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INSIDE JEB

Fighting cichlids size up opposition with lateral line

Cichlid males mouth fighting. Photo credit: Karen Maruska.

When sizing each other up before a confrontation, most males depend on all of their senses to learn more about their opponent – listening, watching and sniffing out strengths and weaknesses. However, Karen Maruska and Julie Butler, from Louisiana State University, USA, explain that fish also explore their surroundings with an additional sense: the lateral line system responds to the ebb and flow of water surrounding the fish's body. Could fish also use this 'touch at a distance' system to learn more about a foe? Maruska and Butler explain that fish adversaries often waft water around while posturing in preparation for an encounter and add, 'The lateral line is poised to provide crucial information for opponent assessment'. However, no one had ever tested whether fish resort to the specialised sense in preparation for combat. '*Astatotilapia burtoni* males use a variety of aggressive behaviors, such as lateral displays, border fights, biting and mouth fights to defend their spawning territory,' says Butler, so the scientists selected this aggressive species to test their theory.

First, the duo investigated the structure of the feisty males' lateral line system and clearly saw the sensory units that detect disturbances in water distributed on the fish's head and along the side of the body. Then they selected dominant males that were keen to defend their territory and deactivated the animals' lateral line systems by immersing them in a solution of cobalt chloride and severing the posterior lateral line nerve. Next, they paired combinations of males, with and without active lateral line systems, in a duel over new territory and filmed the encounters.

Butler explains that for each contest there were three possible outcomes: the fish did not fight; one fish capitulated to the other before full hostilities began; or the fish battled for supremacy. Analysing the outcomes of each confrontation, the duo quickly saw that the lateral line system was an essential component of a successful non-confrontational outcome.

Almost 75% of the pairs where both fish had an intact lateral line system battled. However, when a dueller with a lateral line system was pitched against an opponent that had lost the sense, the duo saw a large increase in the proportion of fish that backed down before a confrontation – up from 5% in two males with intact lateral line systems to 30% where one combatant had lost the use of the lateral line. 'This decreased motivation was likely due to an impaired ability to adequately assess the opponent', say Butler and Maruska, adding that the disabled fish spent more time in close proximity to their opponents than the intact fish and that fish that had lost the lateral line system failed to instigate combat with the fin-flaring display that intact fish perform before a skirmish. And when Butler and Maruska analysed the battle manoeuvres, they saw that the fish with a functional lateral line system avoided contact with their opponents, while the fish that had lost the system bit and rammed each other more.

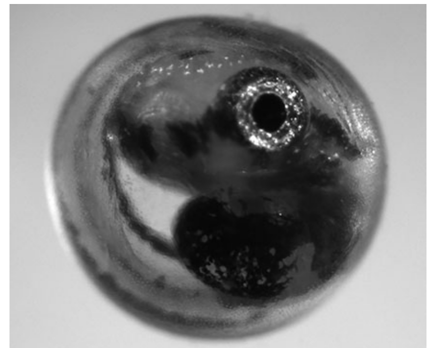
Butler and Maruska were impressed to find that the fish use the additional sense to avoid damaging confrontation and they say, 'To our knowledge, this is the first study to implicate the lateral line system as a mode of social communication necessary for assessment during agonistic interactions'.

10.1242/jeb.132563

Butler, J. M. and Maruska, K. P. (2015). The mechanosensory lateral line is used to assess opponents and mediate aggressive behaviors during territorial interactions in an African cichlid fish. *J. Exp. Biol.* **217**, 3284-3294.

Kathryn Knight

The benefits of being a fish egg out of water



A mangrove rivulus (*Kryptolebias marmoratus*) embryo. Photo credit: Mike Wells.

