

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.

WHALE FEEDING



SENSORY ORGAN DISCOVERY DEMYSTIFIES RORQUAL WHALE FEEDING

The rorqual whale family is composed of the largest animals on Earth with a unique way of eating their prey: they dive into aggregations of small crustaceans and fish at great depths and lunge with their mouths wide open, engulfing kilograms of fish in a single mouthful. The volume of each mouthful can be larger than that of their body and the engulfed water is filtered through baleen plates in a matter of seconds, leaving them to consume the food that is left behind. Over the past couple of decades researchers have found many unique morphological features that allow rorqual whales to perform these feats: enormous heads with large flexible jaws, the ability to invert their tongues and incredibly stretchy ventral (along the front of the body) pouches that extend from the chin down to their belly button. Recently, a new sensory organ involved in this fascinating feeding strategy was discovered by a team of North American researchers led by Robert Shadwick from the University of British Columbia, Canada, and they published their findings in *Nature*.

One intriguing anatomical feature of rorqual whales is that the bones in their lower jaws (mandibles) are not fused at the chin but are held together by connective tissue instead. This gives their jaws more flexibility and the ability to rotate outward, enabling the whales to gulp even more water than if their jaws were fused. Dissecting whale carcasses, the team discovered a round, jelly-filled cavity in the connective tissue between the mandibles. A closer look at the tissue with microscopes revealed that the cavity was innervated, and had many papillae (finger-like projections) and nerve endings reminiscent of other sensory organs.

To get a better idea of the structure of this organ, they then performed magnetic

resonance imaging (MRI) and X-ray computed tomography (CT) scanning on different species of rorqual whales. When they analysed the distribution of bundles of blood vessels and nerves going to the sensory organ, the team discovered an asymmetric distribution – 60% of the nerves and blood vessels originated from the left mandible in fin whales – and they believe that this asymmetry in the innervation is related to the tendency of individual whales to be biased to one side when side gulping or rolling to feed.

Another intriguing anatomical feature is a Y-shaped cartilage structure that emerges out of the chin and protrudes along the bony jaws, providing support for the stretchy ventral pouch. Using the same imaging techniques that they had used previously, the team discovered that the sensory organ was in contact with the Y-shaped cartilage. They propose that mechanoreceptors (sensors responding to mechanical stimuli) in the sensory organ located in the mandibles relay information about the configuration of the jaws to the brain in order to co-ordinate the movements of the jaw bones and the soft tissue of the ventral pouch during lunge feeding.

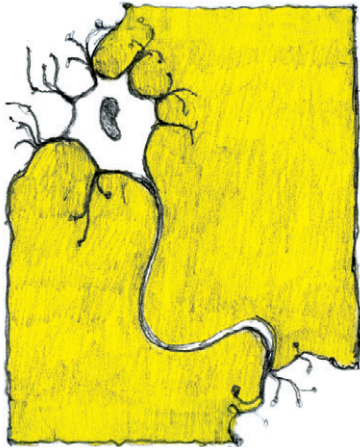
This discovery raises interesting questions about the evolution of this organ. Based on its absence in toothed whales, the research team proposes that it evolved either before lunge feeding or along with other specializations associated with lunge feeding and that this organ is an important contributor to this fascinating behaviour.

10.1242/jeb.064345

Pyenson, N. D., Goldbogen, J. A., Vogl, A. W., Szathmary, G., Drake, R. L. and Shadwick, R. E. (2012). Discovery of a sensory organ that coordinates lunge feeding in rorqual whales. *Nature* 485, 498-501.

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SETTLEMENT LOCATION



THE NEIGHBOURHOOD SOUNDS NICE

As any real estate agent will tell you, there are many important factors to consider when choosing a home. Is the neighbourhood safe? Are there plenty of options for food nearby? Will it be easy to start a family? Many oceanic animals start out life as pelagic larvae, travelling vast distances on currents before they find a suitable location on which to settle and metamorphose into their more sedentary adult form. For these larvae, selecting a home seems an overwhelming task. How can such small animals, at the mercy of tides and currents, select the correct habitat? How can they even discriminate among different options?

Jenni Stanley, Craig Radford and Andrew Jeffs from the University of Auckland's Leigh Marine Laboratory, New Zealand, set out to investigate how larval crabs are able to select an appropriate site for metamorphosis. The researchers hypothesized that as oceanic larvae don't have particularly good vision, and chemical cues drift with currents, larval crabs might be using sound cues to locate the ideal settlement site. Sound is particularly promising as a signal of habitat quality because it carries clearly underwater and provides a consistent directional cue that larvae can home in on.

