The Journal of Experimental Biology 216, 2363-2364

doi:10.1242/jeb.091322

EDITORIAL

Electric fishes: neural systems, behaviour and evolution

Weakly electric fish are a unique model system in neuroethology as musculoskeletal systems and mechanics are not involved in many of their behaviours. Rather, these behaviours are mediated solely by the activity of neurons and other excitable cells in the sensory and motor systems of these fascinating animals. Their electrical behaviours can be recorded easily as variations in the waveform, timing and amplitude of the electric organ discharge. As a consequence, the behavioural roles of specific features of neural circuits and of transmembrane molecules that affect membrane voltages can be measured directly using simple electrodes positioned in the water. This experimental advantage facilitates our ability to study the neural mechanisms that underlie a wealth of behaviour.

In addition, the diversity and phylogenetic history of these animals make them well suited for comparative approaches in the context of evolutionary and neuro-ecological questions. Weakly electric fishes include two major groups, the gymnotiforms in South America and the mormyriforms in Africa. These two groups independently evolved the ability to produce electric fields – electrogenesis – and sense perturbations of these self-generated fields. Starting with the work of Hans Lissmann in Cambridge, it has been shown that weakly electric fish use their active electrosense for orientation, foraging and communication (Lissmann, 1958; Lissmann and Machin, 1958; Moller, 1995). Further, within each of the two clades, there are over 200 species that have unique electrical signatures and behaviours (Crampton and Albert, 2006; Lavoué et al., 2012; Sullivan et al., 2000). Their diversity and the simplicity of recording electric behaviours make these fish uniquely suited for studying questions of ecology, evolution and basic neuroscience, in addition to being 'champion' animals in neuroethology, a role they have served for almost 50 years.

In these early years of the 21st century, we have seen a surge of research on the behaviour, modulation, evolution and neural mechanisms of behaviour in electric fish. This special issue of *The Journal of Experimental Biology* captures a snapshot of many of the exciting recent developments in these fields. Even a quick glance at the articles in this special issue reveals one of the hallmarks of research in electric fish and perhaps the most important trend in research of the 21st century: deeply interdisciplinary approaches and work across different levels of biological organization.

Interesting questions rather than techniques or animal models should, of course, define scientific investigation. Nevertheless, the unique properties of weakly electric fishes make them excellent models for some of the most important questions that continue to face us in the behavioural and cognitive neurosciences. Most of the areas in which we expect significant advances in the next few years are represented in this special issue. For example, we are on the cusp of a deep understanding of the energetics of neural activity and behaviour. The fact that electrical behaviours use the same currency as neural activity may permit us to link the evolution of electrocommunication systems to energetic costs at the level of ionic mechanisms both on the motor side, in electric organs, and on the sensory side, including the circuits that transform 'dense codes' used in the periphery to 'sparse codes' used more centrally (Chacron et al., 2011; Markham, 2013; Salazar et al., 2013; Stamper et al., 2013).

The ease with which electrical behaviours and electrosensory input can be recorded is also a major advantage for the quantification of the first- and higher-order statistics of the sensory world, which is essential for understanding the evolutionary forces that have shaped the mechanisms for sensory processing (Simoncelli and Olshausen, 2001; Stamper et al., 2013; Yu et al., 2012) (H. Fotowat, R. R. Harrison and R.K., unpublished observations). Sensing is an active process, and probably all animals exert some level of control over the input driving their sensory receptors, be it obvious cases, such as bat echolocation where call direction, call rate and duration, and range of frequency modulation are tightly controlled (e.g. Moss and Surlykke, 2010), or less obvious cases, such as olfaction, where sensing turns out to be intricately coupled to sniffing (e.g. Fukunaga et al., 2012). The interplay between motor strategies and sensing appears to be of crucial importance and weakly electric fish promise exciting new insights in this field (e.g. Hofmann et al., 2013; Neveln et al., 2013).

Similarly, weakly electric fish provide a direct window into the modulation of behaviour. Animals continuously adjust to changing environmental and social conditions over many time scales using a spectrum of mechanisms. These processes demand interdisciplinary approaches and integration across different levels of biological organization. Weakly electric fishes facilitate these sorts of integrative studies, ranging from the control of electric behaviours and sensory processing by hormones and neuromodulators (Gavassa et al., 2013; Silva et al., 2013; Smith, 2013; Toscano Marquez et al., 2013; Markham, 2013) to neurogenesis (Dunlap, 2013) and tissue regeneration (Unguez, 2013).

Rüdiger Krahe is an Associate Professor in the Department of Biology at McGill University in Montreal, Quebec, Canada. His research focuses on sensory processing and communication in weakly electric fish and includes laboratory-based neurophysiological and behavioural approaches as well as field work in the neotropics.

Eric Fortune is an Associate Professor in the Federated Department of Biological Sciences at the New Jersey Institute of Technology in Newark, NJ, USA. His research examines the behavioural and neural mechanisms for interactions between organisms. The laboratory uses two model systems, neotropical weakly electric fishes and duetting songbirds.

