Brain Evolution Triggers Increased Diversification of Electric Fishes

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Science

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Electric Fish (Mormyridae)
**Diversity of Signal waveforms**

- Various signal waveforms from a specific species or morph are depicted, showing the variation in electric signals.

**Mormyridae and the evolution of temporal coding**

- **Brief Overview**
- **Relevant Brain Regions**
- **How changes in the brain enable temporal coding**
  - Impact of temporal coding
  - Mechanism of temporal coding
- **How the ability drives signal diversification and speciation**

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**Electric signaling is key**

- Signals are critical for species recognition
- Signals evolve faster than other factors like body shape, size, or trophic ecology.
- *Mormyridae* are the ideal model system for relating brain evolution to diversification. Why?

**Electrical signaling is key**

- Signals are critical for species recognition
- Signals evolve faster than other factors like body shape, size, or trophic ecology.
- *Mormyridae* are the ideal model system for relating brain evolution to diversification. Why?
  - **Easy to study**: a specific sensory pathway exists exclusively for electric communication analysis.

**Electroreceptors**

- An image showing the electroreceptors with labels such as “ampullary,” “knollenorgan,” and “mormyromast” with a scale of 100 μm.
Electroreceptors

- The timing of knollenorgan response on different parts of the body gives information about the stimulus.
- The projections eventually reach a midbrain region called the exterolateral nucleus (EL).

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The Exterolateral nucleus (EL)

- Pathway: the knollenorgan (KO) projects to the nucleus of the electrosensory lateral line lobe (nELL), which projects to the EL

Brain evolution and diversification?

- A comparative analysis of EL anatomy was performed, through standard procedures of obtaining brain slices
  - 26 species

The EL has two forms in Mormyridae

- The EL was identified using topology (spatial relations to other brain regions, regardless of shape/size).
- In some cases, the EL was a single, small unit with no subdivisions. In others, it was divided into the anterior and posterior regions (ELa and ELp, respectively)

Difference in ELp/ELa & EL expression, within subfamilies Mormyrinae and Petrocephalinae
Cytb data suggests a phylogenetic separation between EL and ELa/ELp

Two exceptions

- *Mormyrinae* is a monophyletic group, and all but one have ELa / ELp subdivisions ("Clade A")
  - Exception: *Mormyrinae myomyrus*
- *Petrocephalinae* is a monophyletic group, and all but one show no EL subdivisions
  - Exception: *Petrocephalus microphthalmus*. New discovery in this study.

- But there is a problem...

Parsimony

- **Maximum parsimony** - when facing competing evolutionary hypotheses, choose the one with the fewest assumptions.
  - in this case, the least evolutionary change

So, either EL is the ancestral state and ELa/ELp is derived, or ELa/ELp is ancestral and EL is derived.

Which is more parsimonious?
**Gymnarchus** settles the debate

- New data on the brain structure of *Gymnarchus*, the sister taxon to the Mormyridae, reveals an unseparated EL, demonstrating that EL is the ancestral state.

**Mormyridae** and the evolution of temporal coding

- Brief Overview
- Relevant Brain Regions
  - Exterolateral nucleus
  - Phylogenetic divide between EL & ELa/ELp
- How changes in the brain enable temporal coding
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So why does the presence of an EL division matter?

- **Hypothesis**: EL anatomy is responsible for different distribution of receptors.
- Two patterns of receptor organization
  - Broad distribution throughout body
  - Discrete clusters on head
- Testing the hypothesis
  - Method: mapping knollenorgans of species

EL division & receptor distribution

- **Results**: Clade A & *P. microphthalmus* show broad distribution of receptors
- All other Petrocephalinae show clusters on the head
- Mormyrinae *Myomyrus* is intermediate (one cluster on head, sparse distribution thru body)
- Conclusion: ELa/ELp is responsible for broad distribution

Distribution of receptors

- How does a broad or clustered distribution of receptors affect temporal coding?

- How does a broad or clustered distribution of receptors affect temporal coding?
  - Recall: The EL analyzes electric signals by comparing response times of knollenorgans on different parts of the body
  - So, the broad distribution of KOs should help with signal discrimination
Playback experiment

- Method: Fired 10 bursts (each burst = 10 pulses). The 9th burst was phase-shifted, and changes in behavior from the 8th to 9th recording was recorded.
- Normal response to a conspecific is either 1) increase in electric discharge, or 2) pause in electric output
- Deviations from the normal response (increasing electric discharge rate, or pausing for longer) indicate dishabituation and thus discrimination of the changed nature of the signal

Arnegard et al., 2006

Playback experiment

- Results
  - Clade A & P. microphthalamus exhibited dishabituation (and partial recovery of response)
  - Petrocephalinae did not show a dishabituation
- Conclusion: the evolution of ELa/ELp led to physical changes that improves signal discrimination ability

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Temporal Coding: Mechanism

- Knollenorgans respond differently with the onset of current from one side of the body to the other.
  - The first would respond with the normal polarity (receiving the EOD stimulus), while the opposite side would respond with the reverse polarity (responding to an inverted EOD stimulus)

M. Xu-Friedman & C.D. Hopkins, 1999

Temporal Coding: Mechanism

- Recall: the KO projects to NELL (nucleus of the electrosensory lateral line lobe) which projects to ELa and medialis ventralis (MV)
- ELa is specialized for time keeping
  - Heavy myelination
  - Thick axons

M. Xu-Friedman & C.D. Hopkins, 1999

Temporal Coding: Mechanism

- The ELa contains large cells and small cells.
- NELL contacts a large cell, and after a delay, some small cells
- The ELa large cells form an inhibitory synapse on the small cells.
- The result is that a small cell receives an inhibitory input from the large cell, and a delayed excitatory input from a NELL cell.
Temporal Coding: Mechanism

• The small cell receives one input from each side of the body: a large cell on one side, and a NELL cell on the opposite side. In the case of a sufficiently long negative pulse, the excitatory NELL input will be faster than the large cell inhibition—thus the cell fires.

M. Xu-Friedman & C.D. Hopkins, 1999

Temporal Coding: Mechanism

• The relative length of the pulse and the axon delay is important. A small cell responds if the pulse is longer than a set threshold.

M. Xu-Friedman & C.D. Hopkins, 1999

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Temporal Coding encourages diversification

• Now that individuals can discriminate minute time differences, signal variations are all that are required for diversification.

• Hypothesis: Rapid signal divergence and species diversification should be found in clade A.

Signal Divergence Rates

• Signal Divergence rates were calculated using cross-correlation, and pair-wise similarities were calculated
• Combined with pair-wise phylogenetic distances.
Signal divergence vs Phylogenetic distance

- Mormyrinae (red) show higher divergence in all levels of phylogenetic distance, than Petrocephalinae.
- Conclusion: their temporal coding ability enables Mormyrinae to undergo signal divergence at a much faster rate.

Species Diversification

Take-Home Messages

- Anterior/Posterior subdivisions in the exterolateral nucleus (EL) is a derived character state in many electric fish.
- These subdivisions are predictive of receptor distribution, and lead to better signal discrimination.
- A neural circuit of indirect inhibition and direct delayed excitation is used to cause small-cell firing only if the pulse passes a critical threshold.
- Temporal coding in the brain allows for successive signal divergence and species diversification.

Your thoughts?

- Was the article title too direct?
- Any questions/comments?