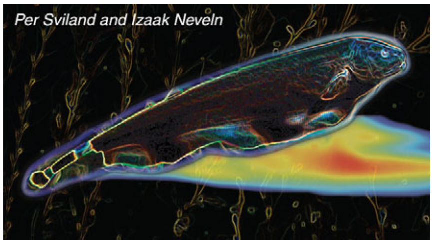
Inside JEB highlights the key developments in *The Journal of Experimental Biology*. Written by science journalists, the short reports give the inside view of the science in JEB.

SEEING AND COMMUNICATING THROUGH WEAK ELECTRIC FIELDS



Weakly electric fish spend their lives bathed in their own internally generated mild electric field, interpreting perturbations in the field as objects pass through and when communicating with members of their own species through high frequency electric ‘chirps’. Rüdiger Krahe, from McGill University, Canada, says, ‘These fish are very cryptic and hard for us to understand because we don’t have this electric sense’. However, he explains that despite our limitations, it is the very nature of this exotic sensitivity that underpins why it can teach us so much about sensory encoding and perception. These weak electric fields are not produced passively; they are an intrinsic behaviour in the same way that bats emit sound for echolocation. But in the case of electric field generation, the signals are easy to record, analyse and mimic, and you can measure the recipient’s behavioural response to the signal and then trace the complex train of neural events that relates the behavioural response to the sensory input. Explaining that this enigmatic system has evolved multiple times, Krahe also lists the two currently existing modern groups of weakly electric fish: one in Africa (Mormyriformes) and the other in South America (Gymnotiformes). With them in mind, Krahe says, ‘We have this fascinating convergent evolution of electro-generation and -sensation in these two groups that evolved this ability independently.’

Explaining that this is the first special issue in *The Journal of Experimental Biology* dedicated to the neuroethology of electric fish since the highly cited 1999 special issue (*J. Exp. Biol.* **202** issue 10), Krahe reflects, ‘There has been amazing progress in a number of fields, for example in the hormonal and neuromodulatory control of electrosensory and electromotor systems, and in the study of the evolution of electric signalling, to name just a few. So Eric Fortune and I wanted to have this exciting and broad array of topics represented in this special issue’. Fortune, from the New Jersey Institute of Technology, and Krahe commissioned review articles in the areas of electric sensory coding and neuromodulation, the physiology of the electric organ, electric fish locomotion and evolution, and assembled them in this comprehensive collection detailing the many intriguing aspects of the natural history of these exotic animals.

Neural coding in electric fish

Bruce Carlson and his colleagues from Washington University in St Louis, USA, explain that electric fish not only convey information about themselves in the structure of each electric pulse but also vary the duration of the interval between pulses to communicate their behavioural state, such as whether they are subordinate or dominant and how aggressive they are (p. 2365). All sensory information is encoded by neurons into patterns of electrical spikes. In the case of electric signal perception by mormyrids, information is encoded by specialised receptors known as knollenorgans into both spike timing differences between receptors and interspike intervals within receptors. Carlson and his colleagues also describe how two subfamilies of pulse-type African mormyrids differ in their ability to distinguish differences in the waveform of emitted electric signals and they explain that these perceptual differences are due to differences in midbrain structures, as well as differences in the distribution of the knollenorgan receptors on the fish’s bodies. The authors conclude by saying, ‘The mormyrid electric communication pathway is a powerful model for integrating mechanistic studies of temporal coding with evolutionary studies of correlated differences in brain and behaviour to investigate neural mechanisms for processing temporal codes.’

