

INSIDE JEB

Termite mound lungs driven by solar power



A *Macrotermes michaelseni* termite mound. Photo credit: Samuel Ocko.

At first glance, a towering termite mound might look like a bustling insect skyscraper, but the insect megalopolis that is home to hundreds of thousands of termites is buried in the ground beneath. For decades, termite mounds had been thought to regulate the climate of their colony; however, Scott Turner, from the State University of New York (SUNY), Syracuse, USA, had suggested that they worked like a lung driven by the wind. Inspired by this, Hunter King, from Harvard University, USA, Samuel Ocko, from the Massachusetts Institute of Technology, USA, and L. Mahadevan, also from Harvard, set out to investigate the airflows through *Odontotermes obesus* termite mounds in India, and discovered that the structure built by this species does function like a lung. However, the flow of air through the mound is driven by the sun moving across the surface of the mound, generating temperature gradients that drive air currents inside the structure, which, in turn, allow gases to move across the mound walls, removing carbon dioxide from the air and bringing in oxygen. Could termites that live in other environments benefit from a similar ventilation mechanism?

Together with collaborators Turner, Paul Bardunias (SUNY), Rupert Soar (Nottingham Trent University, UK) and David Andreen (Lund University, Sweden), Mahadevan, King and Ocko travelled to Otjiwarongo, Namibia, to measure the temperature gradients through *Macrotermes michaelseni* termite mounds and the air currents flowing through them. Ocko recalls that it did not

take the soldier and worker termites long to attack the newly installed airflow sensors, smothering the probes with wet soil. ‘The field work turned into a real hit-and-run game against the termite colonies’, he laughs. In addition to visiting ~30 mounds to collect over 120 internal airflow measurements at different times of day, while also measuring the external wind speed and direction, the team implanted iButton temperature loggers around the circumference of one mound to build an understanding of how the thermal gradients within the structure varied through the day.

Reconstructing the airflows through the Namibian mounds, the team realised that the circulation reversed twice a day, with air in the core rising to the top of the mound before descending through the flank channels during the night, with the flow switching in the opposite direction sometime before mid-day. And when they analysed the temperature gradients throughout the mound, they realised that the warm zone on the surface that was heated by the sun moved over the mound from dawn to dusk, generating shifting temperature gradients to drive the air currents. Instead of being driven by external breezes, the currents in the *M. michaelseni* mounds are solar powered, just like the Indian termite mounds.

The team also measured the carbon dioxide levels at two heights in one of the mounds and in the nest below, and found that the carbon dioxide concentrations within the nest and the mound remained consistently high at 5%, which was different from the Indian mounds, where the gas concentrations ebbed and flowed. ‘If the bulk flow slowed down, as one might expect at some points in the day, the nest would then stagnate and we’d see an elevated carbon dioxide level relative to the mound’, says King. And when the team measured the porosity of the mound walls, the structure was leaky enough to keep the nest well ventilated.

‘Termite mounds are like an inverted lung’, says King, who hopes that we can learn from the termites’ abilities to harness the

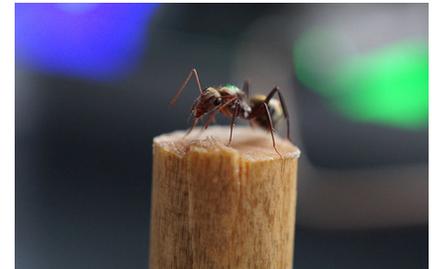
power of the sun to keep their nests well ventilated. He says, ‘This passive termite solution will hopefully inspire human engineering and architecture, especially in coming up with less energy-costly replacements for conventional heating, ventilation and air-conditioning systems’.

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Ocko, S. A., King, H., Andreen, D., Bardunias, P., Turner, J. S., Soar, R. and Mahadevan, L. (2017). Solar-powered ventilation of African termite mounds. *J. Exp. Biol.* **220**, 3260-3269.

Kathryn Knight

Ants prefer UV shades



An ant that has been selected for training. Photo credit: Adrian G. Dyer and Ayse Yilmaz.