To investigate this possibility, the researchers captured the larvae of two species of temperate crab off the coast of New Zealand (*Hemigrapsus sexdentatus* and *Cyclograpsus lavauxi*), and three species of tropical crab off the coast of Australia (*Cyno andreossyi*, *Schizophrys aspera* and *Grapsus tenuicrustatus*). Returning to the lab, the trio housed the larvae in individual vials, each with a roughened floor on which the larvae could metamorphose. Then, they isolated the vials in soundproof waterbaths and exposed the larvae to sounds recorded in the larvae's

natural environment: continuous sound from a high quality reef habitat, sound recorded from a moderate broken reef or mixed beach habitat, the sound of a poor quality open sand habitat, or silence. Finally, the researchers moored some of the vials containing larval residents close to the field locations where they had recorded the sounds, then regularly checked the laboratory and field vials to see how the larvae fared. The question was, would the crab larvae take advantage of a prime real estate opportunity and metamorphose more quickly when moored near a desirable location than when moored near a poor quality habitat? And would exposure to the sound alone cause this effect, or would they require the full spectrum of environmental cues to trigger rapid metamorphosis?

After a week, the team realized that the larval crabs must have good instincts for real estate, because all five species discriminated well among the habitat types. When exposed to the full spectrum of environmental cues in the wild, and when listening to the sound recordings in the laboratory, the larvae metamorphosed more quickly when they heard the high quality site than when they heard a lesser quality habitat or silence. This is probably a highly conserved response across crabs, as all five species, from three different families and two different climate zones, had the same response to sound cues.

When the scientists analysed the sound recordings, they found that the presence or absence of sounds generated by noisy marine animals, such as sea urchins and snapping shrimp, caused the main auditory differences between the habitat types. It is an intriguing possibility that the larval crabs are listening for potential neighbours as they drift past a given habitat. Rather than relying on real estate agents, larval crabs appear to choose their homes based on word-of-mouth recommendations from prospective neighbours.

10.1242/jeb.064360

Stanley, J. A., Radford, C. A. and Jeffs, A. G. (2012). Location, location, location: finding a suitable home among the noise. *Proc. R. Soc. B* 279, 3622-3631.

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GREGARIZATION



LIGHT AND CHEMICAL CUES TRIGGER BIBLICAL SWARMS

Locusts are known for their striking demonstration of the power of epigenetics. Changes in population density cue a sudden shift in their physical form between a smaller, greener, solitary phase and a larger, darker, gregarious phase by changing the expression of their genes. When the population shifts to gregarious phase, vast swarms of locusts can strip entire swaths of vegetation bare, making the control of these phase shifts of interest from both a physiological and an economic standpoint.

In the desert locust *Schistocerca gregaria*, this change can also be initiated between generations when a female locust is stimulated by crowding to produce larger gregarious phase eggs. However, how locusts control this phase switch is unclear. Koutaro Maeno from Tsukuba, Japan, and Seiji Tanaka from Nouakchott, Mauritania, recently showed in a publication in *Physiological Entomology* that solitary locusts require light and chemical cues in order to produce gregarious offspring.

Knowing that touching the chemosensitive antennae, rather than knocking the legs, causes females to lay large gregarious phase eggs, Maeno and Tanaka thought that a chemical cue might be responsible. To test this idea, they blindfolded females with white-out and black nail polish, to prevent them from picking up visual cues. Then they washed the head and thorax of old male locusts – which are known to induce the gregarizing response – in hexane, before brushing the washed and unwashed males against the females' antennae. The duo found that the females had to be touched by the unwashed males to lay gregarious eggs. Similarly, cotton balls soaked in the males' hexane wash induced a similar response, suggesting that a chemical found on the bodies of the males was responsible for the shift, rather than a purely mechanical stimulus. And when the duo repeated the

experiment by touching females with either female locusts or several other insect species, Maeno and Tanaka found that the species that were more closely related to *S. gregaria* (such as other locusts or female *S. gregaria*) induced more gregarization response in female *S. gregaria* than more distantly related species (such as beetles and cockroaches). In addition, only older adult *S. gregaria* seemed to induce the response, while nymphs or sexually immature *S. gregaria* did not.

