INSIDE JEB

Whisking whiskers tell rats about surroundings



Rat investigates surroundings with whiskers. Photo credit: Mitra Hartmann.

Watch a rat's twitching nose and you may think that it's taking a good sniff. However, Mitra Hartmann from Northwestern University, USA, explains that much of the time the animals are deftly exploring their surroundings by whisking their whiskers to and fro. Hartmann is fascinated by how animals perceive objects and how rats interpret deflections as their whiskers brush past obstacles. She explains that measuring the interactions between a rat's whiskers and a structure could shed light on how the rodents build an understanding of their surroundings. However, directly measuring the whisker interaction patterns for all of the possible poses that a rat's head could strike would be almost impossible in real life. So, having previously built a cyber-rat simulation – complete with 62 cyber-whiskers laid out in a grid – to learn more about the rodent's sixth sense, Hartmann teamed up with Jennifer Hobbs and Blythe Towal to calculate the contact patterns as the simulated rat's whiskers explored objects that it encountered.

Explaining that the cyber-rat's head can be positioned in any orientation relative to an object, Hartmann and Hobbs placed a wall and floor in the simulation and embarked on the Herculean challenge of calculating the chance that the rat's whiskers would encounter the surfaces after positioning the head in 83,509 different positions (at distances up to 60 mm from the wall, looking over a range of angles from vertically up to vertically down and looking from 90 deg right to 90 deg left). Next, Hartmann and Hobbs positioned the rat side-on to the wall, explaining that this is the orientation that rats tend to assume

naturally in a burrow, and simulated a tunnel while calculating the probability of the whiskers contacting the wall and floor while whisking.

Analysing the calculations, Hartmann and Hobbs were delighted to see trends emerging in the contact patterns. When the rat faced the wall head on, the adjacent whiskers in the same row or column were most likely to contact the object. However, when the rat turned side-on to the wall, the duo could see that clusters of whiskers laid out in a triangle were most likely to touch the wall. And when the rat was placed in a burrow, the triangular arrangement became even more pronounced.

But how many of the head positions that Hobbs and Hartmann had simulated would a flesh-and-blood rat use when thrown into the complete unknown? This time, Towal placed a rat on a perch near to a wall in the dark and filmed the first few seconds as the animal explored the new location with its whiskers. Measuring the position of the animal's head from the movies, the trio was pleased that the rat's behaviour strongly reflected their simulations. 'We found that the rat tends to put its head at the angles where it is most likely to maximise the number of whiskers in contact with the ground and with a structure in front of it in an uncertain environment' says Hartmann.

Adding that motion is the key to an animal building an understanding of its surroundings, Hartmann explains that sensory systems have been shaped by the way that an animal moves through the environment. She stresses that we can only understand how the brain constructs a map of the objects in the vicinity by studying sensory signals in the context of the movements that generated them. 'If you are going to understand what the brain does, you have to study it in awake animals that are free to explore the world the way they evolved,' she says.

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Hobbs, J. A., Towal, R. B., Hartmann, M. J. Z. (2015). Probability distributions of whisker– surface contact: quantifying elements of the rat vibrissotactile natural scene. J. Exp. Biol. 218, 2551-2562.

Kathryn Knight

DGC not necessarily saving water



The Company of Biologists

Ocneropsis lividipes grasshoppers. Photo credit: Stav Talal

Equipped with a delicate network of tubules that deliver oxygen directly to every tissue in the body, insects open and close the valves (spiracles) at the ends of the tubules (tracheae) to admit oxygen to the body and release carbon dioxide in a series of well-established patterns matched to their activity. One such pattern, known as the discontinuous gas exchange cycle (DGC), occurs when some insects are inactive. The spiracles are initially closed for extended periods as the insect consumes oxygen from the air in the closed tracheae. However, once the oxygen level has fallen sufficiently, the spiracles begin to open and close rapidly (flutter phase), to draw in more air. The carbon dioxide levels in the body then continue rising until they are high enough to trigger the final phase of the cycle, when the spiracles open for an extended period as the insect releases the accumulated carbon dioxide and takes in more oxygen ready to begin the cycle again. Yet, how this particular gas exchange pattern evolved is a mystery. Several competing theories had been proposed, but Eran Gefen says, 'None of the existing hypotheses... is backed by unequivocal support'. Explaining that one theory suggests that DGC evolved to protect insects from dehydration, Shu-Ping Huang, Stav Talal, Amir Ayali and Gefen decided to test whether grasshoppers from three dramatically different environments saved water when using DGC.