The first terrestrial animals were true pioneers. Having heaved themselves out of their swampy homes onto dry land, they were finally able to take full advantage of the metabolic benefits of unfettered access to an abundant oxygen supply. But what advantages could this oxygen bonanza provide for fish eggs laid out of water? Michael Wells, Andy Turko and Patricia Wright from the University of Guelph explain that so long as the developing fish embryos remain moist, they should develop faster than their aquatic counterparts, thanks to the enriched oxygen. However, no one had ever systematically compared the metabolic trade-offs when fish eggs develop in water and air. Explaining that the amphibious fish mangrove rivulus is equally happy laying its eggs in and out of water and that the fish are capable of self-fertilization – producing batches of genetically identical eggs – Wright and her colleagues set about assessing the benefits of a terrestrial versus aquatic start in life for fish embryos.

Suspecting that an abundant oxygen supply would improve the fish's fecundity, Wells measured the egg production of adult rivulus in water and on land and found that the terrestrial fish produced almost three times as many eggs as the fish in water. In addition, the eggs that were exposed to air developed faster than the aquatic eggs, with 95% reaching a stage where they could hatch after 15 days,

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compared with 45% in aquatic eggs. And when Wells compared how much oxygen the two sets of embryos consumed, he was impressed to see that the air-reared eggs consumed 44% less oxygen than the submerged embryos, in addition to retaining larger egg-yolk reserves. Next, Wells tested the fish's activity levels as they wafted oxygen-laden fluid in their eggs with their gill covers (opercula) and noticed that early in development (7 days after egg release) the water-reared embryos moved their opercula far more than the air-reared eggs. And when the air-reared eggs were returned to water, their metabolic rate and movement increased significantly, 'Supporting the hypothesis that *Kryptolebias marmoratus* [mangrove rivulus] embryos use micro-environment manipulation to maintain oxygen uptake,' the team says. They also calculated the metabolic cost of the opercular movements when the 30-day-old air-reared eggs were returned to water, discovering that the embryos consumed 64% more oxygen than embryos that were more static. And when the team compared the body size and survival of the embryos after they developed into adults, they found no ill effects of the different starts in life, showing that oxygen availability in the earliest life stages had little effect on the fish's long-term development.

The air-reared fish eggs seemed to benefit from their oxygen-rich start in life, developing faster while preserving their limited reserves for use after hatching. And Wright says, 'Terrestrial rearing is energetically more favourable and, by extension, the energy savings may have provided the selective pressure favouring the evolution of terrestriality'.

10.1242/jeb.132530

Wells, M. W., Turko, A. J. and Wright, P. A. (2015). Fish embryos on land: terrestrial embryo deposition lowers oxygen uptake without altering growth or survival in the amphibious fish *Kryptolebias marmoratus*. *J. Exp. Biol.* **218**, 3249-3256.

Kathryn Knight

Well-fed larvae switch ion transport in rectal complex

Trichoplusia ni larva. Photo credit: Alton N. Sparks, Jr. via Wikimedia Commons.

The key to a good larval life is to eat as much as possible, regardless of the havoc wreaked on crops. So, gorging larvae have to balance their fluid intake and losses depending on how moist or dry their diet; which is why some species have evolved a specialised organ for reclaiming fluid from the gut, known as the rectal complex. Michael O'Donnell and Esau Ruiz-Sanchez from McMaster University, Canada, explain that the rectal complex also regulates the levels of Na^+ and K^+ ions in the insect's haemolymph, which would otherwise fluctuate wildly when the larvae are gorging and growing rapidly. However, little was known about the fine details of fluid transport between the rectal complex and the larva's other excretory organ, the Malpighian tubule. So, O'Donnell and Ruiz-Sanchez teamed up to build a more detailed understanding of the delicate interplay of fluid and ion transport between the two structures in well-fed and hungry larvae.

Collecting fourth instar larvae from a lab colony of cabbage looper moths (*Trichoplusia ni*), the duo first investigated the relative architecture of the Malpighian tubule and rectal complex. They identified the distributions of two different cell types – known as principal (type I) cells and secondary (type II) cells – in the two structures. Then the duo began the incredibly intricate task of measuring ion transport at different locations across the structures using thin ion-selective microelectrodes positioned with computer-controlled micron precision at different locations on both structures.