Continuing the theme of pulse-type weakly electric fish, Javier Nogueira and Angel Caputi from Montevideo, Uruguay, address the fundamental question of the properties of a neuron and how they enable that neuron to participate in a particular circuit. In this review, they focus on one specific cell type: spherical neurons in the electrosensory lobe of *Gymnotus omarorum* (p. 2380). Having defined the properties of this type of neuron – which is a one-spike-onset neuron – Nogueira and Caputi go on to explain that the cell plays a key role in distinguishing between electric fields that have been self-generated and externally generated. Spherical neurons allow the fish to preferentially process self-generated electric images of their surroundings in the presence of weaker electric fields generated by surrounding fish of their own species. Comparing the function of one-spike-onset neurons in the fish’s electrosensory system

Guy l'Heureux

with the same cells from auditory systems, Nogueira and Caputi say, ‘One-spike-onset neurons may play several functional roles in sensory systems. This role depends on specific adaptation of the “response functions” of the neurons and also on the circuit and the functional contexts in which the neuron function is involved.’

Concluding the section on information encoded in electric fish fields and how the animals process that information, Maurice Chacron, Sarah Stamper and Eric Fortune describe an additional source of information exploited by a second category of gymnotiform fish, which emits a continuous – wave-type – electric field (p. 2393). Chacron, from McGill University, and colleagues explain that low frequency electrical signals produced by social interactions between these fish add an additional frequency component to the electric field that results in a low frequency envelope that modulates the structure of the electric field. The envelopes produced by the movement of a fish’s body have lower frequency properties than envelopes produced by the interaction between close together fish, and the trio adds that congregating fish, ‘respond in robust and stereotypical ways to social envelopes that serve to increase the envelope frequency’. Moving on to consider how the fish extract information from electric field envelopes, the team traces the processing circuit from the response of the electroreceptors that detect electric fields, through to a region of the brain called the torus semicircularis, where the signal is extracted, leading to perception and behaviour.

Communication in electric fish

While we cannot detect electric fields, making electro-perception a sense beyond our own appreciation, weakly electric fish communicate through electric signals, modulating the electric discharges that they produce for a variety of reasons. For example, they vary field strength to convey information about their sex and size, as well as reducing the strength of the electrical signal during the day to conserve energy and protect themselves from electrosensitive predators. Focusing on honesty in sexual signalling, where the cost of extravagant signals should prevent weaker males from boasting dishonestly, Sat Gavassa, Philip Stoddard and colleagues from Florida International University, USA, and Instituto de Investigaciones Clemente Estable, Uruguay, discuss how the fish’s ability to manipulate their electric fields could jeopardise this honesty (p. 2403). After examining how electric fish modulate their electric fields by hormonal regulation and comparing how males and females manipulate their signals, the team then switches its focus to the information that electric fish transmit – about size, reproductive condition and aggressive state – and how signal honesty improves in a social context. The team also explains that when food is plentiful, male electric fish preferentially consume more food to sustain production of boastful electric fields. Yet, when resources are scarce, they are prepared to consume their own body reserves to maintain a strong electric field to ensure that they reproduce, even at the risk of their own survival. Gavassa and colleagues conclude, ‘Signal plasticity remains evolutionarily stable as signallers benefit from saving in costly signalling when return is low and receivers benefit from the improvement in the information quality when the signals are enhanced.’

Next, Ana Silva’s lab turns to the question of how two species of electric fish – with vastly different lifestyles – control their behaviour patterns *via* the same neurohormonal mechanisms (p. 2412). According to Silva, her colleagues and collaborators, one electric fish species – gregarious *Brachyhypopomus gauderio* – only exhibits male-on-male aggression during the mating season, while solitary *Gymnotus omarorum* aggressively defend their territories against intruders for most of the year. The team describes how the responses of the fish to the neuromodulators serotonin (which usually inhibits aggression) and arginine vasotocin (AVT, which modulates aggression in birds, fish and mammals) differ. Serotonin inhibits aggressive territorial behaviour in the solitary species; however, it does not inhibit mating season male-on-male aggression in the gregarious fish. AVT increases the aggression of solitary *G. omarorum* defending their territory while not altering the aggression of mating *B. gauderio* males. The team also analysed the impact of the hormone on the fish’s electrocommunication and found the hormone had different effects on how the two species conveyed their status in the social hierarchy.