In the upcoming years we expect the experimental advantages of electric fish to be exploited to also address questions of higher-order brain function, such as those related to cognition. The first forays in this area have already yielded exciting results on the involvement of telencephalic circuits in long-term recognition of individual conspecifics (Harvey-Girard et al., 2010). Finally, it is a pleasure to be part of the vibrant and supportive community of electric fish researchers.

Rüdiger Krahe
rudiger.krahe@mcgill.ca

Eric S. Fortune
eric.fortune@njit.edu

Guest Editors

References

Chacron, M. J., Longtin, A. and Maler, L. (2011). Efficient computation via sparse coding in electrosensory neural networks. *Curr. Opin. Neurobiol.* **21**, 752-760.
Crampton, W. G. R. and Albert, J. S. (2006). Evolution of electric signal diversity in gymnotiform fishes. In *Communication in Fishes*, Vol. 2. (ed. F. Ladich, S. P. Collin and P. Moller), pp. 647-731. Enfield, NH: Science Publishers.
Dunlap, K. D., Chung, M. and Castellano, J. F. (2013). Influence of long-term social interaction on chirping behavior, steroid levels and neurogenesis in weakly electric fish. *J. Exp. Biol.* **216**, 2434-2441.
Fukunaga, I., Berning, M., Kollo, M., Schmaltz, A. and Schaefer, A. T. (2012). Two distinct channels of olfactory bulb output. *Neuron* **75**, 320-329.
Gavassa, S., Goldina, A., Silva, A. C. and Stoddard, P. K. (2013). Behavioral ecology, endocrinology and signal reliability of electric communication. *J. Exp. Biol.* **216**, 2403-2411.
Harvey-Girard, E., Tweedle, J., Ironstone, J., Cuddy, M., Ellis, W. and Maler, L. (2010). Long-term recognition memory of individual conspecifics is associated with telencephalic expression of Egr-1 in the electric fish *Apteronotus leptorhynchus*. *J. Comp. Neurol.* **518**, 2666-2692.
Hofmann, V., Sanguinetti-Scheck, J., Künzel, S., Geurten, B., Gómez-Sena, L. and Engelmann, J. (2013). Sensory flow shaped by active sensing: sensorimotor strategies in electric fish. *J. Exp. Biol.* **216**, 2487-2500.
Lavoué, S., Miya, M., Arnegard, M. E., Sullivan, J. P., Hopkins, C. D. and Nishida, M. (2012). Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. *PLoS ONE* **7**, e36287.
Lissmann, H. W. (1958). On the function and evolution of electric organs in fish. *J. Exp. Biol.* **35**, 156-191.
Lissmann, H. W. and Machin, K. E. (1958). The mechanism of object location in *Gymnarchus niloticus* and similar fish. *J. Exp. Biol.* **35**, 451-486.
Markham, M. R. (2013). Electrocyte physiology: 50 years later. *J. Exp. Biol.* **216**, 2451-2458.
Moller, P. (1995). *Electric Fishes. History and Behavior*. London: Chapman and Hall.
Moss, C. F. and Surlykke, A. (2010). Probing the natural scene by echolocation in bats. *Front. Behav. Neurosci.* **4**, 1-16.
Neveln, I. D., Bai, Y., Snyder, J. B., Solberg, J. R., Curet, O. M., Lynch, K. M. and MacIver, M. A. (2013). Biomimetic and bio-inspired robotics in electric fish research. *J. Exp. Biol.* **216**, 2501-2514.
Salazar, V. L., Krahe, R. and Lewis, J. E. (2013). The energetics of electric organ discharge generation in gymnotiform weakly electric fish. *J. Exp. Biol.* **216**, 2459-2468.
Silva, A. C., Perrone, R., Zubizarreta, L., Batista, G. and Stoddard, P. K. (2013). Neuromodulation of the agonistic behavior in two species of weakly electric fish that display different types of aggression. *J. Exp. Biol.* **216**, 2412-2420.
Simoncelli, E. P. and Olshausen, B. A. (2001). Natural image statistics and neural representation. *Annu. Rev. Neurosci.* **24**, 1193-1216.
Smith, G. T. (2013). Evolution and hormonal regulation of sex differences in the electrocommunication behavior of ghost knifefishes (Apteronotidae). *J. Exp. Biol.* **216**, 2421-2433.
Stamper, S. A., Fortune, E. S. and Chacron, M. J. (2013). Perception and coding of envelopes in weakly electric fishes. *J. Exp. Biol.* **216**, 2393-2402.
Sullivan, J. P., Lavoué, S. and Hopkins, C. D. (2000). Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. *J. Exp. Biol.* **203**, 665-683.
Toscano Márquez, B., Krahe, R. and Chacron, M. J. (2013). Neuromodulation of early electrosensory processing in gymnotiform weakly electric fish. *J. Exp. Biol.* **216**, 2442-2450.
Unguez, G. A. (2013). Electric fish: new insights into conserved processes of adult tissue regeneration. *J. Exp. Biol.* **216**, 2478-2486.
Yu, N., Hupé, G. J., Garfinkle, C., Lewis, J. E. and Longtin, A. (2012). Coding conspecific identity and motion in the electric sense. *PLoS Comput. Biol.* **8**, e1002564.