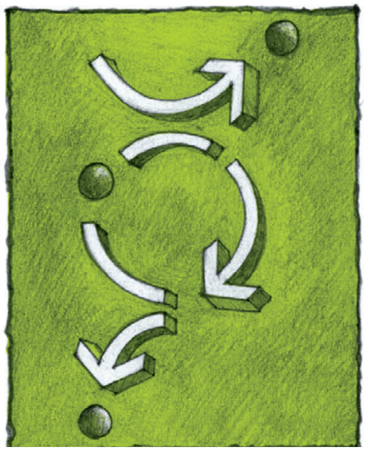
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

OXIDATIVE STRESS



A BIRD'S SECRET TO LONGEVITY

In recent decades, we have made enormous progress toward understanding the cellular basis of aging, and our current knowledge suggests that the very thing that allows cells to survive is also inherently linked to their degeneration. The oxidative stress theory proposes that mitochondria produce, as a natural by-product of respiration, harmful reactive oxygen species (ROS) that accumulate, damaging molecules (proteins, lipids and nucleic acids) and deleteriously affecting cell function over time. Thus, over the years researchers have manipulated the diets or the genetics of animals to alter their susceptibility to oxidative damage, with the aim of extending their longevity. However, nature has provided us with a striking example of differential longevity in the pigeon and the rat; pigeons can live up to 7 times longer than rats. This comparison has baffled researchers for decades as pigeons have a higher metabolic rate and a higher body temperature (both of which promote a higher rate of ROS production and shorten life expectancy), yet they outlive their furry cousins by three decades! Previous comparisons between the capacity of rats and pigeons to detoxify ROS or prevent oxidative damage to biomolecules generated contradictory results. Magdalene Montgomery, Anthony Hulbert and William Buttemer decided to try to reconcile these apparent contradictions and attempt to identify factors that may be responsible for that difference in longevity between rats and pigeons.

The team initially looked at *in vitro* mitochondrial production of ROS in liver, skeletal muscle and heart. Their findings suggest that rats do not consistently produce more ROS in these tissues when compared with pigeons. However, when they compared ROS production with mitochondrial oxygen consumption, only rat cardiac muscles 'leaked' relatively more free radicals than pigeons. Next, the team evaluated the differences in antioxidant defences in the plasma, liver, heart and muscle of the two animals. Overall, the different indicators (enzymatic and non-enzymatic antioxidants) were not consistently higher in one animal or the other across tissues. Montgomery and colleagues then looked at the phospholipid composition of tissues and mitochondria from rats and pigeons to calculate a peroxidation index, a measure of membrane susceptibility to oxidative damage, as some fatty acids are more prone to peroxidation. In most tissues examined, the team found that rat cellular and mitochondrial membranes were more susceptible to peroxidation than the corresponding membranes in pigeon. Finally, the authors looked at oxidative damage at the DNA, protein and lipid level and found that rats had a higher level of mitochondrial DNA damage in the heart and higher protein damage in plasma, while pigeons had higher lipid damage in the liver.

In this comprehensive study, Montgomery and colleagues shed light on some inconsistencies previously reported in the comparison of oxidative stress markers between the long-lived pigeon and relatively short-lived rat. Overall, this work suggests that of all the components of the oxidative stress axis, the membrane peroxidation index is the most consistent with the oxidative stress theory of aging in these animals. More importantly, the variability of the other factors examined certainly warrants comprehensive examination of the different components of the oxidative stress axis in future investigations.

10.1242/jeb.050013

Montgomery, M. K., Hulbert, A. J. and Buttemer, W. A. (2011). The long life of birds: the rat–pigeon comparison revisited. *PLoS One* **6**, e24138.

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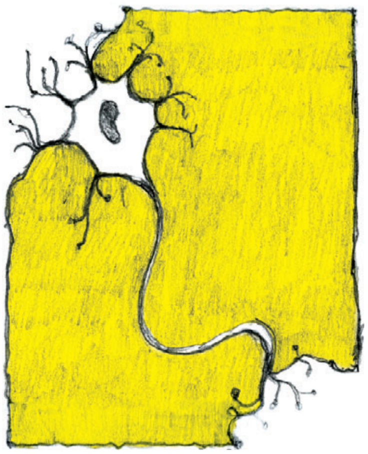
CONTROL OF BEHAVIOUR



SEA SLUG SWIMMING SURPRISE

Since the days of Darwin, we have greatly increased our understanding of how organisms have been shaped by evolution. We can uncover the interaction between genes and the environment by studying fossils and the processes by which animals develop. However, the evolution of behaviour is more difficult to study; progress can only be made by trying to understand and compare how different nervous systems produce behaviours, as the fossil record holds very few clues.