Continuing the theme of signal modulation, Troy Smith from Indiana University, USA, describes how the members of one diverse family, the ghost knifefishes, have each evolved their own signature electric signals, which they use for distinguishing members of their own species from fish of other species (p. 2421). In addition, the males and females of each species modulate the frequency of their electrical signals to produce chirps, which communicate information about their size, social rank, sex and reproductive condition or aggressive intent. However, Smith explains that there is no consistent relationship between the male/female sex differences across all ghost knifefish species. For example, the males of some species produce higher frequency electric signals than their females, while the females of other species produce higher frequency fields than their males. By analysing the sex differences between the electric field structures of different ghost knifefish species and by studying the reception and production of chirps across the family, Smith hopes that we will learn more about the evolution of communication in general and the neural and hormonal mechanisms that regulate it.

Moving on from Smith’s discussion of the evolution of electrocommunication, Kent Dunlap, Michael Chung and James Castellano from Trinity College, USA, discuss how social interactions between electric fish initially cause them to increase their production of electrocommunication chirps; however, this initial increase in chirping declines and returns to normal levels after 2 weeks (p. 2434). Having described how chirping is hormonally regulated, the team explains that it is also associated with the addition of new brain cells to a region of the brain – known as the prepacemaker nucleus – that controls chirp production. Explaining that these new brain cells are born in a nearby region of the brain and migrate to the prepacemaker nucleus, that the process is partially regulated by the hormone cortisol, and that the addition of brain cells declines as the chirp rate declines, Dunlap and colleagues suggest that there is a causal relationship between the appearance of the new cells and the increased chirp rate, although this is still not proven. The team says, ‘Establishing such causal relationships will require developing techniques to experimentally ablate neurogenesis in the CP/PPn and chirp production in socially interacting fish.’

Having addressed neuromodulation of the fish’s encoded responses to electric fields, the collection of articles dedicated to mechanisms of neuromodulation concludes with a discussion of neuromodulation of electrosensory processing in one group of weakly electric fish; the Gymnotiformes. Explaining that sensory neurons continually modulate how they process sensory inputs in response to the animal's individual circumstances, Brenda Toscano Márquez, Rüdiger Krahe and Maurice Chacron say, 'Neuromodulators are thought to mediate such adaptation' (p. 2442). Focusing on the roles of two well-characterised neuromodulators – acetylcholine and serotonin – in signal processing in the weakly electric brown ghost knifefish (*Apteronotus leptorhynchus*), the trio outlines what is known about how these neuromodulators modify signal processing in the region of the brain known as the electrosensory lateral line lobe. However, the scientists point out that other – as yet unidentified – factors are likely to have important functions in modulating sensory signal processing and add that it is essential to understand the relationships between the animals' behaviour and the neuromodulators that they trigger.

Considering neuromodulation of sensory processing in weakly electric fish, Krahe and Fortune are enthusiastic about the questions that can be specifically addressed in these animals. They say, 'We have a good chance of being able to link behavioural context to the release of neuromodulators, the release to specific changes in sensory processing properties of neurons, and the changes in the neurons' processing properties to the action of specific neuromodulator receptors, second-messenger cascades, and ion channels at the cellular level.'

Electric field generation and the electric organ

In his introduction to the section dedicated to discussion of the specialised organ that generates weak electric fields, Michael Markham, from the University of Oklahoma, USA, describes how Hans Lissmann founded the study of weakly electric fish in the 1950s (p. 2451). Not only did Lissmann prove that *Gymnarchus niloticus* produce weak electric fields but also he showed that the fish sense their surroundings and communicate *via* the fields. Reviewing the early work of M. V. Bennett on the physiology of the electric organ, Markham goes on to describe how weak electric fields are produced by the synchronised discharge of large groups of electrocytes. Adding that the electrocyte discharge is coordinated in different ways to produce the two types of field emitted by the fish – regular trains of electric pulses or a continuous 'sinusoidal' field – Markham then goes on to explain how the discharge is hormonally regulated, resulting in sexual dimorphism in electric fields, and controlled at the molecular level by modifying the production of ion channels in the electric organ to alter the waveform of the field.

