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

YOU ARE UNDER MY CONTROL…

Being a mother can be very hard work, and finding enough food to feed your young is risky and time-consuming. But some parasitoid species give their young the best start in life by having an energy-rich meal ready and waiting when they emerge from the egg. The catch is that this very nutritious breakfast is the body of a hapless victim, its muscles paralysed by the mother's venom. However, not all wasp mothers use the same paralytic approach to ensure her brood's future: *Ampulex compressa* uses a sophisticated alternative mechanism; she catches and manipulates her victims. Instead of disrupting the signals between the victim's motor neurons and muscles to paralyse them, *A. compressa*'s venom alters the victim's behaviour by targeting its stings to specific parts of the cockroach prey's nervous system, leaving it at the wasp's mercy. In a review published in the *Journal of Comparative Physiology*, Frederic Libersat describes his work on this intriguing system.

When a female *A. compressa* is ready to provide for her brood, she attacks the cockroach and lands on its back. She then delivers the first of two deadly stings, accurately injecting venom into a part of the nervous system called the pro-thoracic ganglion. This interferes with the synapses connecting to the leg motor neurons and causes temporary paralysis of the cockroach's front legs so that it is unable to fight off the attack. The wasp is now poised to deliver the second sting, injecting the venom directly into the brain and the sub-oesophageal ganglion, causing the cockroach to behave in a strange and unexpected way. Once recovered from the temporary paralysis caused by the first sting, the venom induces the cockroach to groom its antennae very carefully. This continues for about 30 minutes, during which time the cockroach remains where it was stung and does not escape. It is at the mercy of the wasp, who leads the cockroach to a pre-prepared burrow before total paralysis sets in.

The venom is so effective because it works by targeting only certain parts of the nervous system. Firstly, the venom probably activates the neural network that controls grooming because it contains large quantities of the neurotransmitter dopamine; the signalling chemical used in this network. The venom also overrides many other behaviours by stimulating grooming behaviour. Most importantly for the wasp, escape behaviour is stalled. It is almost impossible to provoke the cockroach to run away from danger. The venom probably interferes with the part of the walking network that receives signals from all over the body and makes connections with the motor neurons that control the leg muscles. Specifically, the motor neurons that produce rapid movements are deactivated, so the cockroach can walk but not run to save its life.

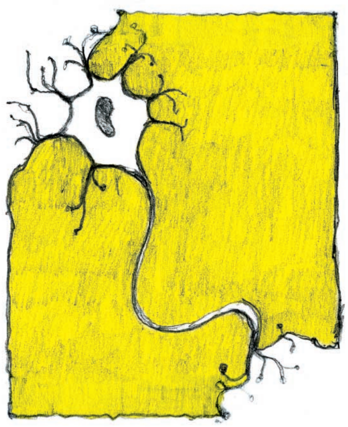
The wasp has developed a highly efficient way of controlling its prey with a cocktail of chemicals, ensuring that when its larva emerges after 6 days of incubation it has a feast waiting to be devoured!

10.1242/jeb.00683

Libersat, F. (2003). Wasp uses venom cocktail to manipulate the behaviour of its cockroach prey. *J. Comp. Physiol. A* **189**, 497-508.

Laura Blackburn
Cambridge, UK
lmlb2@cam.ac.uk

TOUCH



RESONATING WHISKERS TELL A TOUCHY TALE

Anyone who has watched a rat explore an object or environment knows that whiskers play a vital role in the inspection process. Unlike our hairs, whiskers are capable of discriminating between surfaces that differ ever so slightly in texture. With such finely tuned sensory abilities, it is clear that whiskers are more than overgrown hairs that respond to pressure changes. Instead, their acuity relies on a different mechanism. As recent work from two laboratories demonstrates, a whisker's mechanical resonance seems to hold the key to how a rat senses the world.

