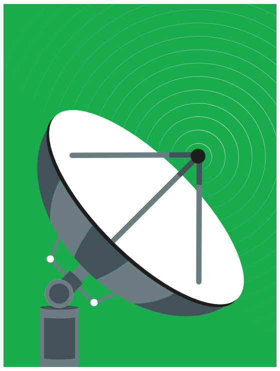
OUTSIDE JEB

# Fireflies' contrast-enhanced colored lights

SIGNAL EVOLUTION



If you have ever been outdoors in the suburban or rural USA, you have probably seen fireflies cheerfully lighting the evening. Fireflies, or lightning bugs (which are neither true flies nor bugs), are actually beetles – and though as a 5 year old I thought they glowed for my own amusement, the fireflies' light organs serve an important purpose. Adult fireflies use their light to find and identify mates, and larval 'glow worms' may keep predators away by using light organs to signal their unpalatability.

Even though firefly light signals serve common purposes, they come in a variety of colors, ranging from green to yellow to light red. Interestingly, variation in light color seems to have little to do with mate attraction and this led David Hall, Sarah Sander and colleagues at the University of Georgia, USA, to ask the next obvious question: why did variation in light color evolve in the first place? Earlier research on signal reception provided one possible explanation: sensory drive.

The theory of sensory drive suggests that evolution should favor conspicuous signals – signals that maximize signal-to-noise ratio and minimize degradation. So, Hall, Sander and colleagues translated the principles of sensory drive into some firefly-specific hypotheses. First, firefly species that are active earlier in the evening should have yellower lights to maximize contrast with the green ambient light reflected from vegetation (increasing signal to noise). Second, fireflies that are active later in the evening – especially ones with sedentary females – should have greener light, to increase the amount of light reflected off plants (minimizing signal degradation).

To test these hypotheses in an evolutionary framework, the researchers sampled the emission spectra (light color) of a massive number of fireflies (including males and females from 25 species and totaling over 750 individuals) across the eastern USA over 3 years. In addition, they collected data on the density of vegetation at each site and the time of day when the tantalizing creatures were active.

The results of all of this data collection proved tremendously rewarding. While the color variation across populations of single species was larger than the authors had anticipated, the species and populations that were active earlier in the day produced yellower light. Further still, populations that live in areas of abundant vegetation (with more green ambient light) emitted yellower signals, enhancing the contrast with their environment. In addition, the fireflies that were active later in the evening produced greener light and the team suspects that in the males, this may be due to ancestral conditions, the sensitivity of photoreceptors, or a number of other hypotheses. However, the researchers wanted to test the specific assumption that sedentary females would produce greener light than males to reflect off their leafy perches. Fortunately, the team had collected the light spectra of enough males and females from two species to test this hypothesis and they found that the females from both species were greener than the males, presumably to minimize signal degradation.

Having demonstrated these relationships both without and with phylogenetic context, Hall, Sanders and their collaborators suggest that light color within and across firefly species has evolved multiple times as predicted by sensory drive. The beautiful colors of these natural lights serve a functional purpose: and it has nothing to do with my childhood lantern preferences.

10.1242/jeb.130328

**Hall, D. W., Sander, S. E., Pallansch, J. C. and Stanger-Hall, K. F.** (2016). The evolution of adult light emission color in North American fireflies. *Evolution* **70**, 2033-2048.

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# What's on the vibrissa abscissa?

MECHANOSENSATION

The face of a rat is peppered with stiff, conical hairs called vibrissae, more commonly known as whiskers. As nocturnal animals that live in dingy, cramped hovels, rats rely on tactile information from their whiskers to get through the night. Using just their whiskers, they can run through complicated mazes and recognize complex objects – tasks that humans typically rely on vision to accomplish.

These feats of tactile perception begin with mechanosensory neurons, whose dendrites reside at the base of each whisker. A longstanding goal has been to understand what information these mechanosensory neurons are extracting from the whiskers. Specifically, do mechanosensory neurons encode object position and whisker movement during touch, or do they simply encode the mechanical forces acting at the base of the whisker?