In the next contribution on the topic of the electric organ and electric field generation, Vielka Salazar, Rüdiger Krahe and John Lewis discuss the energetics of weak electric field production (p. 2459). Starting their review with the startling fact that brain activity can account for up to 20% of resting metabolic rate in some animals and that this high cost is incurred by the maintenance of electrical activity, the trio then recaps the neural circuitry that regulates the electric organ discharge. Next, they review calculations of the amount of energy that is required to maintain the electric fields that arise from various arrangements of electric charge. Based on these calculations, Salazar and her PhD supervisor Philip Stoddard estimated in 2008 that male *Brachyhypopomus* spend 11–22% of their energy budget on electric field production. Given the diversity of electric fish species and the electric fields that they produce, the team concludes by suggesting that electric fish could teach us how energetic constraints might influence the evolution of signal diversity.


Angel Caputi

Robert Güth, Matthew Pinch and Graciela Unguez then address the intriguing question of how weakly electric fish have adapted muscle to produce a tissue that no longer contracts but produces a measurable electric field (p. 2469). As conventional muscle is intrinsically versatile (plastic), performing a wide variety of different functions naturally, the trio explains that the unusual characteristics of the muscle-derived electric organ allow them to answer fundamental questions about the molecular mechanisms that regulate muscle plasticity. Focusing on *Sternopygus macrurus*, Unguez and her students describe how muscle-derived electrocytes produce many of the proteins essential for muscle contraction, but they lack the sarcomere structure that is fundamental to muscle contraction. The team also points out that many of the molecular mechanisms that govern muscle development and maintenance are conserved in the electric organ, although some of the genes that encode essential components of the sarcomere are not translated into functional proteins (despite being transcribed into mRNA). This shows that there are fundamental differences between the regulation of protein expression in conventional muscle cells and electrocytes. The team adds that this suppression of production of key muscle proteins in electrocytes is influenced by the high frequency electric activation of the tissue and they conclude, 'We believe these studies in *S. macrurus* will also provide important insights into the multiple molecular processes that regulate muscle gene expression in other vertebrates.'

As if the ability to convert muscle into an organ that generates electric fields wasn't remarkable enough, Unguez goes on – in a single authored publication – to describe how adult weakly electric fish can regenerate both the electric organ and muscle after part of the tail has been lost (p. 2478). Although tissue regeneration is widespread amongst adult bony fish, their restorative powers are often limited. However, Unguez says, 'Some gymnotiforms can replace all tissues lost after repeated tail amputations, suggesting an inexhaustible regeneration capacity in the adult.' And it is this ability that makes some species of electric fish ideal for teaching us about tissue regeneration. Having explained that tissue can regenerate *via* two mechanisms – morphallaxis, where tissue is reorganised during regeneration, or epimorphosis, where cells multiply – Unguez describes how stem cells, which have the potential to divide and develop into any tissue, occur naturally in association with muscle fibres and electrocytes. She also reviews how these specific stem cells have been shown to rebuild lost muscle and electrocyte tissue by epimorphosis during tail regeneration.

Active sensing and locomotion in weakly electric fish

Although the bioelectric field that is generated by weakly electric fish is fascinating from a scientific perspective, the fishes that evolved electroreception are simply interested in successfully negotiating their surroundings. In the review by Jacob Engelmann and colleagues from Germany and Uruguay, they draw comparisons between the way that echolocating bats and electrolocating fish perceive objects in their environments by modifying the sounds and electric fields that they emit to draw objects out from their surroundings (p. 2487). Describing sensorimotor patterns that maximise electrolocation sensitivity – such as tilting the body at specific angles while foraging, moving the tail and varying the pulse frequency of the electric field to enhance the distortions produced by an object – the authors review our current understanding of the strategies used by these animals to sense the surrounding environment. They describe what is known about the impact that motor patterns have on sensory flow and detail sensory cues that become apparent as a result of the fish's progress through time and space. Engelmann and his team conclude by saying, 'The emerging field of dynamical sensory systems analysis in electric fish is a promising approach to study the link between movement and acquisition of sensory information.'