Some structures have the intriguing property of resonance: when vibrating at their resonant frequency, the amplitude of vibration is disproportionately large. Maria Neimark reasoned that if each whisker vibrates at unique resonance frequencies, a rat might be able to use its whiskers to perform a type of Fourier analysis, decoding the complex stimulus generated by brushing the whiskers over a textured surface. By deploying an array of differently tuned whiskers, vibrational patterns can be transformed into spatial patterns, simplifying the work the nervous system has to do to encode the stimulus.

Neimark and colleagues tested these ideas using whiskers on anesthetized rats and on isolated whiskers mounted on a metal beam. Stimuli were delivered using a piezoelectric device or by deflection with a rod, and the results measured using an optical switch. Whiskers were found to have sharp tuning curves and to resonate at frequencies between about 50 and 750 Hz. This resonance probably functions to amplify tactile signals: stimuli that vibrate a whisker near its resonance frequency increase its deflection as much as tenfold, which should deliver a larger stimulus to the neurons innervating the base of the whisker. Neimark and colleagues also demonstrated that, like a xylophone, the resonance frequencies of whiskers depends on their length, with longer whiskers having lower resonance frequencies. This, along with the fact that rat whiskers are organized into tidy rows, with longer ones towards the back, suggests that rats could use their array of differently sized whiskers to create a map of stimulus frequencies.

In a separate paper, Mitra Hartmann and colleagues mounted rat whiskers on a vibration table and delivered stimuli either at controlled frequencies or by brushing against the whisker with forceps, and recorded the whisker movements on high-speed video. At some frequencies, the tip of the whisker moved disproportionately more than the base, demonstrating the whisker's resonant properties. In addition, the authors examined whisker movements using videotape of a rat exploring a chamber in which a vertical bar had been mounted. This experiment revealed that as a rat passes a nearby object, whiskers deflected by the object oscillate after passing the object, suggesting that whiskers can be used to detect edges of objects and perhaps even to determine the distance between the animal's snout and the object. One of the most intriguing points raised by Hartmann's study is the suggestion that rats may be able to actively modulate the damping on individual whiskers by altering blood flow and muscle activity around the whisker base. If so, the resonance of whiskers can be actively altered, suggesting that the simple spatial map proposed by Neimark and her colleagues may not be so simple after all.

10.1242/jeb.00682

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Hartmann, M. J., Johnson, N. J., Towal, R. B. and Assad, C. (2003). Mechanical characteristics of rat vibrissae: resonant frequencies and damping in isolated whiskers and in the awake behaving animal. *J. Neurosci.* **23**, 6510-6519.

Cynthia A. Wei and Heather L. Eisthen
Michigan State University
weicynth@msu.edu
eisthen@msu.edu

SIGNALLING CASCADE

NO PAIN, NO GAIN?

Wouldn't it be nice to enjoy the benefits of exercise without the effort? For example, endurance physical training results in elevated muscle mitochondrial content for increased aerobic respiration and the transition of fast-twitch fibers into slower oxidative fibers. One step towards the goal of gain without pain is the elucidation of the signaling cascades that increase both metabolic and contractile capacities in muscle. Recently, it has been appreciated that one important signaling cascade during exercise involved AMP-activated protein kinase (AMPK). Indeed, the activation of AMPK can mediate some of the metabolic effects associated with exercise. However, the role of this pathway in modifying muscle contractile properties remains unclear. The paper by Charles T. Putman and collaborators examines this question and further investigates the effects of activating the AMPK pathway on glycolytic and oxidative metabolic profiles.

In order to test these hypotheses, the authors injected rats for a month with a compound, AICAR, that is known to activate AMPK. The team looked at the activity of several mitochondrial enzymes as markers of mitochondrial biogenesis, the expression of uncoupling protein-3 (UCP3), a mitochondrial protein that is associated with the regulation of burning fat and, finally, the proportion of oxidative fibers in muscle.

The first set of results in fast-twitch muscle revealed that the activity of mitochondrial enzymes was elevated in the groups of rats treated with AICAR. This result suggests that AMPK plays a role in mitochondrial biogenesis due to exercise.

