Erratum

Music to his antennae

Douglas Fudge

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There was an error published in *J. Exp. Biol.* **210(5)**, v-vi.

In the second sentence of paragraph 4, the author incorrectly attributed the discovery of the active adjustment of antennal vibrations to Joseph Jackson and Daniel Robert. In fact, it was Martin Gopfert and Daniel Robert that made this discovery.

The sentence should have read as follows:

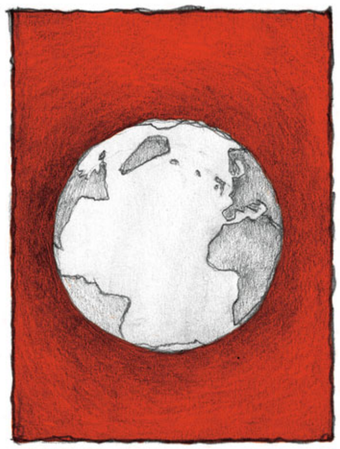
'Scientists previously believed that mosquito antennae vibrated passively in response to sound, however Robert and Martin Gopfert, at Universitaet Koeln, showed that mosquitoes actively adjust how much their antennae vibrate.'

We apologise to readers, in particular Dr Gopfert, for this error.

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

POLARIZATION



POLARIZED SQUID

Being able to continue displaying to members of the opposite sex, while actively hiding from predators, sounds like a tall order. However, Lydia Mäthger and Roger Hanlon from The Marine Biological Laboratory, Woods Hole suggest that this might be possible for squid because of the remarkable anatomy of their skin.

Cephalopods – squid, octopus and cuttlefish – perceive information about the polarization of light using their highly ordered photoreceptors. Because light tends to become polarized when it's reflected, one valuable use of this ability is that cephalopods can see silvery fish from below in high contrast: they are otherwise very difficult to see as they reflect whatever is above them and appear to blend into the sky.

Cephalopods also use polarized light perception for communication, elegantly demonstrated in cuttlefish by Nadav Shashar and his colleagues in 1996 (*J. Exp. Biol.* **199**, 2077–2084). Using a camera capable of spotting the orientation of polarized light, they observed pretty polarization patterns on cuttlefish arms and forehead. These polarization patterns were produced in under one second using specialized cells called iridophores, which are a type of chromatophore or pigment-containing cell. The pigments in iridophores differ from standard pigments in that they are iridescent, reflecting light that is polarized, with a colour dependent on the viewing angle.

Shashar also showed that polarization patterns mean something to the cuttlefish: on seeing a reflection of themselves in a mirror that did not distort their own polarization pattern, cuttlefish were much more likely to move away than if they were faced with their reflection from a mirror that distorted the polarization signal. From their observations that polarization patterns can be quickly controlled and mean something to the animal, and the fact that many cuttlefish predators can't detect polarized light, Shashar and colleagues introduced the concept of polarization patterns as a channel of communication concealed from predators.

Mäthger and Hanlon take this possibility one step further and show that not only can polarization patterns be a concealed communication channel, they can be a channel of communication while concealed. By studying the light patterns reflected from squid skin samples, they confirmed the two expected characteristics of iridophores: that the colour reflected depends on the viewing angle and that the reflected light is polarized. They also show that the overlying chromatophores act as colour filters but leave the polarization unaltered. This means that the squid has the potential to express itself freely using polarization patterns while doing its best to hide from predators by changing colour – as long as the predators aren't polarization sensitive too. Fortunately, predators such as sharks, dolphins, whales and seals appear not to be.

Another implication of this finding is that squid can use filtered reflected light to blend into their surroundings, matching their background more closely. Fish are stuck with appearing 'silvery' when light reflects off them; squid, however, can use the iridophores to reflect up to 90% of the light back through the chromatophores, changing its colour. This means that chromatophores can control a squid's appearance both by determining the reflectance, or colour bouncing directly off, and the properties of light allowed back through after bouncing off the iridophores, or transmission. In effect, this opens up a new way of decoupling a squid's colour from the colour's brightness, potentially enhancing camouflage, giving the chance for a squishy, tasty, slow mollusc to survive in the open seas. This part-reflection camouflage system does start to sound like 'how to build a Bond car', and so perhaps it isn't surprising that some of the funding for this work comes from DARPA, the American military research agency.

10.1242/jeb.000497

Mäthger, L. M. and Hanlon, R. T. (2006). Anatomical basis for camouflaged polarized light communication in squid. *Biol. Lett.* doi:10.1098/rsbl.2006.0542

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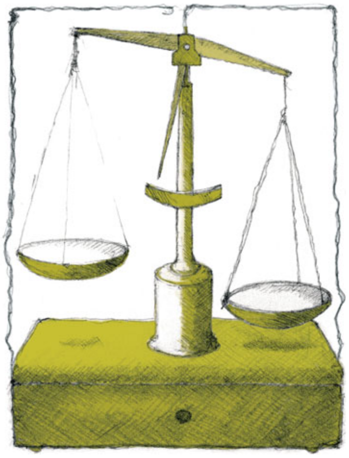
ASYMMETRY



SMELLING ASYMMETRY

Higher organisms are intrinsically asymmetric, and this seems to be important. In humans, partial situs inversus, a medical condition where the body's organs are positioned in a mirror image of normal, is usually an embryonic lethal condition, whereas complete situs inversus often goes undiagnosed until doctors fail to find hearts or appendices in the right place. Simpler organisms may be good places to seek the developmental basis for the decisions that make for asymmetric adults, except that asymmetry may not be immediately obvious.

