OUTSIDE JEB

Getting fatter to stay warm

In the midst of the long Northern Hemisphere winter more than a few of us wish that we could hibernate, shutting off the outside world for the duration of the cold winter. This is the fate of many small mammals, which rather than decide to remain active throughout the cold, barren winters, retreat to hibernacula, emerging only once temperatures have warmed and the spring ushers in fresh food sources.

Hibernation, as it turns out, is about much more than just avoiding harsh environmental conditions, as suggested by a recent study on the edible dormouse by Claudia Bieber and her colleagues at the University of Veterinary Medicine in Vienna, Austria. While most previous research into hibernation has focused on the interactions between the environment and hibernation patterns, this study looked at how energy reserves and predator avoidance affect hibernation. Presenting the results of 4 years of study on both wild-caught and captive females, the study, in press at *Functional Ecology*, looked at the amount of fat the animals stored before they retreated to their burrows for the winter. This was then evaluated against the amount of time spent in hibernation, mass at emergence in the spring and a number of other factors including reproductive success and age.

During hibernation, small mammals enter a state of hypometabolism, called torpor, during which body temperature is lowered to levels nearing that of the environment. In this state many bodily functions are reduced or stopped completely. Although prolonged torpor can result in significant energy savings, it also comes at a price, resulting in a diminished capacity to fight off infections, as well as reductions in basic maintenance – such as protein synthesis – and even brain function. However, these adaptations also incur risks and they are the likely reason why torpor in colder climates never lasts throughout the entire winter. Instead, hibernators frequently warm up to active body temperatures, usually for less than 24 h. This leads to a trade-off between increases in energy savings resulting from lower temperatures during torpor and the physiological costs of prolonged exposure to low body temperatures.

What Bieber and her colleagues discovered was that females with larger fat stores were able to maintain higher body temperatures and rewarm more frequently than their thinner counterparts, lessening the potential costs. They also managed to emerge from hibernation with larger fat stores, which could be used to fuel early reproduction. What is surprising about their results is that even though the fatter females could have emerged earlier, they remained underground for similar periods of time to thinner females, prolonging inactivity well past the point when food became available and spending as long as 8 months in hibernation. It therefore seems that hibernation in these dormice is about more than just saving energy. These results, as well as previous work showing low rates of mortality during hibernation in a number of species, led the researchers to suggest that this prolonged period of hibernation also serves to avoid predation. These results suggest that when predicting how species will respond to environmental conditions, we need to consider not just their physiology but also other aspects of their ecology.

doi:10.1242/jeb.094722

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A noise ordinance in the retina

In the early morning hours of 22 October 1850, a German doctor called Gustav Fechner erupted from sleep in a paroxysm of insight. Fechner, a philosopher and experimental psychologist, had dozed off while contemplating the fundamental relationship between the physical world and human perception. Thirty years earlier, Fechner's former professor, Ernst Weber, had performed an experiment in which he had asked subjects to tell him which of two weights was heavier. Weber was surprised to discover that people found it much harder to discriminate small differences if the weights were large than if they were small, a result that became known as Weber's law.

Fechner's convulsive realization was that Weber's law could be described by a simple mathematical relationship: P=log(I), where P is perception and I is the stimulus intensity. This equation predicts that the smallest noticeable difference between two stimuli should increase linearly as the stimuli get larger. To test this, Fechner performed a classic series of psychophysics experiments in which he demonstrated that visual thresholds increase linearly with increases in background illumination.

Despite the elegance of the Weber–Fechner law, the underlying reason why it describes human visual perception has remained elusive. In addition, experiments by Horace Barlow and others in the 1950s showed that the Weber–Fechner law does not apply to human vision at low light levels. Now, a study of the retina from Juan Angueyra and Fred Rieke suggests a possible explanation for why human vision obeys the Weber–Fechner law, including why it only applies at high light intensities.