Having discovered that the rectal complex unexpectedly reabsorbs Na^+ and K^+ ions from the gut and returns them to the haemolymph, O'Donnell and Ruiz-Sanchez also realised that the larvae's ability to transport Na^+ and K^+ ions varies dramatically – depending on whether or not they are well fed and the location in the rectal complex and Malpighian tubules – despite the apparently identical appearance of many sections of the tubule. In one example, the duo describes how ion transport differs along the section of the gut known as the rectal lead when the larvae are hungry and well fed. They explain that larvae with full guts reabsorb K^+ in the distal rectal lead, but when the larvae's guts are empty K^+ is secreted in the proximal rectal lead. In contrast, well-fed larvae secrete Na^+ ions across the distal rectal lead while reabsorbing the ions across the proximal rectal lead. And when the duo analysed which cell types were involved in ion transport, they found that the type I cells in the section of tubule linking the Malpighian tubule to the rectal complex – known as the ileac plexus – secreted K^+ ions. However, they were surprised that the type II cells reabsorbed K^+ and Na^+ ions, with the type II cells transporting Na^+ at twice the rate of the type I cells.

O'Donnell and Ruiz-Sanchez admit that they are surprised by the complex pattern of secretion and ion reabsorption and they are also intrigued about the change in direction of ion secretion in different regions of the Malpighian tubule when the larvae are fed. However, they are optimistic that they will be able to learn more about these puzzles using the techniques that they have developed in this study and O'Donnell says, 'I see 5–10 years of exciting work ahead'.

10.1242/jeb.132555

O'Donnell, M. J. and Ruiz-Sanchez, E. (2015). The rectal complex and Malpighian tubules of the cabbage looper (*Trichoplusia ni*): regional variations in Na^+ and K^+ transport and cation reabsorption by secondary cells. *J. Exp. Biol.* **218**, 3206-3214.

Kathryn Knight

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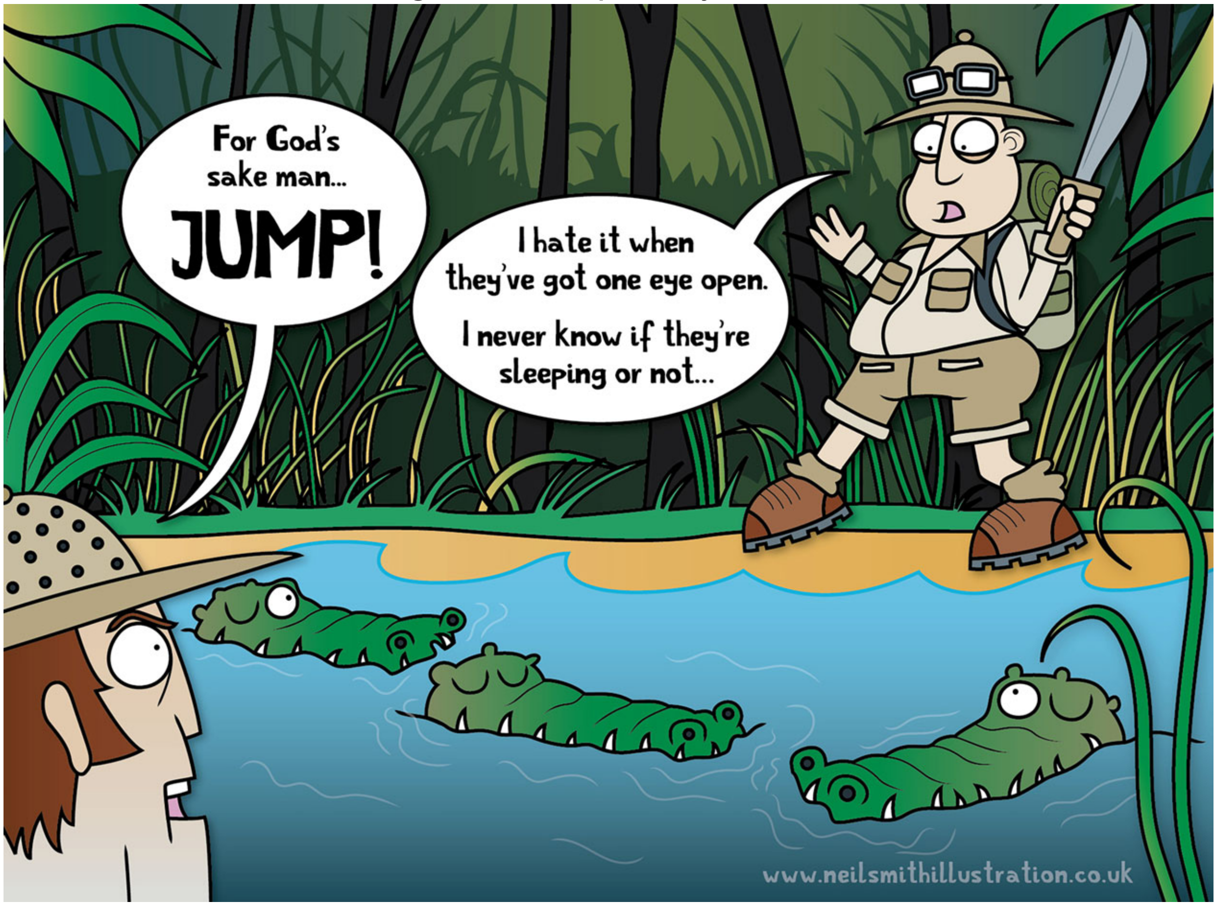
Slumbering crocs keep an eye out for threats



