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Communication: Potassium Channels Define the Dialect

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Weakly electric fishes use electric pulses to interact with conspecifics, but the molecular origin of species-specific communication is unknown. A new study shows that some properties of the electric fish 'language' are dictated by the activity of a voltage-gated potassium channel in electrocytes.

Since the late 18th century, decades before Michael Faraday laid the foundation of the theory of electromagnetism, scientists knew that certain species of fish could generate electricity. Some species, such as the electric eel, use strong electric discharges of up to hundreds of volts to stun their prey [1,2]. To produce electricity, the eel uses the electric organ, a unique structure composed of a series of biological batteries. The 'batteries', called electrocytes, are modified non-contractile myocytes, the cells that normally build muscles [3]. Similar electric organs were also found in a number of then obscure fish species from the rivers of Africa and South America. But in contrast to the eel, these species failed to produce strong electric output, leaving the researchers puzzled regarding the function and biological significance of these structures. Some went as far as suggesting that the 'pseudo-electric organs' of such species evolved "…*most probably not based upon a natural selective basis*" [4].

The conundrum was resolved in the mid-20th century, when Hans Lissmann obtained a single specimen of *Gymnarcus niloticus*, and described a most peculiar feature of its behavior: the fish was able to avoid obstacles while swimming backwards [5]. Lissman hypothesized that this was due to the electric organs in the finger-like tail, which he thought the animal used to detect objects. By placing a pair of electrodes connected to an amplifier into the aquarium, he detected a stream of high-frequency (250–300 Hz) low-voltage (30 mV) electric discharges [5]. Moreover, he noticed that the weakly electric fish not only produced but also sensed electrical pulses produced elsewhere and located their source. This suggested that unlike the eel, who uses electricity as a weapon, *Gymnarcus* uses it in a more subtle way: to navigate in the environment, detect objects and locate prey [6,7].

Lissmann's works laid the foundation for what is currently part of a flourishing field of bioelectricity and electroreception. The majority of weakly electric fish belong to the Mormyroidae superfamily and includes Gymnarchidae and Mormyridae. Currently, there are over 220 recognized Mormyroidae species, organized into more than 20 genera [8]. All the species from this superfamily can sense low-voltage discharges produced by their own electric organ as well as those from other individuals. The electric organ discharges (EODs) have species-specific signatures and serve to mediate communication with conspecifics, provide a means for reproductive isolation, and are used for systematics of weakly electric fishes [9–11].

The temporal features of electric organ discharges serve a purpose similar to words and their order in a human language. The principle components of EODs are the frequency, pattern and shape of the waveform. The frequency and pattern of the EODs can vary depending on the social context, whereas the waveform is species-specific and defined by the morphology, innervation and physiology of the electrocytes [12]. This is particularly evident in the two sister taxons of Mormyroidae. *Gymnarchus niloticus*, the single species of the Gymnarchidae family, generates wide wave-like EODs, while most species from the Mormyridae family generate brief multiphasic EODs (Figure 1) [13]. The EODs result from a concerted discharge of action potentials produced by many individual electrocytes. With the advent of the patch-clamp and voltage-clamp techniques, detailed characterization of the ionic currents underlying electrocyte firing became possible. Similar to neuronal and muscle cells, electrocyte discharge is mainly mediated by voltage-gated sodium and potassium channels [14]. Coordinated shifts in the kinetics of sodium and potassium channel activity were proposed to define EOD pulse shape and duration [15]. However, the identity of the channels as well as species-specific signatures of their activity have remained a mystery. The development of high-throughput sequencing and bioinformatics in the last decade started to reveal the molecular origins of the electric organs' discharge at an unprecedented depth [16–19].

A paper by Harold Zakon and colleagues [11] in this issue of *Current Biology* reports a multidisciplinary approach to zoom in on the molecular origin of the wide *versus* narrow EOD waveform in Gymnarchidae and Mormyridae, respectively. The authors used massively parallel sequencing in combination with differential transcriptome analyses between muscle and electric organs of *Gymnarchus niloticus* and several mormyrids, including *Brienomyrus brachyistius*, to identify transcripts enriched in the electric organ. They found *kcna7a*, the transcript encoding the voltage-gated potassium channel $K_v1.7a$, to be present in large amounts in the electric organ of *Brienomyrus* and other mormyrids. Electrophysiological analysis showed that mormyrid $K_v1.7a$ has novel properties, different from its orthologues from *Gymnarchus* and other species. In technical terms, mormyrid $K_v1.7a$ activates at a hyperpolarized membrane potential and has a steep conductance–voltage dependence (Figure 1). This means that the channel activates shortly after the onset of the action potential, narrowing its duration close to the theoretical minimum. Indeed, when properties of the $K_v1.7a$ orthologues were plugged into a computational model of electrocyte firing, the results were consistent with the observed differences between the wide and narrow action potentials of *Gymnarchus* and *Brienomyrus*, respectively [11].