'We wanted to know whether xeric grasshoppers [that live in dry conditions] "do DGC better", says Gefen, so Huang and Talal headed out to three locations in Israel – ranging from the desiccated

Negev desert to a hill overlooking the Sea of Galilee (where the rainfall is higher), to the wettest location, Mount Hermon on the Syrian border – to collect grasshoppers endemic to each environment. Back in the lab, Huang began the laborious process of measuring the insects' gas exchange patterns and water losses over periods of several hours before scrutinising the carbon dioxide traces to identify examples of DGC and continuous breathing for analysis.

Noticing that 60% of the desert dwelling Tmethis pulchripennis grasshoppers used DGC while only 19% of the grasshoppers from the most humid environment – Ocneropsis lividipes – used DGC, Huang then compared the insects' respiratory water loss rates when they were breathing discontinuously and continuously. If the grasshoppers were breathing discontinuously to protect themselves from desiccation, they would all reduce their respiratory water losses when they used DGC. However, the team was impressed to see that even though the desert species (*T. pulchripennis*) reduced its respiratory water losses, neither of the species that were adapted to more humid conditions (Ocneropsis bethlemita and O. lividipes) did. 'DGC in the two Ocneropsis species did not result in any measureable water savings,' says Gefen, adding 'Our results suggest that DGC has not necessarily evolved as a water-saving mechanism'.

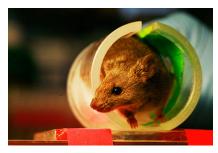
Instead, Gefen suggests that the ability to reduce water loss through DGC in some, but not all, species may be related to differences in tracheal dimensions. He explains that although *T. pulchripennis* may have developed a large tracheal system to conserve water during DGC, there is another possible explanation: that *T. pulchripennis* — which is the only insect in the study that can fly — evolved a larger tracheal system to deliver sufficient oxygen for the high metabolic demands of flight. 'It would be extremely interesting to tease apart the two in the future', says Gefen.

10.1242/jeb.129288

Huang, S.-P., Talal, S., Ayali, A. and Gefen, E. (2015). The effect of discontinuous gas exchange on respiratory water loss in grasshoppers (Orthoptera: Acrididae) varies across an aridity gradient. *J. Exp. Biol.* **218**, 2510-2517.

Kathryn Knight

Nocturnal lifestyle costs measured for mice



An active mouse. Photo credit: Rama, Cc-by-sa-2.0-fr.

It's a long-standing joke that teenagers seem to be nocturnal, but for many animals the switch to a night active bodyclock is more than just a lifestyle choice. Vincent van der Vinne from the University of Groningen, The Netherlands, explains that it is a matter of keeping costs down. Mice that are raised with plenty of food are strictly nocturnal, taking advantage of the night to avoid predators. However, when food becomes scarce and the temperatures drop, the tiny rodents switch to riskier daylight activity. Van der Vinne and his colleagues suspected that the small animals are prepared to gamble with fate to conserve energy when resources are limited by being active when it is warm during the day and snuggling up with nestmates during the cold night. Meanwhile, nocturnal animals should have to invest more energy to stay warm when active at night. However, no one had ever measured the true energetic costs of a nocturnal (versus diurnal) lifestyle, so van der Vinne and his colleagues, Jenke Gorter, Sjaak Riede and Roelof Hut set about measuring the metabolic costs of different mouse lifestyles.

Providing some captive mice with wheels while others had none, van der Vinne and Gorter set the air temperature in the animals' cages at temperatures ranging from a chilly 10°C to a balmy 30°C and measured their energy expenditure while they were active and resting. The wheelrunners burned more calories than the sedentary mice and the active mice conserved more energy when resting than the mice that were less active. Also, the air temperature had a big effect on the mice, with the warm mice using less energy than

the chillier animals. Next, the duo tested the effects on energy consumption of snuggling together by measuring the energy use of mice in nests of 1–3 animals with different amounts of bedding at various temperatures at night. Not surprisingly, the mice that had more nestmates and more bedding stayed warmer; however, the duo found that the air temperature had a significant impact on the animals' energy consumption, with mice in the coldest conditions benefiting most from cosying up in a nest with several others at night. But what impact would these savings have on the animals' activity patterns?