Historically, neuroscientists have designed their experiments based on the assumption that a behaviour found in two related species must be produced by the same neural mechanism. But is this really the case? A team of scientists led by Paul Katz at Georgia State University has tackled this question by looking at how the nervous systems of two closely related species of sea slug (*Melibe leonina* and *Dendronotus iris*) produce their side-to-side swimming behaviour.

The core of the neural swimming machinery of *Melibe* consists of two pairs of cells, swim interneuron 1 (Si1) and swim interneuron 2 (Si2), which are interconnected and fire bursts of action potentials in phase with the swimming motion. The first experiment the team performed was to identify the homologues of these cells in *Dendronotus*, which they did by injecting cells in the homologous area of the brain with a fluorescent dye.

The team found two pairs of cells that fitted the bill. The cells looked similar, had projections to the same areas within the brain, and had the same neighbouring cells as their *Melibe* counterparts.

After identifying the Si1 and Si2 homologues, the team tried to find out whether they could have the same role in the two species by measuring whether the patterns of electrical activity of the cells were similar.

They found that while the *Dendronotus* Si2 homologue did have very similar activity patterns to those of *Melibe*, the Si1 homologue did not. It did not fire action potentials in phase with the swimming movement, which means that it is not part of the core neural swimming machinery and suggests that there are differences in how the two nervous systems produce the swimming behaviour.

To further study the potential differences between the two species, they characterized the pattern of connectivity of Si1 and Si2 in *Dendronotus*.

The team saw that there are a number of differences in how the cells are wired up. For instance, *Dendronotus* overall has fewer inhibitory connections, lacking those between Si1 and Si2 altogether. The cells therefore function differently in the production of a similar behaviour.

The team's findings show that similar behaviours in closely related species do not necessarily have the same underlying neural mechanisms. In order to unravel the evolutionary history of the side-to-side swimming behaviour in sea slugs the team will have to look at other closely related species to see which neural mechanism must have been used by the common ancestor. Furthermore, their findings have important practical implications for neuroscientists and should serve as a cautionary tale for those studying the evolution of behaviour.

10.1242/jeb.050021

Sakurai, S., Newcomb, J. M., Lillvis, J. L. and Katz, P. S. (2011). Different roles for homologous interneurons in species exhibiting similar rhythmic behaviors. *Curr. Biol.* **21,** 1036-1043.

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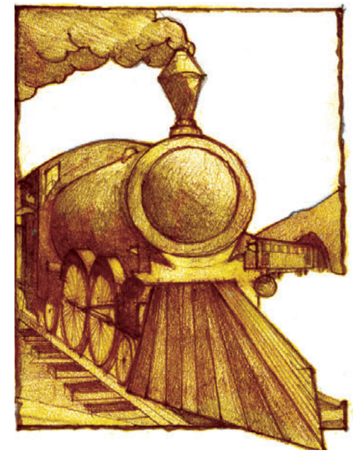
GAIT CHANGES



CHANGING GAITS MECHANICALLY

We usually think that we – meaning our nervous systems – are in control of what our bodies do. Our intuitions lead us astray: in many cases, it seems that body movements only result from interactions among the musculoskeletal system, the external world and the nervous system. In rapid behaviors like running, physical interactions can be dominant, and the nervous system – particularly higher centers in the brain – may only have a small supporting role.

In a recent paper in *Physical Review E*, Shinya Aoi, Tsuyoshi Yamashita and Kazua Tsuchiya provide a nice example of this complex coupling between nervous system, body and environment. Using a computational model, they examined how gait changes come about – why a dog might shift from a walk to a trot or *vice versa* – and found that coupling between the body and the environment could cause the gait to change, with no explicit shift in the neural control pattern.

To examine this effect, the researchers built a computational four-legged animal. It has a 'nervous system' – a simulation of a neural circuit, present in the spinal cord of all vertebrates, called a central pattern generator (CPG), that produces the pattern of muscle activity for locomotion. The CPG controls a 'body' – a mechanical model of the four legs, each with a hip and a knee, but no ankle. Crucially, the forelimbs and hindlimbs are linked by a rotational spring joint at the waist. Each leg can contact the 'environment', which has a slightly springy surface. And finally, the CPG receives sensory input by phase resetting: each time a leg reaches a particular angle forward, the CPG is pushed towards a specific phase in the step cycle.

The researchers set up the model so that each pair of left and right legs alternated with one another, but they didn't specify how the forelimbs and hindlimbs should be coordinated. They found two stable coordination patterns: a pace, in which both legs on the left side alternate with both legs on the right; and a walk–trot pattern, in which the model shifted from walking at low speeds to trotting at high speeds.

There was not a single speed at which the model shifted from a walk to a trot; instead, the shift speed depended on whether the model's speed was increasing or decreasing. If the model speeded up from a slow walk, it only shifted to a trot at a relatively high speed. If it slowed down from a high speed trot, it carried on trotting for a long time, even at speeds much slower than the first transition speed (when speed was increasing and the model shifted up to a trot), until the quadruped finally shifted to a walk at a relatively low speed. This effect, called hysteresis, has been observed in cats, horses and humans, among others.