The mammalian retina consists of two types of primary photoreceptors: rods, which handle vision in low light, and cones, which operate at higher light intensities and contribute to color vision. Recording from primate cone photoreceptors, Angueyra and Rieke investigated how adaptation of cone signals and noise set limits on perceptible intensity differences. The authors varied the background luminance and measured both the noise in the transduction currents during constant light and the signal evoked by a brief light flash. They found that the light-evoked signals were attenuated as background light intensity increased, while noise levels remained relatively constant. These properties are consistent with the Weber–Fechner law and are in stark contrast to findings in rods, in which signal and noise both grow as light levels increase. This difference between rods and cones may explain why cone vision follows the Weber–Fechner law, while rod vision does not.

In addition to quantifying signal and noise in cones, the authors investigated the source of cone noise. By recording from single cones while pharmacologically manipulating the phototransduction pathway, they identified two primary sources of cone noise: gating of the cyclic nucleotide-gated channels that produce phototransduction currents, and fluctuations in the concentration of the second messenger molecules that open these channels. These data provide additional support that, in contrast to rods, spontaneous activation of cone pigments is not likely to contribute to perceptual thresholds.

One-hundred and fifty years after Fechner's pioneering pyschophysics experiments, Angueyra and Rieke have proposed a mechanistic basis for the Weber–Fechner law that relies on detailed measurements of photoreceptor currents and pharmacological manipulation of phototransduction chemistry. An interesting question is whether Fechner, if he were alive today, would accept this reductionist explanation for what he originally considered a phenomenon of the mind. My guess is that Fechner, who was among the first to consider how physiology constrains subjective human experience, would be satisfied.

doi:10.1242/jeb.094706

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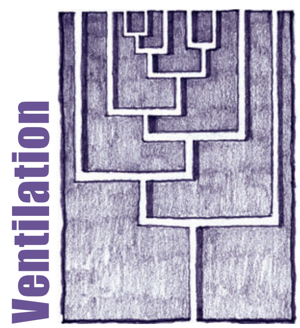
Airway clearance by reducing tensile strength



Vertebrate lungs and insect tracheal systems are respiratory organs that facilitate gaseous exchange between the air and body tissues. During development, when these organs mature and form a three-dimensional tubular network, the tubes are filled with liquid. However, shortly before birth or hatching, the tubes absorb the liquid and become filled with gas, a process that is known as liquid clearance. The underlying mechanisms of liquid clearance were largely unclear. In a study published recently in *Developmental Biology*, a team of scientists from Göttingen, Germany, guided by Reinhard Schuh demonstrated that gas-filling of *Drosophila* tracheal tubes depends on Waterproof, a fatty acyl-CoA reductase, which seems to be required for the production of a hydrophobic coat lining the inner tube wall that reduces the liquid's tensile strength so that gas bubbles are produced to fill the tubes.

The tracheal system of *Drosophila* is a model for studying the development of tubular networks in animals. Its development starts during mid-embryogenesis with the differentiation of groups of tracheal cells that invaginate from both sites of the embryo's lateral body wall. Without further cell divisions, these cells migrate, extend and form branches that finally fuse and interconnect to establish a liquid-filled tubular network. To prevent tube collapse, the tracheal cells produce a ridged cuticle forming the inner tube wall that, in addition, is covered by a coat of hydrophobic waxes. Shortly before hatching, liquid clearance and gas filling are initiated by a single gas bubble, which forms stochastically in one of the trunks, expands and finally fills the entire tubular lumen within 20 min. To uncover genes that are potentially involved in this process, Schuh's team performed an RNA interference screen. They silenced the expression of various genes and inspected the embryos by light microscopy to determine whether gas filling was impaired. In doing so, they identified a gene termed *waterproof*, which was specifically expressed in the tracheal system. Loss of function of the gene completely abolished gas filling while tracheal branching and maturation were unaffected.

