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

BEHAVIOUR AND BEE BRAINS

The question of whether there are links between our genetic makeup and the way we behave has long puzzled humans. With the publication of the human genome we may finally be on the verge of answering this tantalising question. Some scientists hope ultimately to be able to predict behaviour by simply looking at our genetic makeup. Unfortunately, humans are probably too complex to begin answering this problem at the moment. However, undaunted by the enormity of the task, Charles Whitfield and his colleagues at the University of Illinois have set about tackling the problem, while setting their sights a little lower. They have turned their attention to a relatively simple creature, the honey bee (*Apis mellifera*), to start unravelling how (and if) our genes control what we do.

Bees are fascinating because they form complex societies, where everyone has a particular role. For example, worker bees have two distinct forms of behaviour. During the first 2–3 weeks of adult life, female worker bees are confined to the hive, nursing and caring for the demanding young. As they mature, they switch roles and begin foraging, spreading their wings and flying far afield to search for pollen and nectar. The change from nurse to forager depends on the number of hungry mouths there are to feed and the needs of the colony, so the team decided to look at the bee's genetic brain profiles as they switched from one behaviour to the other.

Comparing gene expression patterns across 40% of the genome, the team looked at 5–9-day-old nurses and 28–32-day-old foragers from a typical colony. There were significant differences in brain gene expression for 39% of the genes in the portion of the genome tested. The team then wanted to find out whether these differences were associated with the age of the bees or with the way the bees were behaving. Whitfield and his colleagues turned their attention to single cohort colonies, where all the worker bees are the same age. In these colonies, some bees begin foraging at a very early age in the absence of older bees, while others remain in their nursing role as there are no youngsters to replace them. Knowing that all of these bees were the same age, regardless of their roles, the team measured gene activity in the brains of young and old nurses and precocious and old foragers to see whether the brain expression patterns were due to old age or experience.

What they found was that there is a strong relationship between behaviour and brain gene expression; so it is not how old you are, but what you are doing that is important if you are a bee. Having shown that there is a molecular signature, like a fingerprint, that is strongly related to behaviour, the team were able to identify individual's activities from their molecular fingerprint alone, distinguishing nurses from foragers with a 92–95% accuracy! And with the publication of the honey bee genome pending, Whitfield and his colleagues are optimistic they can unravel the complex web of genetic interactions that transform bees from caring nurses to roaming foragers.

10.1242/jeb.00831

Whitfield, C. W., Cziko, A.-M. and Robinson, G. E. (2003). Gene expression profiles in the brain predict behavior in individual honey bees. *Science* **302**, 296-299.

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MORE THAN MEETS THE EYE

By any standards, strepsipterans are weird. The males' twisted wings definitely give them a distinctive look but it's their eyes that are their most distinguishing feature. In general, insects have compound eyes composed of many ommatidia. For example, the similarly sized *Drosophila* eye is composed of ~700 ommatidia, each of which includes a lens. However, strepsipterans have raspberry-shaped eyes that contain a remarkably low number of lenses. One species, *Xenos peckii*, has only 50 lenses per eye, and the area of each lens is 15 times larger than that of fruit flies. This suggests that images can be formed within each unit, a feature that is remarkably different from the typical compound eye, in which each ommatidium samples just a portion of the visual scene, forming a low-resolution mosaic image.

To better understand these fascinating eyes, Elke Buschbeck, Birgit Ehmer and Ron Hoy have been exploring the anatomy and physiology of *Xenos peckii*'s unusual visual system. These researchers had already shown that, in contrast to compound eyes, which have only 8–10 photoreceptors per ommatidium, below each *Xenos* lens lies a retina with over 100 photoreceptor cells. In this current paper, the team has gone on to describe the optics and physiology of the insect's visual system.

