11-26-2018

Serotonin: Octopus Love Potion?

Lauren E. Nadler

© 2018. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2018) 221, jeb170282. doi:10.1242/jeb.170282

OUTSIDE JEB

Birds and bats: masters of hovering

Flight is an incredibly complex but wonderful mode of transport. Perhaps because of this, and definitely because of our inability to fly, humans are fascinated by it. We have been trying to achieve flight for a long time, with many failures, but also some extraordinary success. While many animals evolved the ability to fly long before humans were around, bats are the only mammals capable of powered flight to get from place to place and to hunt. But remaining stationary while hovering in front of a food source is even more impressive. As some bats are capable of hovering, Rivers Ingersoll and colleagues from Stanford University, USA, were interested to see whether there were any similarities in hovering flight between mammals and birds.

The team travelled to the jungles of Costa Rica to capture 20 bat and hummingbird species. Hummingbirds are well known for their hovering ability; their preferred food of choice is the delicious nectar located deep inside flowers, so hovering is a necessity for extracting the precious fluid. While some hovering bat species chiefly consume fruit, many of them are also partial to nectar. However, bats are less dainty when sipping nectar; they just stuff their whole face into the flower. Once the group had captured their test subjects, they trained the hummingbirds to feed from a syringe filled with sugar water, so they could film the birds while they hovered. Unfortunately, the scientists were unable to train the unruly bats to hover at a flower, but they were still able to film the animals hovering as they moved around a flight chamber.

Once all of the movies of the hovering creatures had been captured, Ingersoll and his colleagues examined the footage to decipher similarities and differences between the hovering techniques of the two groups. Interestingly, the amount of power used by the two while hovering was comparable, but this was where most of the similarities ended. Hummingbirds are better at supporting their weight with the upstroke, when the wings beat upwards. They accomplish this by beating their wings backwards and forwards horizontally, which is a very efficient way to produce lift. Bats, in contrast, create most of the lift they need to support their body weight on the downstroke of the wing beat. Furthermore, bats do not beat their wings horizontally, but at more pronounced angles, and their wings are significantly larger, allowing them to achieve the same power output as hummingbirds.

The disparities in how hummingbirds and bats achieve hovering flight largely boils down to differences in their wing design. Hummingbird wings are covered in feathers and are composed solely of their forelimbs, whereas bat wings consist of a membrane stretched over their forelimbs that is also attached to their legs. This huge variance in flapping appendages makes it even more fascinating that these two groups have converged evolutionarily on a way to feed from a stationary object while flying.

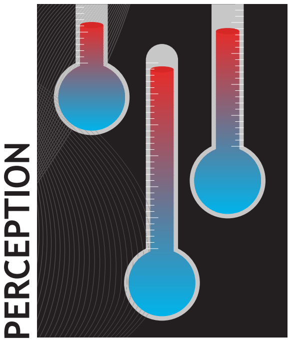
Ingersoll and his colleagues hope that achieving a better understanding of how animals hover may help to create aerial robots that are able to hover just as well. And I recommend taking a look at their supplementary videos of hovering bats and hummingbirds, which are truly captivating.

10.1242/jeb.170282

Ingersoll, R., Haizmann, L. and Letnik, D. (2018). Biomechanics of hover performance in Neotropical hummingbirds versus bats. *Science Advances* **4**, eaat2980.

Clare Stawski (0000-0003-1714-0301)
Norwegian University of Science and Technology
clare.stawski@ntnu.no

Some like it warm – usually women



Science is at its most powerful when it reveals to us some new unknown about the universe. Science is perhaps at its most satisfying, however, when it confirms for us something we sort of knew to be true all along. This is especially true when those suspicions are based on the loose grounds of personal experience. Recently, I had been cobbling together a new temperature theory based on some autumnal experiences with my wife, when, by good fortune, Jenny Visser's team at Erasmus University Medical Center in Rotterdam, The Netherlands, published a paper, the results of which directly supported my theory.

The theory has to do with temperature preference, a topic that in our household tends to flare up in autumn. As the air temperature falls and the thermal gradient steepens, the activity around our thermostat reaches its annual peak. These thermostat adjustments are usually done on the sly because my wife and I prefer different temperatures: she prefers it warm and I prefer it, well, not quite as warm. I've polled friends and family on the topic and the results hinted that males and females may indeed defend their own sides of the thermostat. The work of the Rotterdam team added some welcome rigour to this theory.