Also, the increased mitochondrial biogenesis led to an increase in UCP3 in the treated rats. However, the increase in UCP3 protein level was higher than for other mitochondrial proteins, which suggests that UCP3 might be specifically targeted in mitochondria by the AMPK signaling pathway. The team suspects that as UCP3 expression has been associated with the metabolism of lipids, the preferential upregulation of this protein could be related to the increased oxidation of fatty acids that occurs during exercise.

For the second part of their study, the authors examined the expression of various myosin heavy chain isoforms, which are markers of the different fiber types in fast-twitch muscle. The proportion of oxidative fibers was not increased in AICAR-treated animals. Therefore, activation of AMPK cannot mimic the contractile adaptations that occur in muscle during endurance training.

Overall, this study shows that activation of the AMPK signaling cascade leads to some of the beneficial metabolic effects of exercise, without affecting muscle contractile properties. This type of pioneering study is fundamental to our understanding of how exercise affects organismal physiology. Finally, the search for evolutionary conserved signaling pathways in other organisms should be of great interest for comparative physiologists in the years to come.

10.1242/jeb.00684

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Julie St-Pierre
Dana-Farber Cancer Institute and Harvard Medical School
julie_stpierre@dfci.harvard.edu

SEX REVERSAL

NOT ENOUGH MALES? MONOAMINES CHANGE EVERYTHING!

The saddleback wrasse, *Thalassoma duperrey*, inhabits corals reefs in the Hawaiian Islands. Remarkably, when the ratio of males to females in a population of wrasse becomes too low, the largest female transforms herself into a male over a 6–8-week period. Unsurprisingly, sex reversal in fishes requires a complete reorganization of physical, physiological and behavioural systems. In addition, sex reversal requires the conversion of external social cues into internal chemical cues. While past studies had investigated the roles of various hormones, neurotransmitters and neuromodulators as the trigger for the sex reversal process, an important group of chemicals that had not yet been investigated were the monoamine neurotransmitters such as dopamine, serotonin and noradrenaline. The hypothesis of the study by Larson and coworkers was that sex reversal in the wrasse would be accompanied by changes in the activities of these monoamines within different brain regions.

In order to induce sex reversal in the larger fish and investigate the role of monoamines in the process, a series of floating enclosures were set up and a large and small female were placed in each. The team chose to monitor regions of the brain that are known to be involved in regulating sexual function and behaviour and are homologous to mammalian systems. The team sampled brains from the larger fish at various time points throughout the process of sex reversal and measured the monoamine levels using high-performance liquid chromatography (HPLC).

Larson and colleagues found changes in monoamine metabolism in all of the brain regions that were examined. The most prevalent alterations in monoamine system activation were observed during the first week of sex reversal, at which time the sexual transition is primarily behavioural.

One of the brain regions sampled appeared to be involved in regulating the fish’s physical alterations. In the preoptic area of the brain, linked with male sexual function and behaviour in all vertebrates, the team found changes in both serotonergic activity and noradrenergic activity, which could potentially trigger the reorganization of the reproductive axis.

The remaining four regions of the brain appeared to be involved in altering the female’s behaviour during her sexual transition. The amygdala, an area in the brain that is important with respect to aggression, dominance and stress in vertebrates, exhibited significant changes in serotonin metabolism during sex reversal in wrasse. These changes were probably related to the observable increase in territorial acquisition and defense as the wrasse changed from female to male. In the ventral hypothalamus, noradrenergic activity, which is typically associated with female behaviour in this region of the brain, was reduced. By contrast, the locus coeruleus showed an increase in noradrenergic activity in the later stages of sex reversal, probably in response to an increase in circulating male sex hormones such as testosterone. The raphe nucleus showed an increase in serotonergic activity at the early, behavioural stages of sex reversal. During this time it is critical for the changing female to show dominance over other females, and dominant behaviour results in lower serotonergic activity in many animal models.

