-stroke engine. The team suggests that the warm ventral portion of the muscle pulls the wing down during the first half of the contraction cycle to power flight directly, while the cooler dorsal segment of the muscle releases stored energy during the relaxation half of the cycle to help raise the wings ready for the start of the next wing beat.

10.1242/jeb.069518

George, N. T., Sponberg, S. and Daniel, T. L. (2012). Temperature gradients drive mechanical energy gradients in the flight muscle of *Manduca sexta. J. Exp. Biol.* **215**, 471-479.

Kathryn Knight

HOW LIZARDS TAKE OFF FROM A STANDING START

Lance McBrayer

If you've ever tried to catch a lizard you'll know they move like greased lightening. More like the Usain Bolt of the animal world than Haile Gebrselassie, they swiftly dodge predators and pounce on prey. Eric McElroy, from the College of Charleston, USA, explains that he is intrigued by how muscles power movement and says, 'Most of the thoughts on how lizards move are based on studies of steady speed movement, but what we realised was that burst activity is another aspect of the animal's behaviour. The first step to understanding what their muscles are doing during that burst is to understand the kinematics of them moving.' Teaming up with undergraduate Kristen Archambeau, McElroy began filming lizards in 3-D as they took off from a standing start to begin to understand how they power fast take-offs (p. 442).

Having built a 3 m long racetrack, McElroy was ready to start filming *Sceloporous woodi* lizards when Lance McBrayer delivered 10 of the animals from Florida. Painting white markers on the lizards' hindlimb joints, McElroy carefully covered each animal with a bag to transfer it to the racetrack before gently removing the bag and spooking the animal with a loud clap. Filming the first three strides of each frantic dash at 300 frames s^{-1} from the side and above, McElroy and Archambeau then

painstakingly reconstructed the three-dimensional course of each limb joint to find out how the lizards sprang into action.

Analysing the animals' stride patterns, McElroy and McBrayer realised that instead of pushing off with one foot, the lizards started about half of their escape dashes by pushing off with two. 'Kinematically that first step looks like a jump', says McElroy. And as they analysed the lizards' movements further, they realised that each stride was very different. 'One of the key differences is that the hip, the knee and the ankle seem to really change what they are doing across all three strides. For example, the knee and ankle sweep through huge angles during the first stride and then by the third stride they seem to stiffen and not sweep through very large angles', McElroy recalls.

The animals' accelerations also varied dramatically from stride to stride, peaking during the first stride and falling to almost zero by the third stride. 'The first stride is pure acceleration', says McElroy, and adds that the animals are likely approaching their top speed by the time they hit the fourth and fifth strides and they generate the most power during the first and second strides.

However, when the team searched for correlations between particular aspects of the lizards' movements and their acceleration patterns, they found few. 'We were surprised that the kinematics that we recorded were in general poor predictors of acceleration performance. Our working hypothesis entering this study was that the angular kinematics at the joint should predict acceleration because it is the angular kinematics that presumably reflect what a muscle is doing, and yet the joint kinematics that we recorded had relatively poor predictive power.'

Having measured the fleeing animals' movements as they powered off from a standing start, McElroy is keen to build a computational model of the lizards and their movements. Ultimately, he hopes to use this model to calculate the forces pulling the joints and to understand how muscles in animals with radically different musculature function to move their limbs in similar ways.

10.1242/jeb.069526

McElroy, E. J., Archambeau, K. L. and McBrayer, L. D. (2012). The correlation between locomotor performance and hindlimb kinematics during burst locomotion in the Florida scrub lizard, *Sceloporus woodi. J. Exp. Biol.* **215**, 442-453.

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