What are the molecular origins that dictate the unconventional behavior of mormyrid $K_v1.7a$? The authors noticed that mormyrid $K_v1.7a$ has a cluster of negatively charged amino acids in the extracellular loop near the voltage-sensing domain (Figure 1). By swapping this region between the $K_v1.7a$ orthologues, they found that it is sufficient to interconvert properties of $K_v1.7a$ between the species. While the exact mechanism by which the negatively charged cluster facilitates $K_v1.7a$ activation remains to be determined, the authors provided compelling evidence supporting the idea that it acts by altering outer membrane surface charges,

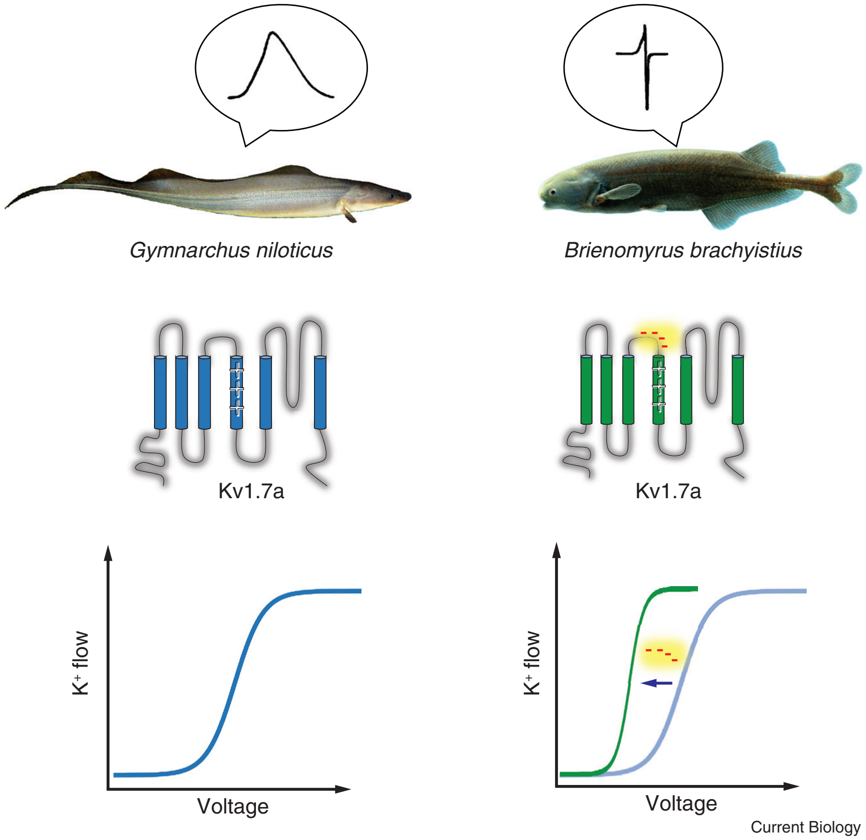

Figure 1. Communication in electric fish.
The weakly electric fishes communicate with conspecifics via electric discharges with characteristic waveforms: wide for *Gymnarchus* and narrow for *Brienomyrus*. The plasma membrane of the fish electrocytes contains voltage-gated potassium channels $K_v1.7a$, which regulate the duration of the wavefom. A patch of negatively charged amino acids near the positively charged voltage-sensing domain of *Brienomyrus* $K_v1.7a$ facilitates channel opening at more negative voltages, shortening the duration of the electric discharge.

which in turn facilitates movement of the voltage-sensing domain in response to small depolarizations [11]. This paradigm is not without a precedent: a similar mechanism was proposed to be at play in the L-type calcium channel found in the electrosensing ampullary organ in little skate [19]. The apparent similarity between the mechanisms potentiating voltage sensitivity of the ion channels from different classes highlights a common pathway targeted in the course of evolution to confer novel properties via a minimal number of amino acid changes.

The new study raises interesting questions. Mormyirids are a very diverse group, and some species have independently evolved wide EOD pulses similar to *Gymnarchus* [20]. Does K_v1.7a from these species have properties similar to those of *Gymnarchus*, and if so, what additional compensatory mutations are responsible for these changes? It will also be interesting to know whether K_v1.7a alone is sufficient to fully change the duration of the action potential discharge, or whether other channels play an equally important role. Recent advances in genomic manipulations, such as the CRISPR-Cas9 genome editing technology, should provide an impetus for studies of non-conventional species that possess unique functional specializations. These studies are in need as they lend a novel standpoint to better understand processes that govern speciation and evolution at the molecular level.

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Social Behavior: How the Brain Thinks like a Mom

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Becoming a parent changes our choices and actions. Identifying the underlying neural circuits is necessary to understand the transformation of an animal's behavior post-parenthood. Multiple nodes of the 'parenting circuit' have now been identified to reveal the workings of a single brain region key to the orchestration of parent-specific behaviors.

We begin the first phase of life, through adolescence and beyond selfishly concerned with our own wants and needs; until we become a parent and our behavior radically changes. Caring for newborns necessitates putting the demands of others ahead of our immediate desires, and requires a change of behavior to prioritize selfless action without immediate personal reward. In