Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

FORAGING

THE ELECTRIFYING BUZZ OF BEES

Springtime is abuzz with the activity of pollinating bees, travelling between flowers whose advertisements are bright, sweet-smelling and shapely. The combination of these sensory inputs help bees to discriminate between rewarding and unrewarding floral patches and thus forage more efficiently. Simultaneously, these signals ensure that plants are only visited by the right pollinators at the right time. However, these well-known sensory modalities are only part of the story. New research published in *Science* by Dominic Clarke and colleagues at the University of Bristol in the UK finds that bees and flowers are not only buzzing with activity, they are also literally buzzing with electricity.

Insects and plants are not electrically inert. Flying insects, it turns out, are positively charged while plants have a negative charge. It is known that these differences can facilitate pollen transfer between bees and flowers. Until now, however, it has been unclear whether this electric potential was also used as a component of a flower's sensory appeal.

To test the role of floral charge on bee foraging decisions, the team created artificial flowers, e-flowers, that were charged or uncharged and supplemented, respectively, with either a sweet or bitter 'nectar' reward. Strikingly, when bees were allowed to choose between these options, they rapidly learned to associate charge with the sweet reward. By contrast, when the scientists pulled the plug on the charged flower, thereby rendering it electrically equivalent to the bitter flower, the ability for bees to correctly choose e-flowers containing the sweet reward was no better than random. Bees, the team found, are even able to distinguish between e-flowers with different charge patterns, for example a flower with uniform charge and another with a charge gradient like a dart board. In short, if bees want a sugar buzz, charge matters.

But how does the ability to detect charge play out in nature? As yet, this remains unanswered. However, the team has taken two important steps forward. First, using electrostatic powder, they revealed that flowers from several plant species vary markedly in their charge pattern. Moreover, just like a heat map, some parts of flowers are charge-hot, while others are charge-cold. Second, the team showed that when charge is paired with a second sensory cue, floral hue, a bee's ability to discriminate rewarding from unrewarding flowers is enhanced. Together, these results suggest that charge patterns and perception, like colors or odors, have evolved as part of the sensory signaling occurring between plants and their pollinators.

Thus far, the story is somewhat one-sided. Recall, however, that bees are also charged. When they alight on a flower they induce nearly instantaneous charge changes in flowers that persist for more than a minute. Within this time window, do flowers withdraw their charged welcome? And do bees, in turn, modify their foraging choices? A blindfold has been lifted with this study, and in the next few years there should be exciting progress in translating the electrical chatter between insects and plants.

10.1242/jeb.077909

Clarke, D., Whitney, H., Sutton, G. and Robert, D. (2013). Detection and learning of floral electric fields by bumblebees. *Science* **340**, 66-69.

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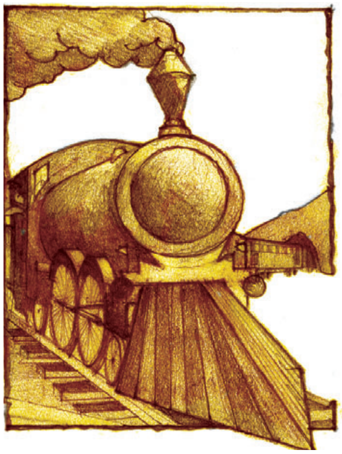
CLIMBING



AHEAD OF THE GAME: HOW KNOCKED INSECTS STICK

While watching an insect skitter straight up a wall may cause jitters in the squeamish, this remarkable feat fascinates scientists interested in animal biomechanics. Because insects have immensely sticky feet capable of clinging to smooth vertical surfaces, to be able to run they must be able to rapidly attach and detach their feet. They do this by rapidly inflating and deflating the adhesive pads on the bottoms of their feet using a claw flexor muscle running through their legs. But it turns out the adhesive pads can still inflate and deflate rapidly even without flexing the muscle – a useful skill for arboreal insects when sudden wind gusts could send an inadequately sticky insect flying.

To take a better look at this ability, Thomas Endlein from the University of Glasgow, UK, and Walter Federle from the University of Cambridge, UK, placed unsuspecting weaver ants and stick insects into a booby-trapped upside-down Petri dish. The lid of the dish had a cutout containing a glass coverslip, which was glued to a cantilevered beam. Whenever an insect stepped on the coverslip, it triggered a bolt that knocked the side of the beam, rapidly jolting the insect. A high-speed camera mounted above allowed the researchers to record and then later measure the size of the adhesive pad on the order of milliseconds.