First, the team measured the distance behind each lens at which images were focused and found that it corresponded well to the position of the retina behind the lens. While each tiny *Drosophila* ommatidium is only capable of sampling a point from an image, which the brain then integrates into a visual mosaic, *Xenos*'s large lenses are capable of much more. The authors' calculations demonstrated that the lenses capture enough light to make image formation possible within each 'eyelet', at least when *Xenos* is active during daylight. Most intriguingly, the optics of this design may also allow for a combination of high sensitivity and resolution that is difficult to achieve in compound eyes.

In addition, other features of *Xenos*'s visual system don't conform to the insect standard. In insects with compound eyes, the lamina, the first visual relay in the central nervous system, is compartmentalized, with no overlap of input from other ommatidia. However, in *Xenos*, no compartments are seen, and the inputs from each eyelet overlap at the borders. Although this organization is odd, it fits well with the authors' calculations suggesting that images falling on neighboring eyelets may also overlap at the borders. These observations suggest that the images formed by individual eyelets are maintained in the central nervous system.

The origin of strepsipteran eyes, which share architectural features of both compound eyes and image-forming single eyes, remains a mystery. Unfortunately, a resolution to the problem is hampered by disagreement about the group's phylogenetic position, although strepsipterans must have evolved from ancestors with compound eyes. Some of the authors' data suggest that strepsipterans might have passed through a nocturnal phase, possibly resulting in poor visual resolution and altering their eyes' design. If this scenario is correct, the authors suggest that Strepsiptera could have regained higher resolution by improving the resolution within each eyelet rather than by adding more lenses. With such profound structural changes, strepsipteran eyes may provide us with unique insight into the evolution of arthropod eyes.

10.1242/jeb.00832

Buschbeck, E. K., Ehmer, B. and Hoy, R. R. (2003). The unusual visual system of the Strepsiptera: external eye and neuropils. *J. Comp. Physiol. A* **189**, 617-630.

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WALK ON FOUR LEGS NOT ON TWO

When walking, most mammalian quadrupeds use lateral-sequence gaits, where hindlimb footfall is followed by the ipsilateral (same-side) forelimb. By contrast, primates generally use what is known as a diagonal-sequence gait; after one hindlimb makes ground contact, the contralateral (opposite-side) forelimb is the next to touch down. But why is the gait of primates distinct from that of other mammals? What selective forces might have led them to develop this alternative gait? In a recent paper, Pierre Lemelin and colleagues from Duke University provide empirical support that diagonal-sequence gaits probably evolved in arboreal habitats, where fine-branched canopies select strongly on locomotor morphology and gait.

Interestingly, rather than working on primates, Lemelin and colleagues used didelphid marsupials (American opossums) to test for functional links between arboreality and diagonal-sequence gaits. Why opossums? Because they include species known to use diagonal-sequence gaits. Additionally, opossums can be found in a broad range of habitats, including forest canopies. Lemelin and colleagues reasoned that if there is some causal link between arboreality and diagonal-sequence gaits in primates, a similar link should be found in opossums.

They studied two species: *Monodelphis domestica*, the short-tailed opossum, which generally forages on the ground, and *Caluromys philander*, the woolly opossum, which spends much of its time on the thin branches of tree canopies. The team filmed 3–4 animals from each species walking on

three surfaces: a flat runway (to simulate the ground), a 28 mm-diameter pole and a 7 mm-diameter pole (representing tree branches of differing size). The team then analysed the locomotor sequences and calculated the degree of diagonality in each gait as the percentage of the locomotor cycle in which ipsilateral forelimb footfalls followed hindlimb touchdowns. Values of 0.25–0.5 imply low diagonality (lateral-sequence walking) whereas values of 0.5–0.75 imply high diagonality (diagonal-sequence walking).

The more terrestrial species, *Monodelphis*, commonly exhibited diagonality values less than 0.5 and was nearly incapable of coordinated movement across the poles. By contrast, the arboreal species, *Caluromys*, generally used diagonal-sequence gaits on all surfaces. Moreover, it exhibited greater diagonality when moving on poles than on the flat surface and had no trouble negotiating the slender 7-mm pole. The authors suggest that the use of diagonal-sequence gaits in the woolly opossum and many primates is not coincidental. Rather, the need for moving about and foraging on narrow tree branches has led to the evolution of this gait.