Sleep can be a blissful release, but it can also leave animals vulnerable to opportunistic attack. Yet, some creatures have come up with a remarkable solution to the problem: only one half of the brain sleeps while the other remains vigilant – a phenomenon known as unihemispheric sleep. John Lesku and colleagues from La Trobe University, Australia and the Max Plank Institute for Ornithology, Germany, explain that some birds and aquatic mammals that have the knack remain attentive by leaving the eye that is connected to the conscious half of the brain open to survey their surroundings, while the closed eye is connected to the slumbering half of the brain. Many sleeping reptiles also appear to keep an eye on events, although it is less certain whether they are half awake. Knowing that crocodiles are more closely related to birds than other reptiles, Lesku and his colleagues wondered whether crocodiles also nap with an eye open.

Filming young crocodiles over a day and recording their responses to other crocodiles and a potentially threatening human, the team could see that the animals usually slept with both eyes closed. However, during the early part of the day they often opened one eye briefly and when the team introduced another crocodile into the tank, the crocodile pinned the open eye on the intruder. 'This is consistent with a vigilance function', explains the team, adding that young crocodiles have a better chance of remaining with their crèche if they open one eye while sleeping , in much the same way that dolphins train an eye on their pod to stay in touch when taking half a snooze. And when a human entered the crocodile's enclosure while the crocodiles appeared to slumber, the animals really took notice, keeping their vigilant eye trained on the threat for several minutes at a time.

So, crocodiles keep an eye on events while they appear to sleep, suggesting that that one half of the brain may be active – although the team adds that measurements of brain activity are required to confirm whether the half of the brain connected to the closed eye is genuinely asleep while the other half is awake. They also say, 'Unihemispheric sleep may have first evolved in the archosaur lineage with the appearance of birds by elaborating upon a pre-existing behaviour inherited from a common ancestor with non-avian reptiles'.

10.1242/jeb.132548

Kelly, M. L., Peters, R. A., Tisdale, R. K. and Lesku, J. A. (2015). Unihemispheric sleep in crocodilians? *J. Exp. Biol.* **218**, 3175-3178.

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