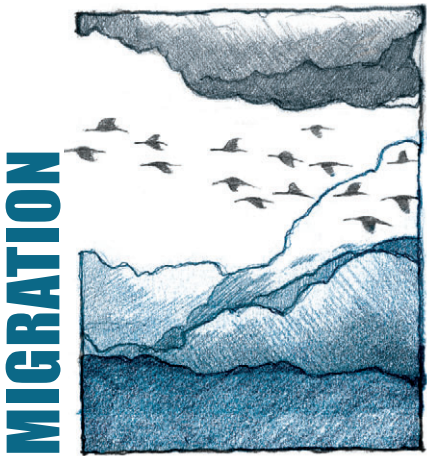
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB



HIGH-FLYING GEESE: HOW HIGH IS HIGH?

Bar-headed geese (*Anser indicus*) migrate thousands of kilometres twice a year from their breeding grounds in Mongolia, northern China and the Tibetan Plateau to their wintering grounds in India and back again. During this migration, bar-headed geese have to fly across the highest mountains in the world, the Himalayas, where the amount of oxygen is a fraction of that available at sea level. These birds have been spotted flying at high altitudes by mountain climbers, but these accounts can be inaccurate. To determine more about these incredible birds and their arduous migration, Lucy Hawkes from the University of Bangor, UK, along with a team of international collaborators used GPS satellite transmitters and reported their findings in a recent issue of *Proceedings of the Royal Society B*.

Hawkes and her colleagues attached GPS satellite transmitters to 91 bar-headed geese captured in India, China and Mongolia, in order to track their migration both to and from their breeding grounds. First, the team used the GPS data in combination with land elevation data to determine whether bar-headed geese performed their remarkable migration through the lower mountain passes or whether they were flying over mountain summits. Hawkes and colleagues found that the birds' migration was on average 3000 km and it took about 47 days. Most geese travelled in areas below 6000 m, which are some of the lowest elevations available in this area, indicating that most geese choose the low mountain passes during their migration. However, 10 birds flew higher than 6000 m, with one goose flying at a record 7290 m. The researchers suggested this was possible because the flight was recorded during the night, when air temperatures are colder and the air is denser, conditions that assist flight at high altitude and increase available oxygen.

Flying is a very metabolically demanding task and bar-headed geese are active flyers that do not use gliding. The researchers therefore wanted to determine whether the birds used tailwinds during their migration to help reduce energy expenditure and oxygen needs in an already oxygen-limited environment. Hawkes and her colleagues used their GPS data in combination with modelled weather data to answer this question. Contrary to expectations, the geese did not appear to use tailwinds during their southbound migration to their wintering areas as the wind speeds and directions were no different when the birds were flying from those when they were stationary. Bar-headed geese migrating northbound to their breeding areas also did not use tailwinds. These geese chose to fly when wind speeds were significantly lower than those when they were stationary. The researchers have previously suggested that flying during low wind conditions is safer and allows the birds more control over flight without interfering winds.

Despite bar-headed geese choosing the lower mountain passes during their biannual migration, these birds are still performing a remarkable feat. Even at these lower elevations the available oxygen is only half that at sea level, and the birds' energy demands are increased by actively flying. Despite this, they do not seem to take advantage of tailwinds. The endurance flight of bar-headed geese at these heights is incredible when compared with the performance of humans, who can only accomplish mild exercise at these altitudes even with acclimatization. It goes to show that the sky isn't the limit for the bar-headed goose!

10.1242/jeb.077743

Hawkes, L. A., Balachandran, S., Batbayar, N., Butler, P. J., Chua, B., Douglas, D. C., Frappell, P. B., Hou, Y., Milsom, W. K., Newman, S. H. et al. (2013). The paradox of extreme high-altitude migration in bar-headed geese *Anser indicus*. *Proc. Biol. Sci.* **280**, 20122114 (doi:10.1098/rspb.2012.2114).

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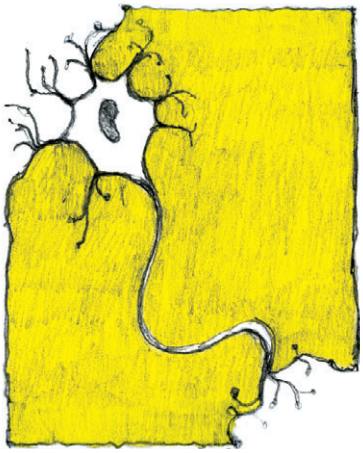
CONTROL



FLY LARVAE EXPLORE THE WORLD WITHOUT A BRAIN

You've just arrived in a new city, and you are rather hungry, so you start exploring the streets to find a suitable place to eat. All moving creatures need to inspect their surroundings and they have developed distinct motor exploratory strategies to do so efficiently. But where in the central nervous system are the neural networks that generate and regulate these exploratory routines located? In a recent paper published in *Current Biology*, Jimena Berni, Michael Bate and their colleagues at the University of Cambridge, UK, have explored this question by using the simple and genetically tractable nervous system of the *Drosophila* larva.