What advantages might diagonal-sequence gaits provide on narrow unpredictable supports? Lemelin points out that earlier workers had proposed that diagonal-sequence gaits reduce yaw, which may be important for stability. Additionally, recent work by Cartmill's group suggests that diagonal-sequence gaits, in conjunction with grasping hindfeet, allow animals such as *Caluromys* and many primates to maintain a firm grip with a grasping hindfoot while the contralateral forelimb tests out potentially risky footing. If a branch were to give way under the forelimb, the animals could readily pull themselves back and save themselves from taking a potentially nasty tumble.

10.1242/jeb.00833

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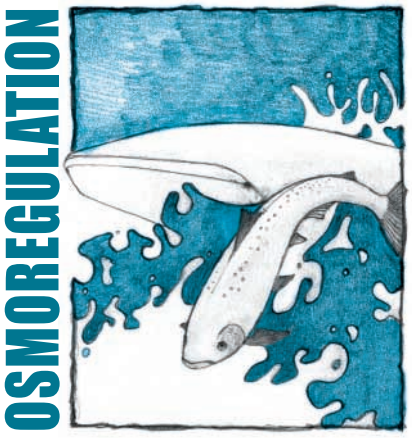

OUABAIN: A NEW FISH HORMONE?

Remarkably, many fish have the ability to move easily between freshwater and seawater, despite the demands these two extreme environments make on their physiology. For example, in freshwater, fish constantly lose salt and gain water from the environment, requiring them to have special mechanisms to take up salts and excrete water in order to maintain salt and water balance. The complete opposite occurs in seawater, where fish continuously gain salt and lose water to the environment. Consequently, marine fish need to actively excrete excess salts and drink water to maintain hydromineral balance. Determining the mechanisms that allow the same fish to acclimate quickly to these two very different environments has been an intense area of research for decades.

To date, the hormone cortisol has been shown to play an important role during acclimation to seawater by causing changes in gill cell morphology and stimulating the enzyme Na^+/K^+-ATPase to help in the extrusion of salts. The hormone prolactin is important during acclimation to freshwater as it reverses the morphological modifications caused by cortisol and decreases gill permeability. Yet, these two hormones alone cannot account for all the changes that occur in fish during salinity change. In mammals, evidence has accumulated suggesting a role for ouabain, a familiar Na^+/K^+-ATPase inhibitor, in the regulation of hydromineral balance. S. Kajimura and colleagues decided to examine whether a ouabain-like substance is present in fish and to determine whether ouabain is involved in hydromineral balance during seawater or freshwater acclimation.

Choosing to work with tilapia, a fish that is found in both freshwater and marine environments and moves between the two, the team exposed the fish to a rapid salinity change and then took blood samples at 2, 4, 8 and 24 h after the transfer. The team measured the plasma and tissue concentrations of ouabain using a radioimmunoassay with a specific antibody against ouabain.

Interestingly, ouabain was detected in all of the tissues examined, regardless of salinity. The highest concentration was found in the head kidney, which is the area of cortisol production in fish and is analogous to the adrenal gland in mammals.

When freshwater-acclimated fish were transferred to seawater, the team saw a significant increase in plasma osmolality. Plasma ouabain and cortisol levels also rose and all three increases were significantly correlated. By contrast, seawater-acclimated tilapia that were transferred to freshwater showed a significant decrease in plasma osmolality although there was no significant correlation between plasma osmolality, ouabain or cortisol levels, possibly because there was little change in plasma cortisol and ouabain levels.

Kajimura and the team have shown for the first time measurable ouabain levels within the circulation and tissues of fish. Ouabain may be involved in the regulation of hydromineral balance in tilapia, in conjunction with cortisol, and, if so, could potentially be more important during acclimation to seawater than to freshwater. However, the physiological function of ouabain is still yet to be determined. It will be exciting to learn the implications of this possible new hormone on the physiology of fish!

10.1242/jeb.00834

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