The team investigated the thermal perceptions and shivering thresholds of 20 men and 23 women participants. The experimenters outfitted each participant with skin temperature sensors and shiverdetecting electromyography electrodes, and then wrapped them in a precise temperature-controlled thermal blanket and vest. They then gradually dialed down blanket and vest temperatures from 24°C to 9°C over 45 minutes and let the sensors and electrodes do the rest. As the temperature gradually fell, the team asked the participants to score their thermal sensation and comfort on seven-point scales ranging from ‘hot’ to ‘cold’ and ‘very comfortable’ to ‘very uncomfortable’, respectively.

The results revealed that women felt cold at higher experimental temperatures than men did (18.3 versus 14.6°C). Previous work has shown that temperature-sensitive TRPM8 receptors on the skin are more sensitive in women than men, and the Rotterdam team suspects these receptors are at play here too. Beyond just feeling cold, women began shivering at higher temperatures than men (11.3 versus 9.6°C). The way in which skin temperatures fluctuated across the sensors signified to the team that women maximally constrict surface blood vessels at higher temperatures than men do, indicating women begin losing body heat at higher temperatures than men and consequently supplement that lost heat with shivering. As for why women begin losing heat at higher temperatures than men, the team implicates physics; the women in their study – like women generally – had higher body surface area-to-mass ratios, meaning each gram of heat-producing tissue had a larger surface area over which the heat it generated could be lost. The result was higher rates of heat loss and, therefore, higher temperatures at which the body started compensating by producing extra heat through shivering.

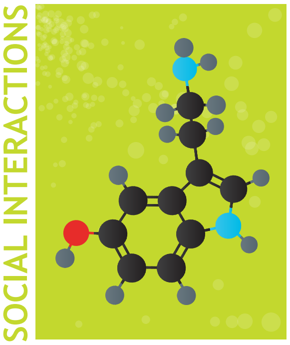
These results have timely implications both generally and personally. Generally, climate change-related studies often include experimental temperature change protocols similar to those used by the Rotterdam group. If their results show sex-specific variation in temperature responses, so too might those of other studies, indicating male and female conspecifics may respond slightly differently to climate change. And personally, I have been a little more careful when defending my side of the thermostat this autumn because, as my wife now reminds me, what I am quibbling with is an actual physical law: surface area-to-volume scaling. It’s easy to quibble about some things; physical laws aren’t one of them. I’m anticipating a warm winter.

10.1242/jeb.170290

Kaikaew, K., van den Beukel, J. C., Neggers, S. J. C. M. M., Themmen, A. P. N., Visser, J. A. and Grefhorst, A. (2018). Sex difference in cold perception and shivering onset upon gradual cold exposure. *J. Therm. Biol.* **77**, 137-144.

Matthew D. Regan (0000-0001-9341-5747)
University of Wisconsin-Madison
mdregan@wisc.edu

Serotonin: octopus love potion?



When you think about human social behaviour, what animals do you immediately think of as most similar to us? Apes, dolphins, wolves? Sure, these animals display incredibly complex social interactions, just like us. But Eric Edsinger from the Marine Biological Laboratory, USA, and Gül Dölen from Johns Hopkins University, USA, teach us in their latest study that we aren’t actually all that different from our more distant cousin: the octopus. While octopuses typically hang out by themselves and fight when they come across each other, they let bygones be bygones during the mating season. Until now, we had no idea why octopuses suddenly set aside their aggressive tendencies during this ‘special’ time. Using a unique combination of molecular and behavioural studies, Edsinger and Dölen delved into the brain of the octopus to uncover the neurological mechanisms that regulate their social behaviour.

The duo suspected that the neurotransmitter serotonin may be involved. A neurotransmitter is a chemical in animal brains that helps to communicate signals between neurons. In many animal species, from insects to humans, serotonin is known to play a key role in regulating social behaviour by inhibiting aggression and spontaneous activity. To investigate whether octopuses use this chemical messenger, Edsinger and Dölen constructed an evolutionary tree for key genes involved in serotonergic signalling among 21 species, including their study animal, the California two-spot octopus (*Octopus bimaculoides*). They uncovered incontrovertible evidence that the octopus carries a gene for a key protein involved in transporting serotonin between neurons, with amazing similarity to the human gene for this protein. The fruit fly, the roundworm and a number of vertebrate species also share these gene sequences, probably as a result of evolution from common ancestors. Interestingly, social insects like the honeybee lack these genes, illustrating the complex progression of sociality across evolutionary history.