This larva displays an exploratory behaviour that consists of straight crawling – generated by forward wave-like contractions of its body wall – interspersed by turns. Turns are decision-making points during which the larva stops, swings its head to sample the environment, and then commences crawling along a new trajectory. Like other animals, the larvae can modify their exploratory strategy in response to different environmental conditions and internal states by varying the duration of forward crawling and the frequency and direction of turns. To understand the differential role of brain and ventral nerve cord circuits underpinning this behaviour, the authors genetically engineered larvae in which the anterior part of their central nervous system – the brain and suboesophageal ganglion – could be remotely switched off in a reversible way in freely behaving animals.

The team first showed that when they inhibited the activity of all brain neurons the larvae could still perform normal peristaltic waves. Thus, the circuits producing crawling do not reside in the brain, but in the ventral nerve cord.

But what about the networks controlling the key decision of when and how to turn? The authors counted the number and angle of turns performed by these effectively 'brainless' larvae and found that turning frequency and angle were indistinguishable from those of larvae with functioning brains. This demonstrates that the networks producing the default exploratory locomotor programme in the larvae reside in the ventral nerve cord, and can operate normally without a functioning brain. But how is this exploratory behaviour modified by the larva under changing environmental conditions?

The researchers first assayed the exploratory abilities of the temporarily 'brainless' larvae in response to the odour of a drop of yeast, which is a powerful natural modifier of exploratory behaviour in larvae. It is well established that the networks responsible for the key processing steps of olfactory information reside in the brain. Therefore, unsurprisingly, the 'brainless' larvae were unable to modify their exploratory routine in response to the odour. The authors then decided to try using a stimulus that might be less dependent on brain processing, so they turned to light. An array of light receptors covers the larval body wall, and although the way in which this visual information is processed remains unknown, it is possible that some processing might occur locally within the ventral nerve cord. Berni and colleagues found that 'brainless'larvae display a completely normal and coordinated avoidance response to light.

These results reveal that the ventral nerve cord of the larva contains all the necessary circuit elements to produce an effective exploratory strategy and to modify it in response to environmental cues, such as light, without involving the brain. However, the brain is responsible for adjusting the larva's exploration strategy in response to other environmental sensory inputs, such as olfactory information, during goal-directed behaviour.

The elegant use of *Drosophila* genetic tools by Berni and co-workers has for the first time made it possible to remove brain function reversibly in a freely behaving animal. This led to the unexpected finding that the brain is dispensable for the explorative behavioural programme displayed by larvae. In the future, similar approaches might become feasible in vertebrate model organisms to find out just how brainless some of our own behaviour might be.

10.1242/jeb.077750

Berni, J., Pulver, S. R., Griffith, L. C and Bate, M. (2012). Autonomous circuitry for substrate exploration in freely moving *Drosophila* larvae. *Curr. Biol.* **22**, 1-10.

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APPETITE REGULATION

SIGNAL TO OVER-EAT

According to the Organisation for Economic Co-operation and Development (OECD) report, 'Obesity and the Economics of Prevention: Fit not Fat', published in 2010, one person out of every 10, or 500 million people worldwide, is defined as obese. In order to understand the motivation behind empty eating – the tendency of animals to over-indulge when they do not physiologically require additional calories – scientists are investigating the body's natural mechanisms for evaluating satiation and hunger. In a recent study published in *Current Biology*, a group of scientists from the University of Michigan, USA, contribute to our understanding of over-eating by reporting that they have found a highly targeted brain region, the anteromedial quadrant of the dorsal neostriatum, where an opioid neuropeptide, enkephalin, serves as a signal to eat.

Based on previous work implicating the dorsal neostriatum as a region involved in reward and addiction, Alexandra Difeliceantonio, Omar Mabrouk, Robert Kennedy and Kent Berridge designed a study to measure the neuropeptides that are naturally released in rat brains during eating. In order to measure peptide release, the team implanted probes in the dorsal neostriatum of the rodents and measured the extracellular levels of neuropeptides (including enkephalin) while the rats consumed chocolate candies.

The team found that compared with the baseline measurements – taken before a meal in mildly hungry rats – the enkephalin measurements of the chocolate-consuming rats reached 150% of the pre-meal levels and remained elevated while they ate. Furthermore, they found that the faster the rat began consuming its first chocolate, the higher the relative increase in enkephalin. Intrigued by the possibility that enkephalin might stimulate the rats to over-eat, the

team performed microinjections of a synthetic opioid peptide, DAMGO, into different sites within the dorsal neostriatum region of the brain to mimic enkephalin and monitored the rat's appetites. The DAMGO injections, specifically within the anteromedial quadrant of the dorsal neostriatum, proved to produce the most intense over-consumption of chocolate, with the rats increasing their intake by more than 250% compared with rats that had received no DAMGO.