Ants are remarkably busy creatures, ranging from navigators that scamper across vast desert pans to aphid-farming garden ants and wood-infesting species, yet little is known about their use of colour vision as they rush around. Although several species have eyes that are equipped with light-sensitive cells that are tuned to ultraviolet, green and even blue shades, Ayse Yilmaz, from the University of Würzburg, Germany, says, ‘No attempt, so far, has been made to analyse how ants form memories of colour’. Knowing that several *Camponatus* species (popularly known as carpenter ants) have a well-developed memory for odours, Yilmaz and colleagues Adrian Dyer, Wolfgang Rössler and Johannes Spaethe decided to investigate whether *Camponotus blandus* have a favourite colour and how long they can recall memories of colours that they associate with a tasty treat.

Having selected *C. blandus* – because of their relatively large eyes and day-active

lifestyle – from the University of Würzburg’s current collection of 15 ant species, Yilmaz identified keen foragers that were prepared to scale a vertical stick in the centre of their foraging arena in search of food to ensure that they were motivated to participate in her experiments. Then she offered these individuals a choice between two colours (combinations of UV, blue and green) and found that the ants had a strong preference for UV shades.

However, this fondness presented problems when the team was trying to figure out whether the insects could genuinely distinguish between UV and the other two colours, or were simply selecting their favourite colour. Yilmaz offered the ants a choice between two of the colours and rewarded them with a sugary treat until they reliably identified one of the two shades. They quickly learned to distinguish UV from the two other colours, even when the brightness was turned down. However, the insects were never able to distinguish blue from green. And when Adrian Dyer, from RMIT University, Australia, built computer simulations of how the ants might respond to different colours if they were equipped with one, two or three photoreceptors tuned to various wavelengths, it was clear that the simulation of two photoreceptors (tuned to 360 nm for UV and 390–560 nm for blue/green wavelengths) reproduced the ants’ abilities to distinguish UV from blue and green hues.

But how long would the ants hold on to their colourful memories? This time, Yilmaz took advantage of the ants’ UV preferences and trained them to recognise blue or green in favour of UV before checking their memories between an hour and as much as 7 days later. Impressively, the ants were still able to select the colour that they had been trained to recognize 7 days later and were equally capable after 1 h, 12 h, 1 day and 3 days, suggesting that the ants are capable of storing the recollection in their medium- and long-term memories.

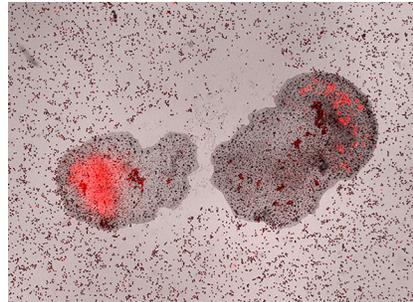
‘Our results show that ants can use chromatic information in a way that should promote efficient foraging in complex natural environments’, says Yilmaz, who is now keen to learn more about the molecular and neuronal basis of long-term visual memory.

10.1242/jeb.168112

Yilmaz, A., Dyer, A. G., Rössler, W. and Spaethe, J. (2017). Innate colour preference, individual learning and memory retention in the ant *Camponotus blandus*. *J. Exp. Biol.* **220**, 3315–3326.

Kathryn Knight

Trichoplax neuropeptide controls movement without nerves



Two paused *Trichoplax adhaerens* feeding on a bed of microalgae (dark particles). Photo credit: Carolyn Smith.

Gliding on microscopic beating hairs as it grazes upon microalgae coating surfaces in warm oceans, tiny *Trichoplax adhaerens* is one of the most ancient and simplest animals on the planet. Lacking a brain, gut and nervous system, the 1 mm diameter flat creatures are composed of only six different cell types that perform a variety of roles, including sensing their surroundings, digestion and movement. Without nerves to coordinate their actions, it was unclear how the small animals organise their basic grazing lifestyle and cease moving when they encounter food. Another ancient family of animals, jellyfish, release short protein-like molecules – called neuropeptides, which can trigger nerve signals – from sensory cells to control their actions, so Carolyn Smith, from the National Institutes of Health, USA, and her colleagues Adriano Senatore and Thomas Reese began investigating whether *Trichoplax* also produce neuropeptide-like molecules to control their movements without the benefit of a nervous system.