To distinguish between these possibilities, Nicholas Bush, Christopher Schroeder and colleagues from Mitra Hartmann's lab at Northwestern University, USA, used single-unit

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extracellular recordings to measure the spiking activity of mechanosensory neurons that innervate whisker follicles. They investigated two types of whisker wiggling: active movements in awake, behaving rats and manual movements, in which they deflected the whiskers of anesthetized rats. By tracking the position of the whiskers with video, the authors were able to precisely measure kinematic variables of whisker movement, such as the angular position, velocity and distance to an object. They also used a biomechanical model of whisker bending to estimate the mechanical forces and moments at the base of the whisker.

The authors then examined how the spike trains of mechanosensory neurons encode tactile stimuli. They employed a framework called a generalized linear model that allowed them to estimate which input variables were best at predicting the firing rate of each mechanosensory neuron. Their models revealed that different neurons encode different combinations of kinematics and mechanics. Overall, however, the activity of most mechanosensory neurons was better predicted by mechanical rather than kinematic variables.

This finding alters our view of tactile processing in the whisker system. Previous studies have shown that rodents can use their whiskers to precisely localize the position of objects and that object position can be decoded from neurons in the somatosensory cortex. Thus, it was thought that sensory neurons might directly encode object position. However, these results indicate that additional processing may be needed to transform the code for mechanical force into a code for position and movement.

Where might this transformation take place? Each whisker is innervated by hundreds of mechanosensory neurons that fall into at least eight different classes, based on their anatomy and physiology. These sensory neurons project into the trigeminal nucleus of the brainstem. From here, central neurons route whisker information to multiple different brain regions, including the somatosensory cortex by way of the thalamus. Perhaps as early as the trigeminal nucleus, integration of diverse whisker signals could underlie a transformation from a mechanical to a kinematic code. Cracking this problem will require a detailed understanding of different mechanosensory neuron classes and the logic of their integration within circuits of the central nervous system.

Another possibility is that the brain does not need to transform the neural code from mechanics to kinematics, because these two codes are tightly correlated in a rat's normal life. In this paper, the authors compared manual and active whisking in order to sample a broad range of whisker movements. In awake, behaving rats, whisker movements are far more constrained. Perhaps the limited range of natural whisking could allow downstream circuits to decode object location directly from a code based on mechanics. Testing this idea might require teaching rats to whisk outside of their comfort zone, a noble but unenviable task for which volunteers may not be forthcoming.

10.1242/jeb.130336

**Bush, N. E., Schroeder, C. L., Hobbs, J. A., Yang, A. E., Huet, L. A., Solla, S. A. and Hartmann, M. J.** (2016). Decoupling kinematics and mechanics reveals coding properties of trigeminal ganglion neurons in the rat vibrissal system. *Elife* e13969.

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## Bumblebees have a sweet tooth


There is nothing like a bit of candy to satisfy a craving for sweet treats. Humans, along with many other animals, can taste their food and use this sense to detect when food is energy rich, containing carbohydrates like sugar. For a bee, a garden of blooming pollen-laden flowers presents a smorgasbord of potential food sources. However, flower pollen is also highly variable in its chemical composition, suggesting that pollens may have unique tastes for pollinators, yet we know very little about the role that pollen flavour and bee taste play in pollen collection.

Felicity Muth, Jacob Francis and Anne Leonard of the University of Nevada, USA, investigated whether bees used taste to decide which flowers to visit. The researchers used bumblebees (*Bombus impatiens*), a pollinator species that consumes flower pollen, to answer their research questions. The team created three pollen blends – a sweet blend (including sucrose), a neutral blend (with added cellulose) and a bitter blend (flavoured with quinine) – with similar nutritional value, to test the bees' preferences. Then, they presented the flavoured pollen blends to bees in fake flowers and assessed the bees' preferences, their willingness to visit new flowers after their initial pollen experience and the amount of pollen that they collected.

Having observed the frenetic insects' activities and preferences, the team concluded that bees do have a sweet tooth. The insects spent more time collecting pollen from the flower with sweetened pollen than from the flowers with unflavoured (added cellulose) or bitter pollen. The bees also visited sweet- and neutral-flavoured flowers more often. In addition, the bees that had been provided with the quinine-flavoured pollen collected the smallest amount of pollen: they appear to dislike bitter flavours. And when the scientists presented the bees with additional flower choices, they were more likely to sample a new flower if they had just experienced the bitter pollen.