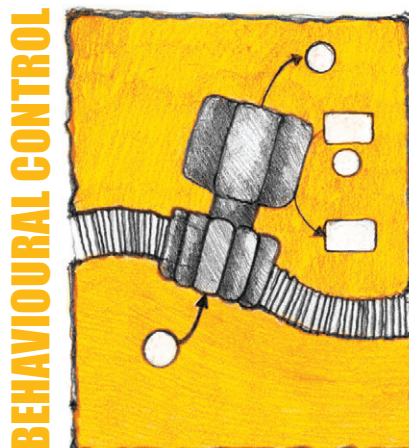
As the females' eyes were covered with paint in the initial experiments, the authors went on to test the effect of light and visual cues on the females' ability to receive a gregarization signal. Maeno and Tanaka analysed the size of the eggs produced by crowded non-blindfolded females in bright and dark conditions, and were surprised to find that crowding only induced gregarization (large eggs) in the light. Finally, to exclude the possibility that natural light intensity changes during the day caused the change, and to track down the part of the body responsible for receiving the signal, the scientists painted the female locusts with phosphorescent paint, so that they glowed in the dark. Then they tested the locusts' receptivity to the crowding cue and found that the females with phosphorescent heads produced large gregarious eggs while non-glowing females did not. Taken together, the authors suggest that a light-sensitive organ on the head must also be responsible for receiving the cue.

So, adult *S. gregaria* females produce gregarious offspring in response to chemical and light cues. As there must be both light and chemical signals to induce gregarization between generations, the authors suggest further research into how light perception influences processing and integration of chemical cues in insects in the hope that we might one day be able to control biblical locust plagues.

10.1242/jeb.064352

Maeno, K. and Tanaka, S. (2012). Adult female desert locusts require contact chemicals and light for progeny gregarization. *Physiol. Entomol.* **37**, 109-118.

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SODIUM/POTASSIUM PUMPS HELP FROGS PACE THEMSELVES

Track and field athletes can either sprint for a short time or run slowly for a long time. This simple trade-off between performance and endurance is a fact of life for all moving animals. But how does an animal's motor system remember what it has done in the past and regulate future movements to avoid exhaustion? Hong-Yan Zhang and Keith Sillar at St Andrews University, UK, recently explored this question by studying motor networks in *Xenopus* tadpoles. They published their work in a recent edition of *Current Biology*.

Locomotion in *Xenopus* consists of swimming bouts triggered by sensory stimuli interspersed with pauses. Swimming episodes can last from a few seconds to several minutes. The team first simply controlled how long tadpoles rested after each swim bout. They found a very strong linear relationship between the interswim interval (rest time) and swim bout duration. The longer the network is active, the longer it rests afterwards. This suggests that tadpoles pace themselves. To do this, the frog locomotor system must retain a memory of what it has done in the past and dictate future output.

To examine the mechanisms underlying this network memory, the team recorded from neurons in the rhythmic circuits driving locomotion during fictive swimming (swim motor patterns evoked in a preparation isolated from sensory feedback). Following swim bouts, most neurons firing during swim rhythms showed an 'ultra slow' after-hyperpolarization (usAHP). For up to a minute after a swim bout, the usAHP made it harder for the network to maintain

swimming. This cellular 'hangover' was directly and exclusively proportional to the amount of time the cell spent firing action potentials during swim bouts. The more action potentials a neuron fired during swimming, the longer the cell stayed hyperpolarized.

In other species, similar activity-dependent slow AHPs are mediated by electrogenic activity of the Na⁺/K⁺ pump. These pumps actively move K⁺ ions into cells and Na⁺ ions out. They have traditionally been considered to be unglamorous workhorses that regulate the baseline electrical potential of cellular membranes, but they have also been shown to generate activity-dependent inhibitory currents in a variety of invertebrate neurons. Zhang and Sillar next tested whether the Na⁺/K⁺ pump mediates the tadpole usAHP. Indeed, the usAHP has electrophysiological properties and pharmacological sensitivity consistent with it being mediated exclusively by a Na⁺/K⁺ pump current.

Finally, the team wanted to determine whether there is a causal relationship between Na⁺/K⁺ pump function and homeostatic regulation of swim episode and pause durations. To test this, they examined both fictive and actual swimming rhythms in the presence of a pharmacological inhibitor of Na⁺/K⁺ pump function. They found that the presence of the inhibitor increased the duration of swim bouts and decreased the duration of pauses. The delicate balance between performance and endurance was disrupted and the swim network essentially ran itself to exhaustion.

The work of Zhang and Sillar demonstrates that Na⁺/K⁺ pumps can dynamically set the excitability of cellular components in relation to previous activity. This provides the *Xenopus* locomotor system with a simple yet elegant cellular mechanism for controlling future behaviors in light of recent activity. Given that Na⁺/K⁺ pumps and action potentials are ubiquitous features of all brains, this mechanism might very well be a highly conserved feature of neural networks across animal phyla.

10.1242/jeb.064378

Zhang, H. Y. and Sillar, K. T. (2012). Short-term memory of motor performance via activity dependent potentiation of Na⁺/K⁺ pump function. *Current Biology* **22**, 526-531.

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