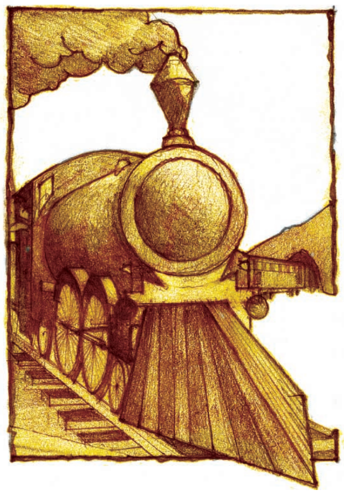
The present study is the first to investigate monoamines and their role in environmentally stimulated sex reversal and has revealed that monoamines in different brain regions are important in both behavioural and gonadal sex reversal in the saddleback wrasse.

10.1242/jeb.00685

Larson, E. T., Norris, D. O. and Summers, C. H. (2003). Monoaminergic changes associated with socially induced sex reversal in the saddleback wrasse. *Neuroscience* **119**, 251-263.

M. Danielle McDonald
University of Miami
dmcdonald@rsmas.miami.edu

FLIGHT EVOLUTION



ROW, ROW, ROW YOUR WINGS

Birds do it, bees do it, but unfortunately we cannot. I'm alluding to the capacity for self-powered aerial flight, an activity that we humans can only appreciate from a foreign perspective. Nonetheless, because we have designed our own flying machines from scratch, we recognize all too well the difficulties inherent in getting something aloft and keeping it there. Hence it makes perfect sense that questions relating to the origins of flight in various animal groups perennially pique our interest. In a newly published study, James Marden and Michael Thomas draw upon numerous sources (paleontology, behavior, developmental genetics and morphology) to make the case that flying insect's wings evolved from the gills of aquatic or amphibious ancestors.

As with the origins of bird flight, myriad hypotheses have been proposed regarding the evolution of flight in insects. Two leading hypotheses differ markedly in their approach to understanding this remarkable event. One proposes that insects are a sister-group of myriapods (e.g. millipedes and centipedes) with wings that evolved from lateral protrusions of the thorax. Implicit in this hypothesis is the notion that wings would have arisen in a terrestrial environment, after progressing through a sequence of functional stages like parachuting, gliding and ultimately through to flapping flight. The other hypothesis, and the scenario that Marden and Thomas favor, suggests that insects are a sister-group of crustaceans (e.g. crabs, brine shrimp and copepods) whose wings were derived from gills, presumably in an aquatic or amphibious environment. How might a gill evolve into a wing? Marden and Thomas address this by developing a 'wings from gills' model based on their study of *Diamphipnopsis samali*, a species of stonefly that possesses wings on its thorax and gills on its abdomen, a condition considered primitive for flying insects.

Marden and Thomas first collected a number of live specimens from southern Chile and performed tests of their locomotor capacity in air and water. Their ability for flight is only marginal, but on the water surface they create lift- and drag-based forces for propulsion using their hindwings and forewings respectively (see video sequences at http://www.bio.psu.edu/People/Faculty/Marden/movies/rowing.mov). The drag-based rowing locomotion of the forewings is intriguing because it may serve as an analog for an intermediate step in the evolution of insect flight.

As I understand it, their 'wings from gills' scenario goes something like this: (1) ancestors of flying insects were aquatic, bore moveable thoracic and abdominal gills and relied on a blood-based gas exchange system rather than the tracheal system seen in insects today; (2) to take advantage of high aerial oxygen content, pterygote ancestors began to exploit the water surface where their gills could be exposed to air as well as water; (3) once at the air–water interface the tracheal system began to evolve, reducing the need for external gills in gas exchange and allowing them to become specialized for other tasks; (4) structurally sound and mobile thoracic gills began to be used as locomotory structures involved in various forms of water-surface travel (e.g. skimming, rowing, sailing) and eventually were co-opted for more sophisticated 3-dimensional aerodynamic function.

Like any evolutionary scenario, this one requires several major assumptions, not least of which is that insects at one time used a blood-gas exchange system. Regardless, by blending varied modern analyses and a bit of imagination, Marden and Thomas have opened a new window into how insects might have evolved not only flight but their wings as well.

10.1242/jeb.00686

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Gary B. Gillis
Mount Holyoke College
ggillis@mtholyoke.edu

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