Van der Vinne built a computer simulation – incorporating factors such as how much warmth active animals generate, the impact of huddling in nests and the effect of environmental temperature – and found that switching to a daytime lifestyle and using the warmth to be active allowed normally nocturnal mice to save up to 10% of their energy budget. And when van der Vinne factored hunger into the equation, the mice could boost their energy savings to an impressive 20% by dropping their body temperature and going into a minihibernation at night. Switching their active periods from night to day and cuddling up with nestmates makes perfect metabolic sense for cold mice when food is scarce.

But what does this mean for mice out in the wild? When are they most likely to trade in a low risk but metabolically costly nocturnal way of life for a more risky but low energy cost daytime existence? Collecting temperature data from weather stations across Europe, van der Vinne found that functioning during the day could save mice as much as 14% of their energy budget in Spain in spring and autumn, but only 3% in Norway. So it makes more sense for Spanish mice to become active during the day when food is scarce than Norwegian mice, which are just as well off sticking to life in the dark.

10.1242/jeb.129262

van der Vinne, V., Gorter, J. A., Riede, S. J. and Hut, R. A. (2015). Diurnality as an energy-saving strategy: energetic consequences of temporal niche switching in small mammals. *J. Exp. Biol.* **218**, 2585-2593.

Kathryn Knight

Oh! Maybe I should mind my dive behaviour!

High nitrogen solubility in jaw fats puts whales at risk

Diving mammals are superbly adapted to their submarine lives. With their hearing finely attuned to waterborne sound and lungs that can compress at extreme depth, they seem well protected from their highpressure lifestyle. However, all is not well beneath the waves. In recent years there have been reports of mass strandings of whales and dolphins - some of the animals showed symptoms that resembled decompression sickness - that coincided with the Navy's use of sonar in the vicinity. Gina Lonati and colleagues from the University of North Carolina Wilmington, USA, suspected that the animals may have changed their diving behaviour, affecting how nitrogen is stored in tissues where it may have accumulated during a dive. Knowing that fat absorbs nitrogen and that the amount of gas that fat can hold depends on its chemical make-up, the team decided to find out how much nitrogen can be absorbed by the fats that pack around the

jaws of whales and dolphins – which carry sound to the ear – to find out how vulnerable the animals may be to decompression injuries.

Collecting samples of jaw fat from small Atlantic spotted dolphins to mighty sperm whales, the team was impressed when they measured the nitrogen solubility and found that it ranged from

 $0.066 \text{ ml N}_2 \text{ ml}^{-1}$ in pygmy sperm whales to an impressive $0.101 \text{ ml N}_2 \text{ ml}^{-1}$ in the short-finned pilot whale – compared with 0.062– $0.075 \text{ ml N}_2 \text{ ml}^{-1}$ in the animals' blubber. And, when the team tested the composition of the fats, they found that high levels of wax ester fats – which do not occur in other mammals – increased the nitrogen solubility. However, when they looked at the fat composition in more detail, they found that specific chemical components of the fats (such as fatty acids and alcohols) also contributed to the nitrogen solubility in the jaw fats,

especially in the spotted dolphins, pilot whales and beaked whales.

Lonati suspects high nitrogen solubility in the jaw fats of beaked whales and pilot whales combined with their deep-diving lifestyles leads them to accumulate nitrogen in the jaw fats, which leaves them prone to decompression-related injuries. She also hopes that these new measurements will help us to understand how nitrogen circulates in whales during dives to identify other species that may be at risk of decompression injury as a result of human activity.

10.1242/jeb.129270

Lonati, G. L., Westgate, A. J., Pabst, D. A., and Koopman, H. N. (2015). Nitrogen solubility in odontocete blubber and mandibular fats in relation to lipid composition. *J. Exp. Biol.* **218**, 2620-2630.

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