As many of these neuropeptide-like molecules are produced as inactive precursors, which are then activated by trimming, Smith and her team selected a range of off-the-shelf neuropeptides that are similar to neuropeptide precursors that had previously been identified in the *Trichoplax* genome, including two

versions of the activated mammalian neuropeptide, endomorphin. After being injected into the animals’ water, both of the mammalian endomorphin neuropeptides caused the microscopic hairs that propel the flat creatures along to cease moving, and the animals paused. But could the trio find evidence of genes that are similar to the endomorphin neuropeptide in *Trichoplax*?

A search of the animal’s gene database turned up a gene that could produce an inactive endomorphin-like neuropeptide molecule, and when the team produced an artificial version of the neuropeptide and injected minute quantities of it into the water immediately surrounding *Trichoplax* individuals, the animals paused within 30 s: the synthetic endomorphin-like neuropeptide seems to control the animal’s ability to pause when feeding. Also, when the team filmed clusters of grazing *Trichoplax*, they noticed that as soon as one animal paused, other animals in close proximity did so too. The team then used fluorescent antibody tags to reveal that the endomorphin-like neuropeptide was located in tiny granules in sensory cells that are clustered around the edge of the animal’s disk-shaped body.

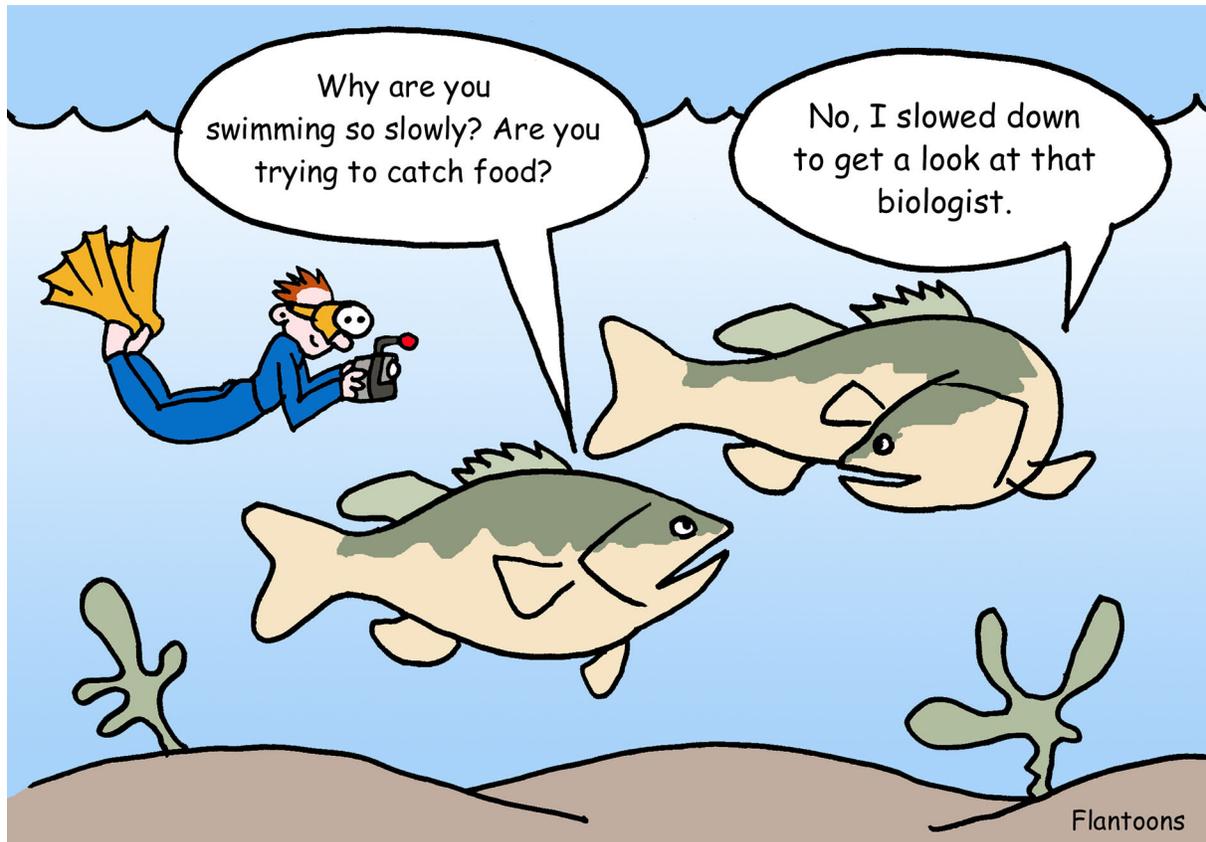
But one question puzzled the team: how could secretions from a small number of endomorphin-like neuropeptide producing cells on the *Trichoplax* surface trigger all of the hairs distributed across the animal’s surface to stop beating? ‘The answer we propose comes from the observation that animals in groups pause in coordination’, says Smith. She suspects that when *Trichoplax* encounter algae, the sensory cells that detect the algae release the endomorphin-like neuropeptide, which then triggers other nearby sensory cells to release more neuropeptide, sparking a cascade of neuropeptide release across the animal, stopping it in its tracks. ‘By these means, a small number of secretory cells detecting algal cells can arrest ciliary beating across the entire animal’, says Smith, adding that these secretory cells ‘share many of the molecular characteristics of sensory neurons in more complex animals and appear to perform a similar function’.