Richard Poole and Oliver Hobert describe an intriguing example of asymmetry in the simple nematode *Caenorhabditis elegans*, where every single cell, and its progenitors, is known from the groundbreaking work of Brenner and colleagues. Although the nervous system appears to be symmetrical, some of the neurones within it show functional asymmetry. In particular, there are a pair of gustatory neurones, ASEL (left) and ASER (right) that are morphologically symmetrical and which sense distinct water-soluble molecules. While the paper by Poole and Hobert doesn't address why these neurones are asymmetrical, it does explain how this asymmetry is set up, and it is proven to result from a decision taken in the very early embryo.

The authors wanted to differentiate between two theories: whether the asymmetry is established in the very early embryo, long before the ASEL/ASER pair differentiate, or whether it is a late event that involves communication between the ASEL and ASER neurones themselves. These ideas draw from two rival theories of how bilateral animals develop: either that embryos are intrinsically symmetrical, and that asymmetry is imposed on this symmetrical ground state, or conversely that embryos are intrinsically asymmetric, and that symmetry is an acquired complex trait. How can these theories be tested?

The authors drew on the detailed knowledge of embryonic development in the worm and laser-ablated either the precursor of ASEL or of ASER to establish whether communication between the two neurones was necessary to establish asymmetry. In these organisms, one of the two neurones was completely absent but the other developed normally. So communication between ASEL and ASER was not required for them to differentiate.

Another possibility is that there is some molecule present in a spatially asymmetric way that cells can sense and so 'read' their identity. To test this, the authors looked at mutants of a G-protein alpha (*gpa-16*), which participates in very early asymmetry decisions in the embryo. In *gpa-16* mutants, the intrinsic slight asymmetry of the 6-cell embryo was randomized, as were the ASEL/ASER fates in the developed worms. However, was the randomization of ASEL and ASER fates due to a very early decision at the 6-cell stage, or were the ASEL/ASER cells reading environmental cues much later on? The authors made use of a temperature-sensitive mutant of *gp-16*. Knocking out *gp-16* with higher temperatures after the 6-cell stage only had no impact on ASEL/ASER fate, showing that a decision at the 6-cell stage must be critical.

Further experiments showed that even this early asymmetry depended on the very first cell division of the fertilised egg, in which the anterior/posterior axis is established. Interestingly, the authors implicated *Notch* as a key player in these early decisions: the *Drosophila* homologue is a rather famous developmental gene that codes for a membrane receptor that binds several proteins, and interactions between these proteins help cells to decide their cell fates relative to their neighbours. *Notch*-like genes are found in many organisms, so this led the authors to speculate that their model of intrinsically asymmetric lineages arising from the very earliest stages of the embryo might have a general validity beyond gestation in this simple worm.

10.1242/jeb.000463

Poole, R. J. and Hobert, O. (2006). Early embryonic programming of neuronal left/right asymmetry in *C. elegans*. *Curr. Biol.* **16**, 2279-2292.

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MOSQUITO ACOUSTICS

MUSIC TO HIS ANTENNAE

The whine of a mosquito in one's ear is one of the most annoying and unwelcome of sounds, yet to a male mosquito, this high-pitched buzzing is music to his ears, or at least his antennae. Joseph Jackson and Daniel Robert at the University of Bristol report in a recent paper some of the acoustic mechanisms that male mosquitoes use to detect nearby females and keep them in range during a pursuit.

Most insects use their antennae to detect sound, and mosquitoes are particularly well-endowed in this area. Sounds cause insect antennae to vibrate, and these vibrations are detected by a large cluster of sensory neurons at the base of the antennae, called Johnston's organ. In a male mosquito, each organ is made up of 16 000 sensory neurons, which is as many as are in the human cochlea. This is quite remarkable considering that humans are about 100 million times bigger than mosquitoes.

This fact is perhaps less surprising when one considers that a male mosquito's *raison d'être* is to listen for a female, track the sound of her buzzing and mate with her. Also significant is the fact that female mosquitoes are inefficient sound emitters due to their small size relative to the wavelength of the sound they produce. The physics underlying this effect is the same as that which makes a large subwoofer loudspeaker better at pumping out bass notes than a small tweeter speaker ever could.