Following on from these molecular studies, Edsinger and Dölen performed behavioural tests to better understand the role of serotonin in octopus sociality. Using methodology designed for rats, the scientists gave the octopuses a choice between a ‘novel object’ (which, in this study, were Star Wars figurines of Chewbacca or a Stormtrooper) and an unfamiliar octopus (either a male or a female) of the same species and recorded which ‘object’ the octopus preferred to hang out with. They found that both males and females preferentially associated with the female octopus. But if presented with a male, both sexes preferred to hang out with the Star Wars figurine.

Then, they used MDMA, the main ingredient in the drug ecstasy, to ramp up the octopus’s serotonin, to see whether they could stimulate the octopus to associate with the male that they had previously dodged. Amazingly, this avoidance of males was reversed with a healthy dose of serotonin-boosting MDMA. Following treatment with the drug, all of the octopuses (both male and female) interacted enthusiastically with the male octopus, which they had avoided previously.

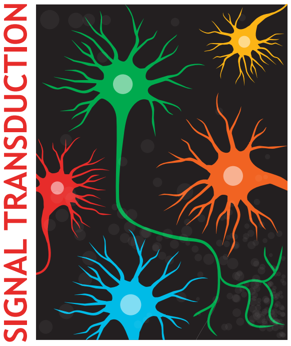
Excitingly, these findings support the scientists’ theory that octopuses become lovey-dovey during the mating season as a result of a boost in serotonergic activity. Edsinger and Dölen speculate that while octopuses maintain all of the necessary machinery to express serotonin, they suppress signalling by this neurotransmitter outside of the mating season. So, potentially, serotonin is just the right love potion to kindle octopus romance.

10.1242/jeb.193698

Edsinger, E. and Dölen, G. (2018). A conserved role for serotonergic neurotransmission in mediating social behavior in octopus. *Curr. Biol.* **28**, 3136-3142.

Lauren E. Nadler (0000-0001-8225-8344)
Norwegian University of Life Sciences
lauren.nadler@nmbu.no

Size slows animals' response to surprise



Life is full of surprises. For an animal in the wild though, surprises could cost dearly; lurking predators might attack or rough terrain could turn every step into a precarious balancing act. As such, an animal's ability to quickly sense trouble and respond accordingly is crucial. Given that neural information must travel longer distances in larger animals, how do larger animals cope with these apparently longer delays? Heather More and Max Donelan from Simon Fraser University, Canada, decided to find out by studying how the size of an animal influences the delay between sensing and generating movements.

To test the delay between sensing and movement, the team decided to study the stretch reflex – the animals' equivalent of the human knee-jerk reflex – that maintains favored muscle lengths by sensing length changes to the muscle and correcting the length accordingly. The reflex can be broken down into a series of events: sensors in the muscle generate an electrical signal when a tap of the tendon stretches the muscle; a nerve fiber transmits the signal to the spinal cord; another nerve fiber transmits the signal back and stimulates the muscle fibers so that they produce force and generate movement. Previously, the team had studied the reflex in a range of terrestrial animals, but to test their new hypothesis they searched the scientific literature to include stretch reflex delays from more animals, spanning a 5 g shrew to a 5000 kg elephant, to bolster their analysis.

Plotting animal size against total reflex delay, More and Donelan found that the delay strongly increased with animal size: a shrew had a 10 ms delay compared with an elephant's 180 ms delay – an 18-fold increase in delay across the size range. To understand why the reflex delay got longer with size, the team took a closer look at the time course of the signal's path from the stretch sensors and back to the muscle and found that large animals' longer nerve fibers, spanning their longer limbs, mainly explained the longer delays. In contrast, other portions of the reflex's path, such as the time it took the stretch sensors to generate the electrical signal and the time it took the electrical signal to cross between the nerve fibers and from the nerve fiber to the muscle, remained about 1 ms and, therefore, made a negligible contribution to the total delay in large animals. This showed that the total delay increases strongly with animal size, despite partial delays not scaling uniformly with size.

Next, the team calculated the reflex delay relative to the contact time of the animals' legs with the ground to account for the larger animals' slower movement. As larger animals move more slowly, their reflex delay expressed as a percentage of the animals' contact time did not increase 18-fold across the entire 5 g to 5000 kg size range, but only doubled. This means that larger animals benefit from their slower movements because the long movement times accommodate their longer delays – if they moved faster they wouldn't be able to use the reflex information to correct their movement.