10.1242/jeb.168146

Senatore, A., Reese, T. S. and Smith, C. L. (2017). Neuropeptidergic integration of behavior in *Trichoplax adhaerens*, an animal without synapses. *J. Exp. Biol.* **220**, 3381–3390.

Kathryn Knight

Free largemouth bass are profligate swimmers



Running on a treadmill in the gym isn't quite the real thing, and now it turns out that fish may have the same problem. David Ellerby, from Wellesley College, USA, is concerned that experiments in flow tunnels (the fish equivalent of treadmills), which had suggested that fish naturally prefer to swim at a speed that consumes the least energy, may not be telling the whole truth. 'Almost all measurements of fish swimming costs are made at constant speeds imposed by the researchers, not those preferred by the fish. Although this is valuable information, we know very little about how the lab data actually relate to swimming behaviour in the field', he says. Realising that they were going to have to get out of the lab and go swimming with free largemouth bass in Lake Waban to find out how realistic lab-based studies are, Ellerby and two undergraduate students, Angela Han and

Caroline Berlin, devised an impromptu stereo camera system by strapping a pair of GoPro cameras to a camera head, donned their snorkels and went swimming.

Back in the lab, the trio estimated the length of each fish from the video and then measured each fish's speed, the directness of the path that they had taken and how fast they beat their tails. However, when the team compared the speeds that the fish had been swimming in the lake with the most economical speeds that had been recorded in a flow tunnel in the lab, they were astonished to see that the majority of the free fish were swimming at slower, less economical speeds ($\sim 0.3\text{--}0.4\text{ m s}^{-1}$) than the optimal speeds that had been recorded in a flow tunnel ($0.4\text{--}0.5\text{ m s}^{-1}$).

Wondering why the free fish might have opted for a more profligate swimming speed, Ellerby suggests that they may have to accept a more costly slower speed to increase their chances of snapping up tasty morsels as they pass by. Alternatively, it is possible that the fish that were swimming in the flow tunnel when their metabolic rates were measured were not behaving as naturally as the freely swimming lake fish. Either way, Ellerby warns that the behaviour of fish in the real world may be subtly different from that of fish pounding a metaphorical treadmill.

10.1242/jeb.168120

Han, A. X., Berlin, C. and Ellerby, D. J. (2017). Field swimming behavior in largemouth bass deviates from predictions based on economy and propulsive efficiency. *J. Exp. Biol.* **220**, 3204-3208.

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