Previous work by the authors demonstrated that mosquitoes make use of some of the same tricks that vertebrates use to filter and amplify sounds. Scientists previously believed that mosquito antennae vibrated passively in response to sound, however Jackson and Robert showed that mosquitoes actively adjust how much their antennae vibrate. In their latest paper, they attempted to put some of these mechanisms in their ecological context by measuring the response of male antennae to the sound of a passing female. To do this, they presented tethered males with sounds that replicated a female making a linear flyby. As a male listened to this louder and then softer sound signal, they measured his antennae's vibrations using a microscanning laser Doppler vibrometer.

The investigators found that the vibrations of the male antennae didn't vary linearly with the strength of the female signal, which is what you would predict if the antennae vibrated only passively with sound. Specifically, they found that there were two moments during a female flyby when the antennae deflected more than you would predict from the sound input alone, which suggests a process of active mechanical amplification. This phenomenon occurred during approaches when the female signal appeared to be about 2 cm away and getting louder, and again when the female appeared to be about 2.4 cm away and getting softer. The authors point out that the distance at which these effects dominate are far closer than the detection threshold, which is about 10 cm. They suggest that amplifying the signal at this close range may function as an 'autofocus auditory telescope' that allows males to lock onto a nearby female's acoustic signal and track her before she gets away.

While it is clear that the mechanical amplification of sound signals by mosquito antennae is an active process (dead mosquitoes don't amplify), it is not known exactly how this is achieved. Because the vertebrate ear is also capable of active amplification, studying mosquito hearing might ultimately help us understand how you detect that faint whine somewhere in your bedroom just after you get into bed, pull up the covers and turn out the light.

10.1242/jeb.000455

Jackson, J. C. and Robert, D. (2006). Nonlinear auditory mechanism enhances female sounds for male mosquitoes. *Proc. Natl. Acad. Sci. USA* **103**, 16734-16739.

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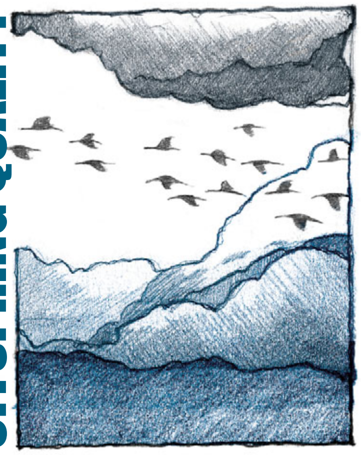
OFFSPRING QUALITY



UGLY DAD? INVEST IN EGGS!

Finding a mate with desirable qualities is big business for humans. In today's society, advertisements are rampant for businesses promising to find you the perfect mate. Of course, whether we are conscious of it or not, the underlying driving force for this human behaviour is our biological desire to successfully transmit our genes. But, what if one didn't have to find the perfect mate? What if it were possible to improve the quality of young produced with a lower-quality mate to maximize reproductive success? Apparently, female birds have figured this 'trick' out and can alter offspring quality before they hatch by manipulating the amount of vital nutrients present in their eggs. Kristen Navara and colleagues from the Department of Biological Sciences at Auburn University, Auburn, Alabama were interested in understanding this phenomenon in female birds.

Female birds invest in offspring by one of two contrasting strategies. Which strategy they use depends on environmental and social conditions, as well as the resource being allocated, for example nutrients. Some studies observed that females invest more resources in offspring sired by better-quality males; a phenomenon termed the 'differential allocation hypothesis'. Conversely, in other studies, females contributed resources in a compensatory fashion, supplying more resources to offspring sired by lower-quality males and enhancing the offsprings' quality, making up for the poor quality of the father.

The team wanted to know what strategy wild female house finches (*Carpodacus mexicanus*) use to allocate antioxidants to their eggs. Antioxidants are chemicals important in protecting organisms against oxidative stress, which is caused by reactive oxygen species that damage cells and tissues. Knowing that males with more colourful plumage are more attractive, the team set out to find how the patterns of yolk antioxidants – vitamin E, vitamin A and three carotenoids – were affected by male quality and attractiveness. They measured the quantity of these nutrients in 36-h-old eggs and compared the antioxidant levels to the attractiveness of the father.

The team found that female house finches deposited antioxidants in their eggs in a compensatory fashion, putting more into eggs sired by less-attractive males. The team argues that this strategy enables females to improve the quality of young fathered by less-attractive males and take the edge off the unfavourable conditions experienced by these offspring. For example, the team explains that less-attractive finch males provide less food. Since house finches are short-lived individuals, the team proposes that focusing on current attempts at reproduction, rather than investing in future attempts, may be the only viable strategy to maximize the number of offspring that they can produce. In essence, females choose from the males that are currently available and make the most of what they have, rather than waiting for a better quality male to come along.

10.1242/jeb.000471

Navara, K. J., Badyaev, A. V., Medonca, M. T. and Hill, G. E. (2006). Yolk antioxidants vary with male attractiveness and female condition in the house finch (*Carpodacus mexicanus*). *Physiol. Biochem. Zool.* **79**, 1098-1105.

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