To their surprise, the researchers found that insects were able to massively increase the contact area of their sticky pads to the coverslip within the first 2 ms after a jolt. Neuromuscular responses in insects usually take 5–15 ms, suggesting that the increase in adhesion was not related to triggering the claw muscle. Instead, the researchers propose that the insects utilize a 'preflex' – a mechanical response that can occur passively without the control of the insect's nervous system.

The researchers also observed an increase in the contact area 10–15 ms after the jolt, which they believe represented the action of the claw muscle. In addition, the researchers found that the more aligned an ant's foot was to the direction of the jolt, the greater the increase in contact area, while stick insect feet responded more evenly to jolts from different directions. The researchers suggested this might be due to differing mechanisms of the preflex in each species.

Running is a complicated balancing act for animals that climb vertically: too sticky and they cannot move, not sticky enough and they fall. But in an uncertain world filled with sudden gusts of wind and inconvenient raindrops, having a little preflex insurance can make all the difference.

10.1242/jeb.077917

Endlein, T. and Federle, W. (2013). Rapid preflexes in smooth adhesive pads of insects prevent sudden detachment. *Proc. R. Soc. B* **280**, 20122868

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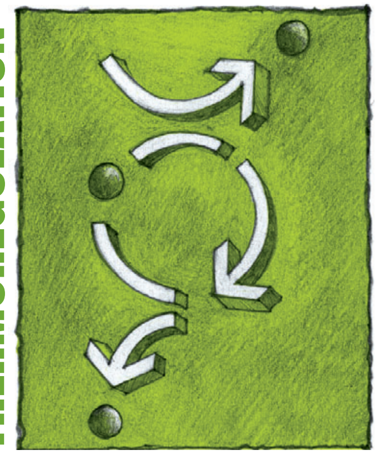
THERMOREGULATION



EMPEROR PENGUIN PLUMAGE CHILLS BELOW AIR TEMPERATURES

The iconic emperor penguin is renowned for braving the Antarctic winter to incubate its young, facing temperatures as low as –40°C. Despite their frosty surroundings, emperor penguins maintain core body temperature near 37°C, in large part due to their impressive, insulating plumage. Intrigued by the complexity of heat transfer dynamics in this warm-blooded creature in such a chilly environment, Dominic McCafferty, from the University of Glasgow, UK, and his colleagues set out to measure the direction and magnitude of heat flux and gain further understanding on the effects of weather and climate on the energetics of this extreme species. In their latest study published in *Biology Letters*, they decided to measure surface temperature variation of free-ranging emperor penguins.

McCafferty and crew braced for the cold, heading to the Dumont d'Urville emperor penguin colony (Terre Adélie, Antarctica) in the austral winter. The team deployed a thermal imaging camera and a digital camera at the colony to capture infrared and digital images of 40 birds, taking advantage of this non-invasive means of investigating thermoregulation. Using images of birds separated from each other by at least one body length, they used image analysis software to determine mean surface temperature of the front and rear trunk, wings, head and feet. They also logged the surface temperature of the surrounding ice, air temperature, relative humidity, wind speed and cloud cover. The images revealed that nearly the entire penguin exterior was below the temperature of freezing (i.e. below 0°C), with the exception of the eye region. Despite this trend, there were differences in how the temperatures of various body parts compared with that of the surrounding, and well below freezing, air. The head, wings and feet were warmer than the surrounding air temperature, but trunk temperatures were even colder than that of the air. Higher air temperatures meant warmer plumage, and stronger winds made for colder wings and feet.

Next, the team used a heat transfer model to estimate the direction and relative magnitude of heat fluxes. Their model showed that radiative heat loss was greatest from the body trunk, followed by the head, wings and feet. They explain that the cloudless sky can act as a radiative sink, causing the penguin's surface temperatures to drop below that of the surrounding air, as seen in other species under similar environmental conditions. The team predicted that the cool trunk feather surface would then actually gain heat from the surrounding, warmer air *via* convection. However, because of the low thermal conductivity of feathers, little of this heat will reach the skin. This low heat conductivity of the emperor penguin's tuxedo-like coat works both ways though, and also helps prevent internal heat loss. Only the un-feathered areas (feet, eyes and beak) and sparsely feathered wings lose heat from the body interior.