The scientists were fascinated by this finding, because *waterproof* encodes a fatty acyl-CoA reductase, which is required for synthesis of the long-chain fatty alcohols that are essential for the production of the waxy coat on top of the tracheal cuticle directly facing the tracheal lumen. Indeed, when they analysed the ultrastructure of the tracheal cuticle by electron microscopy, they observed that in *waterproof*-deficient flies this innermost layer was damaged. To further analyse the function of *waterproof*, the researchers designed a set of elaborate genetic experiments that allowed them to direct expression of the *waterproof* gene in specific regions of the tracheal system. These experiments clearly indicated that regardless of where *waterproof* is expressed in the tracheal system, it always rescues the loss of the gas-filling phenotype of *waterproof*-deficient embryos, indicating that Waterproof acts in the entire tubular system regardless of the genotype of individual tracheal cells.

Taken together, these findings suggest that the tracheal gas-filling process depends on the presence of a hydrophobic coat on the surface of the tracheal cuticle. This coat presumably reduces the tensile strength of the liquid inside the tracheal lumen, which triggers the formation of a gas bubble that acts as a nucleation point for gas to permeate the entire tubular network. As Waterproof is also conserved in vertebrates, it is tempting to speculate that orthologues may have a similar function in lung airway clearance.

doi:10.1242/jeb.094714

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Visually guided landing on plants: no faceplants

A bee takes off from its hive and lands on a flower. This apparently effortless landing, however, is no mean feat. It requires a considerable amount of sensory feedback and fine speed control – miscalculations can be catastrophic. In order to land successfully, bees must slow down at just the right rate, and they require sensory information to control their final descent. When landing on a flat surface, the information comes in the form of optic flow. As a bee flies over the ground, patterns on the ground move past it. The speed of this largely translational movement informs the bee how quickly it approaches its target. But bees don't always land on flat surfaces; flowers and hives can be at any orientation. This raises the question, what information do bees require, and how do they use it, to prepare for landing?

Emily Baird from Lund University, Sweden, and her collaborators from Germany and Australia thought that another visual cue, a more complex version of optic flow, might just answer this puzzle. The group noted that, as a bee flies towards its intended landing site, that site's image will appear to grow in the bee's eyes. This visual expansion could help the bee gauge its approach speed and deceleration.

To test this theory, the team of researchers devised a series of experiments using optical illusions. While visual expansion could provide information about an approach, not all images are equally informative – and some are plain misleading. A checkerboard pattern will appear to expand strongly as you approach it: bees flying towards a checkerboard target slow down and land with very little variation in their approach trajectories. However, a circle of equally sized wedges of alternating color provides very few cues of apparent expansion and the bees that fly toward this target approach with highly variable speeds; some didn't even slow down until they had practically crashed into it.

These results were a vote in favor of Baird and her collaborators' visual expansion hypothesis, but they weren't enough. The team wanted to know whether the bees landed successfully by holding the rate of visual expansion of their target constant. The team returned to their bag of optical illusions and devised spiral-patterned targets with misleading 'apparent' visual expansion. These patterns appeared to expand or contract when rotated during the insect's approach. If the researchers were correct and the bees were using visual expansion to guide their landing speeds, the bees would land according to their illusory visual cues.

And that is exactly what the bees did. When approaching a rotating spiral that appeared to be expanding, the bees slowed their flight much earlier than they did without the misleading visual cues. Similarly, when bees approached a spiral that appeared to contract, they approached at higher speeds. The bees were indeed relying on visual expansion to modulate approach speed.

The beauty of Baird and colleagues' findings lies in their simplicity. By modulating approach speed based on visual expansion, bees can slow to safe landing speeds with minimal information. One parameter, visual expansion, is sufficient to guide a landing without additional information, such as distance, orientation or even the bee's own speed. In fact, Baird and colleagues think this system may be guiding flight landings in other species, and could be easily applied to robots. Visual expansion is an elegant solution to the complicated problem of safe landings; it just took a little bit of visual trickery to figure it out.

doi:10.1242/jeb.094698

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