Clearly, movement is an essential component when weakly electric fish interpret perturbations in their surrounding electric fields, and in order to learn more about the fish's unique manoeuvrability Malcolm MacIver and several other groups have built model electric fish fins. Explaining that one group of fish – the knifefishes – hover, reverse and move forward by rippling a long fin that runs the length of their undersides, MacIver and his US-based co-authors review models that have been designed and built by various international teams to simulate the fin's rippling motions (p. 2501). Using these models, it has been possible for scientists to analyse the propulsive forces exerted on knifefish as they manoeuvre. MacIver's group has also simulated the electric fields emitted by fish and the sensors that detect their own fields in order to determine the electric properties and shapes of objects in the surroundings. 'One of the goals underlying the work in knifefish robotics was to build an autonomous underwater vehicle of enhanced capability over current designs', says MacIver. He goes on to describe a mechanical robot, known as Ghostbot, which successfully simulates the manoeuvrability of knifefish, which he hopes to develop further by integrating an electronic circuit to recreate the fish's electro-receptive system.

The evolution of electrosensory systems

According to the UK-based group of Clare Baker, Melinda Modrell and Andrew Gillis, electroreception is, 'an ancient sense with a fascinating evolutionary history'. The trio describe both types of electroreceptors that are found in teleosts – ampullary organs, which detect low frequency environmental electric fields, and tuberous organs, which detect self-generated high frequency electric fields used for communication and electrolocation (p. 2515). They present evidence from bony and cartilaginous fishes showing that the ampullary electroreceptors found in non-teleost jawed vertebrates are derived from the same embryonic structures, known as lateral line placodes, supporting the hypothesis that they evolved from a single common ancestor. The trio also reviews the arguments suggesting that both types of teleost electroreceptors evolved from touch-sensitive hair cells in the lateral line – which senses fluid flow – although they point out that this current hypothesis requires further testing.


Volker Hofmann

Following on from Baker and co-workers' discussion of electroreceptor evolution, William Crampton, Alejo Rodriguez-Cattaneo, Nathan Lovejoy and Angel Caputi discuss the physiological and ecological mechanisms that have underpinned the evolution of the electric fields emitted by gymnotiform electric fishes (p. 2523). Based on a study of the evolutionary relationships between *Gymnotus* species and an extensive field study – where 1157 electric organ discharges from 29 *Gymnotus* species were recorded – the authors of the review show that the electric fields have diverged between different branches of the family. Next, after outlining the cascade of physiological events that precedes an electric discharge, the team discusses how these processes vary among species to yield the wide range of electric discharge patterns seen today. Crampton and colleagues then review the evolutionary pressures acting on electric organ discharges, and conclude that environmental factors, such as the physical structure of the surroundings, are likely to have had little impact on *Gymnotiform* electric field evolution. However, biological factors, such as predation by other electroreceptive species and sexual selection – which promotes the evolution of elaborate communication signals – are probably strong contributors to the evolution of the diverse assortment of electric field patterns produced by living *Gymnotus* species.

Weakly electric fish into the future

Looking to the future and considering the impact that research into weakly electric fish will continue to have, Rüdiger Krahe says, 'Electric fish are excellent models for studying sensory processing and motor control and their plasticity as well as many other aspects of behaviour and physiology. Recent research shows that they can also teach us many interesting things about tissue regeneration and brain cell proliferation. The key advantage these animals have as experimental organisms is that they produce electric signals as behavioural output, which is easy to measure and relate to nervous system function.' Reflecting on the reviews published in this collection, Krahe adds, 'We wanted to bring lab and field researchers, physiology, behaviour and evolution together … and one of the things that I hope will come out of this special issue is increased interaction between researchers who are laboratory based and those who are field oriented to work together on emergent, cross-disciplinary problems.'

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