Next, the team wondered whether the rats were actually enjoying their sweet over-indulgence following the DAMGO injection. By measuring the rodent's reactions to their diet of chocolate (including rhythmic tongue extensions and lip licking, typical responses to sweetness and pleasure), the team was able to quantify their responses to find out how much they were enjoying their chocolate binge. Interestingly, they found that DAMGO microinjections into the dorsal neostriatum region of the brain failed to elicit the stereotypical set of 'liking' reactions typical for sweet tastes: the rats were not enjoying the chocolates as they over-indulged. In fact, whether the team used sucrose solution infused directly into the mouth or actual chocolates, they could not make the rats that had been treated with DAMGO behave as though they were enjoying the experience when eating, demonstrating that as the rats gorged they failed to derive any gratification from it. Essentially, enkephalin was stimulating the rats to over-eat, but their over-indulgence gave them no pleasure.

Berridge's exciting report has in essence begun the meticulous mapping of the mammalian brains' relationship to food; by finding where the neuro-chemical signaling of wanting but not enjoyment resides, their work helps to pinpoint the empty eating at the heart of the current obesity crisis.

10.1242/jeb.077768

Difeliceantonio, A. G., Mabrouk, O. S., Kennedy, R. T. and Berridge, K. C. (2012). Enkephalin surges in dorsal neostriatum as a signal to eat. *Curr. Biol.* **22**, 1918-1924.

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FEEDING FROGS, TONGUES AND TEMPERATURE

My proficiency at eating is not usually determined by temperature, unless it's one of those ridiculously hot summer days on which a little air conditioning can go a long way. The same cannot be said for ectothermic vertebrates, whose digestive processes and skeletal muscle contractions depend heavily on ambient temperature – warmer generally means more effective and colder the opposite. However, in the last few years, work out of Steve Deban's laboratory at the University of South Florida, USA, has highlighted how a number of ectotherms get around this temperature dependence of their feeding systems. By relying on stored elastic energy rather than muscle work directly, chameleon, toad and plethodontid salamander tongues can project rapidly and forcefully across a wide range of temperatures. Elastic energy release is not nearly as susceptible to temperature as a contracting muscle. Continuing along this intellectual thread, Deban and his student Paula Sandusky recently studied the effects of temperature on the feeding behavior of the frog *Rana pipiens*.

A total of 46 feeding events from five frogs were imaged at 6000 frames s^{-1}. Feeding trials were performed at three temperatures (10, 15 and 25°C) with crickets as prey held at varying distances from the animal. Movements of the frog itself, its lower jaw and its tongue were characterized during each feeding, and the amplitude, speed and timing of these movements were compared statistically across temperatures. A temperature coefficient (Q_{10}) was calculated for each of the various performance variables as an indicator of the degree to which they were affected by temperature.

During feeding, frogs extend their legs, lunge toward the prey and rapidly open their mouths. Rapid depression of the lower jaw (9–24 m s^{-1}) propels the tongue out of the mouth and onto the prey, after which the tongue is retracted with the prey into the mouth. Movement amplitudes including lunge, gape and tongue protrusion distance were not especially sensitive to temperature. However, the durations and speeds of those movements were. For example, the mean velocity of mouth closing at 10°C was ~0.1 m s^{-1} and at 25°C it was ~0.3 m s^{-1}. But not all durations and speeds were equally sensitive to temperature. Velocities and accelerations associated with mouth opening had Q_{10} values less than 1.25, indicating a relatively low sensitivity to temperature, while those associated with tongue projection were much higher. The higher Q_{10} values indicate the relative importance of muscle contraction in driving the movement because we know muscle contractile performance depends heavily on temperature. Thus, while mouth opening appears to be driven largely by elastic energy release (i.e. is not especially sensitive to temperature), tongue projection presumably relies more heavily on muscle contraction for its power. This is quite distinct from what has been found for tongue protrusion in toads, lungless salamanders and chameleons, where elastic energy is the main driver.

While Deban's work highlights the diverse ways in which ectothermic vertebrates power feeding movements, another very appealing aspect of his work is that it demonstrates how temperature can be used as a means of teasing out the importance of muscle *versus* elastic energy in all kinds of biomechanical systems.

10.1242/jeb.077776

Sandusky, P. E. and Deban, S. M. (2012). Temperature effects on the biomechanics of prey capture in the frog *Rana pipiens*. *J. Exp. Zool. A.* **317**, 595-607.

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