Interestingly, the hysteresis also arose when the researchers changed the stiffness of the waist joint. At low stiffness, the model would trot; at high stiffness, the model would walk; but in between, it depended on whether the stiffness was increasing or decreasing.

In Aoi's model, the hysteresis in the gait transition was purely an effect from the body's interaction with the ground. For animals, the nervous system probably contributes to some degree, but these results suggest that mechanics may play a crucial role in determining how and when a gait changes.

10.1242/jeb.050047

Aoi, S., Yamashita, T. and Tsuchiya, K. (2011). Hysteresis in the gait transition of a quadruped investigated using simple body mechanical and oscillator network models. *Phys. Rev. E* **83**, 061909.

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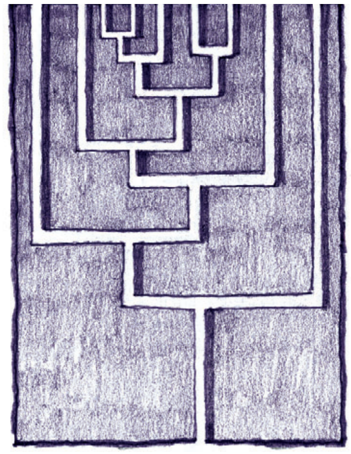
OLFACTION



JUMPING BRISTLETAILS – A GLIMPSE INTO THE ANCIENT INSECT NOSE

In order for aquatic organisms to have made the transition from living in water to surviving on land, mutations in several physiological processes needed to occur. For one sensory system, that of smell, olfactory brain structures that detect odors based on sensing air-borne, volatile and hydrophobic molecules evolved from structures that had the ability to detect aqueous hydrophilic solutions. The necessary evolutionary adaptations that occurred in the ancient insect nose are the focus of a recent paper by Christine Missbach, Steffen Harzsch and Bill S. Hansson from the Max-Planck-Institute, Germany, published in the journal of *Arthropod Structure and Development*.

Insects use their sense of smell for almost every aspect of survival, from mating, predator avoidance and communication, to finding food. The antennae house sensory neurons that send projections to the antennal lobe, deep in the insect brain. Hansson's team analyzed the antennal lobes of insects within the Order Archaeognatha, the wingless insects known as jumping bristletails. Because the Archaeognatha are considered the least evolutionarily changed insects, the team hypothesized that jumping bristletails would provide clues to the minimal changes within the olfactory system that allowed one of the oldest insect groups to evolve the ability to smell on land.

First, the team collected a colony of *Lepismachilis y-signata* (a representative of the Archaeognatha), from a forest in Germany. They set out to analyze the brain architecture of the olfactory system in *L. y-signata* by several techniques. To get a picture of the outermost structures, the group used scanning electron microscopy and closely examined the different types of antennal sensilla – hair-like structures on the antennae that insects use to detect odors. The team found the same types of sensilla covering the antennae of *L. y-signata* that have also been found in higher order insects, suggesting that the antennae, in part, may function as the main olfactory organ in these primitive insects too.

Next, Hansson and his group decided to find out whether these primitive insect brains are organized as they are in more modern insect species. Sensilla house the olfactory sensory neurons that send their projections into the antennal lobe, which is considered to be the primary olfactory brain center. Connections between the olfactory sensory neurons and antennal lobe occur in organized regions called glomeruli, where odor detection and discrimination are processed and where different smells are represented as a chemotopic map in the brain – such that different odors activate different glomeruli. Using histological section series to generate three-dimensional reconstructions of the brain, immunohistochemistry to label neurons and follow their projections in the brain, and antennal backfills to determine where the antennal nerve enters the brain, the team compared the structure of *L. y-signata* brains with the brains of other modern insects.

Interestingly, they found the glomeruli of *L. y-signata* differ in shape and possess far fewer glomeruli overall. Compared with almost all other insects that have been studied so far – and have been found to contain between 40 and 170 individual glomeruli – *L. y-signata* contain less than a dozen. Assuming that more glomeruli translates into a greater array of olfactory receptor proteins (and the ability to detect a wide range of odor molecules) expressed in distinct subpopulations of olfactory sensory neurons, Hansson's team suggest that Archaeognatha may represent a most primitive terrestrial and undifferentiated olfactory model, one with the lowest number of olfactory receptors found in any insect studied to date.

10.1242/jeb.050039

Missbach, C., Harzsch, S. and Hansson, B. S. (2011). New insights into an ancient insect nose: the olfactory pathway of *Lepismachilis y-signata* (Archaeognatha: Machilidae). *Arthropod Struct. Dev.* doi:10.1016/j.asd.2011.03.004

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