Muth and colleagues' work shows that bees preferentially collect sweeter, rather than bitter, tasting pollens. This discovery may partially explain the diversity in the chemical composition of pollens. Plants may be ensuring that pollinators remove a little pollen at a time (it tastes good), while ensuring they don't remove it all at once (it can't taste too good). This strategy would also maximize pollen transfer to other plants of the same species to ensure successful pollination and reproduction. This study opens up new avenues for exciting future research that will allow us to understand the basic mechanisms that underlie plant–pollinator interactions.

10.1242/jeb.130344

**Muth, F., Francis, J. S., Leonard, A. S.** (2016). Bees use the taste of pollen to determine which flowers to visit. *Biol. Lett.* **12**, 20160356.

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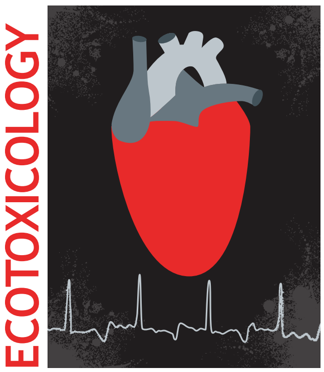
## Salmon versus dilbit: it's a matter of the heart




When it comes to the rush for 'black gold', the oil sands of the Western Canada Sedimentary Basin are one of the largest crude oil reserves in the world. Most of this oil is found in the form of bitumen, which when diluted is known as dilbit – for diluted bitumen – ready for transport via a transcontinental pipeline network for refinement. Proposals are currently underway to expand the existing pipeline network into the Pacific Northwest of North America, potentially taking it through critical freshwater habitats and the migratory routes of economically important fish, such as the Pacific salmon. Although spills from pipelines in the aquatic environment are rare, it is hard to decontaminate pollution when they occur. In addition, dilbit contains a mixture of chemicals, such as metals, naphthenic acids (NAs) and polycyclic aromatic hydrocarbons (PAHs), that are known to be toxic to fish. Low doses of PAHs in particular have been shown to impair swimming ability and cardiac function in fish, which can have long-term implications for migratory species, such as salmon. These fish rely heavily on their highly performing cardiovascular system to power their exertions as they migrate out to sea as juveniles and return to their native freshwater stream as adults.

Sarah Alderman, a postdoctoral fellow at University of Guelph, Canada, and her colleagues set out to identify the potential risks of accidental exposure of Pacific salmon to dilbit and the possible impact on their ability to migrate. Working with sockeye salmon (*Oncorhynchus nerka*), the team exposed juvenile fish to sub-lethal and environmentally relevant concentrations (of a few parts per billion) of dissolved contaminants from dilbit for 1 and 4 weeks. To test the hypothesis that exposure to low doses of dilbit impairs the migratory ability of salmon by inducing cardiotoxicity, the authors conducted swim performance tests on the exposed fish to assess their swimming ability. This was then followed by an examination of the heart tissue, to look for changes that may impair the fish's ability to sustain the high levels of exercise that are required during migration. In addition, Alderman and colleagues conducted an analysis of the fish's liver tissue, to determine whether chemical detoxification pathways were affected by the exposure.

The team was able to demonstrate, for the first time, that exposure to low and environmentally relevant levels of dilbit impairs the cardiovascular system, and that this effect is dependent on both the dose and the length of the exposure. While low doses of dilbit had no effect on swimming performance, higher doses induced heart remodelling and did impair swimming, thus affecting the migratory capacity of the exposed fish. In addition, the authors noted that all doses of dilbit induced an increase in cellular detoxification pathways in the liver, increasing the risk of producing secondary cellular compounds that may induce toxicity if the exposure to crude oil occurs for an extended period of time.

While previous studies have shown that crude oil components do affect heart shape and induce changes in the structure of the heart muscle when exposure occurs at the embryo life stage, the current study is the first to show that these effects also occur in juvenile fish and may be an indicator of dilbit or crude oil exposure. Therefore, in the case of salmon versus dilbit, it appears that it is all a matter of the heart.

10.1242/jeb.130351

**Alderman, S. L., Lin, F., Farrell, A. P., Kennedy, C. J. and Gillis, T. E.** (2016). Effects of diluted bitumen exposure on juvenile sockeye salmon: from cells to performance. *Environ. Toxicol. Chem.* doi: 10.1002/etc.3533

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