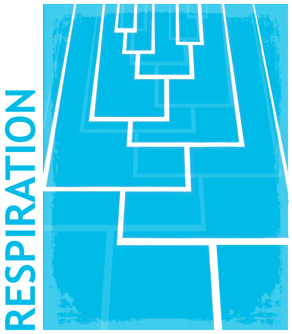
Together, More and Donelan have shown that delays between sensing and movement increase strongly with animal size. Even though the larger animals' slower movements reduce the severity of the delays, delay periods likely remain challenging for all animal sizes and for large animals in particular. Therefore, large animals might especially benefit from moving slowly to prolong the time in which their delayed information can usefully be implemented. Alternatively, large animals could avoid long delays by predicting the consequences of their movements – thereby relying less on slow sensory information – so that they better handle life's inevitable unwelcome surprises.

10.1242/jeb.170233

More, H. L. and Donelan, J. M. (2018). Scaling of sensorimotor delays in terrestrial mammals. *Proc. R. Soc. B Biol. Sci.* **283**, 20180613.

Jan Stenum (0000-0002-0088-8703)
University of Massachusetts Amherst
jstenum@umass.edu

A breath of fresh air for lungless salamanders



About two-thirds of salamander species have relinquished their lungs, but despite this potential handicap, members of this surprisingly diverse group occupy a variety of habitats in locations around the world, from European caves to Neotropical cloud forests. As aquatic embryos, they can subsist on oxygen taken up from water across their skin, whereas the lungless adults breathe air with the lining of their mouths. In a recent study, Zachary Lewis and a team then based at Harvard University, USA, explored how the larval skin and adult mouth have been repurposed for respiration in lungless salamanders.

The lungs of most air-breathing animals are coated with a thin layer of a wetting agent, know as a surfactant, which helps mucus spread and enhances absorption of oxygen into the blood. Wondering whether surfactants may contribute to breathing in the lungless salamanders, Lewis and his colleagues decided to study the production of mRNA – which is the first step in the production of proteins from genes – from the gene for a crucial surfactant component, surfactant protein C, in salamanders with and without lungs.

In their first breath-taking finding, the Harvard team established that all of the salamanders that were available to them (with and without lungs) were endowed with two genes for this surfactant protein. Some time in early salamander evolution, the gene duplicated, so all salamanders hold a spare copy. Apart from that, the expression of the original gene in a salamander with normal lungs – the axolotl – was typical of that of every other air-breathing vertebrate: mRNA from the original copy of the surfactant protein C gene was exclusively present in the lung and it was produced in the animal's lung throughout embryonic development and adulthood. mRNA from the copied gene was also produced in axolotl lungs, but only at low levels, and only in adults.

However, in the lungless salamanders, the copied gene came into its own. Most strikingly, the embryos produced mRNA from the new copy of the gene all over their skin surface, but as the salamanders grew larger, the mRNA production subsided on the skin surface while it began to appear in the animals' mouths. The adult lungless salamanders produced the new mRNA exclusively in their mouths and throat. Meanwhile, there was hardly any mRNA produced from the original version of the surfactant protein gene. In other words, the pattern of gene expression mirrored the transition from aquatic to aerial breathing as the amphibians metamorphosed into adults.

The authors believe that the new gene may help lungless salamanders absorb oxygen through their skin and mouths. However, as this study only confirmed that the gene is translated in the mouth to produce mRNA, they must hold their breath until they can confirm that a functional protein is produced. Nevertheless, this work may provide a remarkable example of 'historical contingency', an idea popularised by Stephen Jay Gould, which suggests that events in the evolutionary history of an animal group can constrain their future trajectory. Long before the first lungless salamanders evolved, this surfactant protein gene was duplicated, but the copy was not fully exploited at first. This earlier event may then have later facilitated the evolution of lunglessness by helping salamanders breathe through other areas of their bodies.

10.1242/jeb.170308

Lewis, Z. R., Dorantes, J. A. and Hanken, J. (2018). Expression of a novel surfactant protein gene is associated with sites of extrapulmonary respiration in a lungless salamander. *Proc. R. Soc. B* **285**, 20181589.

William Joyce (0000-0002-3782-1641)
Aarhus University
william.joyce@bios.au.dk