Other adaptations such as effective heat exchange networks in the blood vessels of these birds and the thick, scaly skin encasing their feet certainly contribute to this bird's ability to retain heat where feathers cannot help. Behaviour is also key to keeping warm; the scientists found that heat loss from the feet was reduced by 15% when the penguins leaned back, lifting their toes off the frozen floor, and during windy, cloudy conditions, the well-known huddle is vital against potential large convective heat losses. Despite its chilly exterior, the penguin's feathered coat remains its most crucial adaptation to the icy Antarctic – as anyone with a feather-filled parka will testify!

10.1242/jeb.077925

McCafferty, D. J., Gilbert, C., Thierry, A.-M., Currie, J., Le Maho, Y. and Ancel, A. (2013). Emperor penguin body surfaces cool below air temperature. *Biol. Lett.* **9**, 20121192.

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PERCEPTION

FRUIT FLIES ARE IN TWO MINDS ABOUT CARBON DIOXIDE

What we 'like' is often dependent on how we are behaving at any given moment. Odours and gasses seem particularly subject to such changes in hedonic valence (i.e. preference). The smell of sweat, for example, normally repulsive, suddenly doesn't seem so bad once one is out on the basketball court or halfway through a 5 km run. In a recent article published in *Current Biology*, Sara Wasserman, Alexandra Solomon and Mark Frye have made inroads into understanding the neural bases for state-dependent changes in sensory perception by studying what fruit flies think of carbon dioxide (CO_2).

Previous work has shown that fruit flies will run away from a CO_2 source. This is puzzling given that CO_2 is a by-product of rotting fruit (a favourite fly food). Wasserman and colleagues first decided to test whether flies are repulsed or attracted by CO_2 once they leave the ground. The team tethered individual flies within flight simulators that allowed animals to fly in place but also rotate freely. When the team exposed these animals to plumes of CO_2 they found that the flies always turned upstream into the CO_2 regardless of starting orientation. Fruit flies do exactly the same thing when they are attracted to odours on the wing. However, when given a chance to walk on a small glass slide, the flies, as expected, tried to walk their way out of the gas stream. Flies are clearly attracted to CO_2 while flying, but are then repulsed by the gas as soon as they hit the ground running.

What receptors allow flies to sense and track CO_2 molecules during flight? The team knew that the receptors that mediate aversion to CO_2 during walking reside in a segment of the fly antenna. Flies were not able to track CO_2 plumes in the flight simulator when this segment was covered over with glue. The team then used genetic targeting techniques to selectively inhibit synaptic release in a subset of antennal neurons that contain identified CO_2 receptors. Surprisingly, this did not stop the little fliers from tracking CO_2 plumes. The team decided to look for alternative receptors that might be involved, looking at two receptor pathways thought previously to be dispensable for sensing CO_2. They found that mutations in both carbonic acid (a CO_2 metabolite) receptor and co-receptor involved in odorant sensing prevented the airborne flies from tracking CO_2. The two pathways come online during flight and cooperate to mediate responses to CO_2.

To investigate what causes the switch in pathways, the team genetically inhibited the synaptic release of octopamine, a neuromodulator upregulated during flight. They found that these flies also actively avoided CO_2 while flying. Reducing octopamine release essentially made a flying fly behave as if it were walking in the presence of CO_2. This suggests that octopaminergic signalling modulates and reconfigures CO_2 detection circuitry as flies shift between different locomotor modes.

The work of Wasserman and colleagues resolves the paradox of why flies would be put off by an environmental cue that could lead them to food. When flies are on the ground, CO_2 is repulsive (perhaps because it is a cue that is proportional to overcrowding). But once in the air, CO_2 is attractive to flies, presumably because it can lead them over long distances to food sources. Overall, this work shows that a single molecule can trigger exactly opposite behavioural responses depending on the neuromodulatory state of an animal and reminds us of the extent to which neural circuits can be completely and utterly reconfigured by neuromodulation.

10.1242/jeb.077933

Wasserman, S., Solomon, A. and Frye, M. A. (2013). *Drosophila* tracks carbon dioxide in flight. *Current Biology* **23**, 301-306.

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